

Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness

Olaf Blanke,^{1,2,*} Mel Slater,^{3,4} and Andrea Serino^{1,*}

¹Laboratory of Cognitive Neuroscience, Center for Neuroprosthetics and Brain Mind Institute, Ecole Polytechnique Fédérale de Lausanne (EPFL), 9 Chemin des Mines, 1202 Geneva, Switzerland

²Department of Neurology, University of Geneva, 24 rue Micheli-du-Crest, 1211 Geneva, Switzerland

³CREA-University of Barcelona, Campus de Mundet, 08035 Barcelona, Spain

⁴Department of Computer Science, University College London, Malet Place Engineering Building, Gower Street, London, WC1E 6BT, UK

*Correspondence: olaf.blanke@epfl.ch (O.B.), andrea.serino@epfl.ch (A.S.)

<http://dx.doi.org/10.1016/j.neuron.2015.09.029>

Recent work in human cognitive neuroscience has linked self-consciousness to the processing of multisensory bodily signals (bodily self-consciousness [BSC]) in fronto-parietal cortex and more posterior temporo-parietal regions. We highlight the behavioral, neurophysiological, neuroimaging, and computational laws that subtend BSC in humans and non-human primates. We propose that BSC includes body-centered perception (hand, face, and trunk), based on the integration of proprioceptive, vestibular, and visual bodily inputs, and involves spatio-temporal mechanisms integrating multisensory bodily stimuli within peripersonal space (PPS). We develop four major constraints of BSC (proprioception, body-related visual information, PPS, and embodiment) and argue that the fronto-parietal and temporo-parietal processing of trunk-centered multisensory signals in PPS is of particular relevance for theoretical models and simulations of BSC and eventually of self-consciousness.

Introduction

Brain activity causes subjective experience, and over the last two decades, research has investigated some of the major neuronal mechanisms of conscious processing (Koch, 2004; Dehaene and Changeux, 2011). Early data regarding the neural correlates of consciousness arguably came from clinical observations in neurological patients (i.e., (Poppel et al., 1973; Weiskrantz et al., 1974; Bisiach et al., 1979), empowered by psychophysics and, more recently, brain imaging (i.e., Kim and Blake, 2005; Sergent and Dehaene, 2004). Although these studies have led to a better understanding of visual consciousness, the interaction of conscious and unconscious vision with other senses has remained largely unexplored, although it is a crucial element given the multisensory nature of consciousness (Deroy et al., 2014; Faivre et al., 2014, 2015).

Importantly, the observer, or subject of conscious experience, is also generally not accounted for in these models of perceptual consciousness, although a fundamental property of consciousness is its link with a self as subject of conscious experience. Conscious perception, indeed, is not only a multisensory experience of an object (McGurk and MacDonald, 1976; Bertelson, 1999) but also includes a subject of experience: that is, the implicit and pre-reflexive experience of being the subject of a given experience. Thus, an object of perception is experienced by someone, by the self, or by the subject of experience. The latter is localized within a body, which is felt as one's own, occupying a given location in space. Recent research has revealed that this important aspect of conscious experience—the implicit and pre-reflexive experience of being the subject of a given experience—is based on multisensory brain mechanisms underlying the integration of bodily signals; it has been the target of much recent research and conceptual work in cognitive neuroscience

and philosophy of mind, and we refer to it as bodily self-consciousness (BSC) (Christoff et al., 2011; de Vignemont, 2011; Gallesse and Sinigaglia, 2010; Blanke and Metzinger, 2009; Jeanerod, 2003; Knoblich, 2002; Legrand, 2007; Damasio et al., 2009). The associated experimental approach to BSC in healthy subjects has also been influenced by empirical work in behavioral neurology and altered states of consciousness. We note that by focusing on BSC we deliberately do not refer to or review cognitive or conceptual higher-level notions of the self, as targeted by other important lines of research in cognitive neuroscience (Gallagher, 2000; Goldberg et al., 2006; Heatherton et al., 2006; Legrand and Ruby, 2009; Mitchell et al., 2005).

Studies of multisensory bodily processing allow the investigation of the subject of experience and have successfully induced illusory states of BSC, such as the illusory feeling of an artificial body part as one's own (illusory body ownership or self-attribution). By manipulating visuo-tactile inputs, an illusory feeling of ownership can be induced for an artificial hand (rubber hand illusion; Botvinick and Cohen, 1998) or for another person's face (enfacement illusion; Tsakiris, 2008; Sforza et al., 2010). Viewing another person's hand (face) being stroked in synchrony with strokes applied to one's own corresponding non-visible hand (face) can induce illusory self-attribution of the seen hand (face). Moreover, participants perceive their hand to be at a position that is displaced toward the fake hand's position (proprioceptive drift) or judge another person's face as similar to their own.

One of the main new arguments of the present paper is that rubber hand and enfacement illusion rely on processing sensory information from the space immediately surrounding the body (or peripersonal space [PPS]), which is a particularly important spatial compartment for BSC. Multisensory perception studies (Spence and Driver, 2004) showed that tactile processing is

strongly modulated by visual or auditory stimuli (for reviews: [Macaluso and Maravita, 2010](#); [Occelli et al., 2011](#)) and that such modulation occurs in particular when these are presented close to (within PPS), as compared to far from, the body. Neuroimaging studies ([Macaluso and Driver, 2005](#); [Makin et al., 2007](#); [Serino et al., 2011a](#); [Serenio and Huang, 2014](#)) associated these effects with brain regions in human posterior parietal and premotor cortices, hosting bimodal and multimodal neurons, as revealed by earlier neurophysiological work in non-human primates ([Duhamel et al., 1998](#); [Graziano et al., 1994](#); [Rizzolatti et al., 1981](#)). Similar regions also process signals involved in self-attribution of the hand ([Ehrsson et al., 2004](#); [Tsakiris et al., 2007](#); [Evans and Blanke, 2013](#)) and face ([Cardini et al., 2011](#); [Apps et al., 2015](#)).

More recent research has investigated trunk-related multisensory processing, as it allows researchers to investigate brain mechanisms that target the body as a global and unitary entity. The importance of this latter approach was motivated by conceptual work in philosophy of mind ([Metzinger, 2004](#); [Blanke and Metzinger, 2009](#)) and clinical data in neurological patients suffering from disorders of BSC ([Brugger et al., 1997](#); [Blanke et al., 2008](#)). A series of studies in healthy volunteers revealed that trunk-related bodily processing is of particular relevance for key aspects of BSC, involving brain mechanisms beyond ownership for a given body part (hand, leg, face). These experimental studies also exploited visuo-tactile and visuo-vestibular stimulations at the trunk for the induction of more global changes in BSC, such as “full-body,” “out-of-body,” or “body-swap” illusions ([Ehrsson, 2007](#); [Lenggenhager et al., 2007](#); [Petkova and Ehrsson, 2008](#); [Aspell et al., 2013](#)). Typically in these paradigms, tactile stimulation is repeatedly applied to the back or chest ([Lenggenhager et al., 2009](#)) of a participant who is being filmed and so simultaneously views (on a head-mounted display [HMD]) the stroking of a human body in a real-time video or virtual-reality animation, in front of her/him, at a farther location. When exposed to the full-body illusion, participants self-identify with the seen virtual body (change in self-identification) and show a forward drift in self-location (the experience of where “I” am in space) toward the position of the virtual body. In particular, behavioral and questionnaire data show that participants perceive themselves to be located “in front” of the position where they had been standing physically during the experiment. Here, we argue that bimodal and multimodal neurons that integrate visual, tactile, and vestibular information as defined in monkey posterior parietal and premotor cortex are of key relevance for these aspects of BSC. Neuroimaging data in humans found such integration in fronto-parietal and temporo-parietal regions, reflecting experimentally induced changes in self-identification and self-location ([Ionta et al., 2011](#); [2014](#); [Petkova et al., 2011](#); [Gentile et al., 2015](#); [Guterstam et al., 2015](#)).

In this review, we develop four major neuroscientific constraints of BSC and apply them to (1) body ownership or self-attribution of a body part (hand, face), (2) self-identification with the full body, and (3) self-location ([Blanke and Metzinger, 2009](#); [Blanke, 2012](#)). For this, we will describe the behavioral laws of multisensory processing of bodily stimuli in PPS, the major neuronal properties of bimodal and multisensory neurons at the level of single neurons, the major brain regions and net-

works involved in the processing and integration of such signals, and the major computational approaches to BSC.

We note that other mechanisms contribute to self-consciousness and BSC, such as the sense of agency for bodily actions that is based on the additional integration with motor signals. Interoceptive body-related inputs are also an important additional mechanism in BSC. Both have been the topic of a large number of studies and reviews (agency, e.g.: [Jeannerod, 2003](#); [Gallese and Sinigaglia, 2010](#); [Haggard and Chambon, 2012](#); [Marcel, 2003](#); interoception: [Craig, 2002](#); [Damasio, 2003](#); [Seth, 2013](#)). Current research has also started to study global aspects of BSC (self-identification and self-location) based on interoceptive signals ([Aspell et al., 2013](#); [Ronchi et al., 2015](#)) and sensorimotor signals ([Kannape et al., 2010](#); [Kannape and Blanke, 2013](#)). However, in the present paper we focus on multisensory brain mechanisms of exteroceptive bodily signals as, we believe, this is the simplest account for BSC (see also [Blanke and Metzinger, 2009](#)).

Major Behavioral Laws of Multisensory Processing, Multisensory Bodily Processing, and BSC *Multisensory Integration*

Information from different senses is integrated in order to improve perception ([Fetsch et al., 2013](#); [Ernst and Bühlhoff, 2004](#)), and there are at least three general laws of multisensory integration. Inputs from different modalities are more strongly integrated the closer they occur in space (spatial law) and in time (temporal law), and the weaker each unisensory input signal is (inverse effectiveness) ([Stein and Stanford, 2008](#); [Stein et al., 1989](#); [Frassinetti et al., 2002](#)). For example, in audio-visual perception, participants are faster and more accurate in localizing the source of a visual target when a concurrent auditory cue is presented at the same location, at the same time, and when the intensity of the visual and the auditory stimuli is weak ([Spence and Driver, 2004](#); [Calvert et al., 2004](#)).

Concerning multisensory stimulation involving bodily signals, several studies have shown that a visual ([Spence et al., 2000](#)) or an auditory ([Zampini et al., 2007](#)) cue affects the perception (i.e., it improves accuracy and speeds up reaction times) of a tactile stimulus delivered to the hand; an effect termed crossmodal congruency effect (CCE). CCE magnitude increases with decreasing temporal delays between the multisensory stimuli, in line with the temporal law of multisensory integration. In addition, the spatial arrangement of tactile targets and visual cues determines CCE magnitude, with stronger CCEs when both multisensory inputs are presented at the same spatial location and weaker if the visual cue is presented further away from the hand that has received the tactile stimulus ([Spence et al., 2004](#)), in line with the spatial law of multisensory integration.

Multisensory Integration of Bodily Signals Is Constrained by Proprioception and Body-Related Visual Information

Although previously reviewed studies suggest that the integration of multisensory signals including bodily signals (i.e., tactile and proprioceptive signals) share similar laws of multisensory integration ([Van der Stoep et al., 2015](#)), we argue that multisensory integration of bodily signals relies on additional constraints that are absent or minimal for exteroceptive events. Consider the case of visuo-tactile integration. If we want to

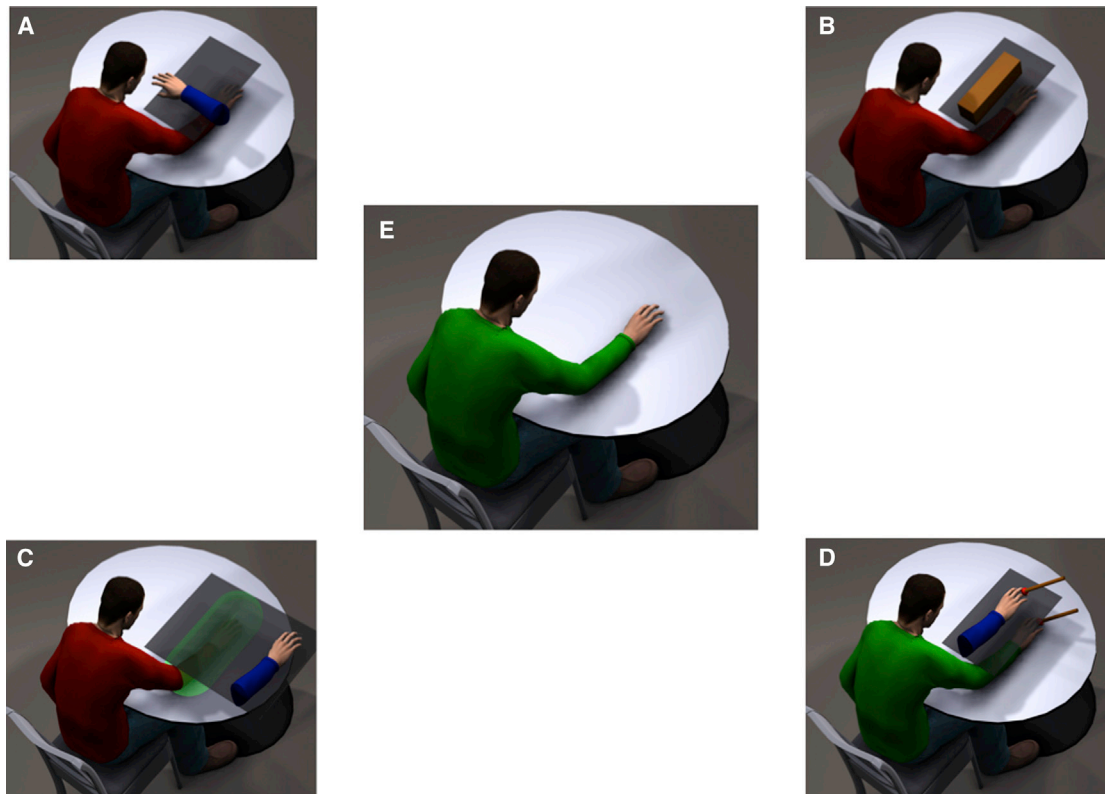


Figure 1. Four BSC Constraints Determining Hand Ownership

(A–E) Stimuli applied to an artificial hand (blue hand) are integrated with stimuli on the physical hand, if the artificial hand is placed coherently with the posture of the physical hand, whereas no change in hand BSC (i.e., illusory hand ownership) occurs if it is placed in a non-matching body posture ([A], proprioceptive constraint). No change in hand BSC occurs for an object with a non-bodily shape ([B], body-related visual information constraint) or if the artificial hand is presented outside the PPS of the real hand ([C], PPS constraint). A change in hand BSC is obtained if the real hand and the artificial hand receive synchronous and prolonged visuo-tactile stimulation ([D], embodiment constraint). Note that, normally, these four constraints apply to the parts of one's own physical body, leading to the normal sense of body ownership (E). Red and green body of the participant indicates, respectively, absence or presence of BSC for the hand.

determine the location of an object touching our body, the position of the skin receptors detecting touch needs to be re-mapped continuously from its fixed position on the skin to its position in external space, where the visual cue is located (Soto-Faraco and Deco, 2009; Heed et al., 2015). Thus, besides visual and tactile cues, other inputs, such as proprioceptive signals, impact multisensory integration, defining the position of the body in space and whether stimuli are related to the body or not. In the case of auditory-visual integration, the auditory and the visual cues both occur in external space, and their location is determined by visual information in retinal coordinates, auditory information in head coordinates, further integrated based on eye position signals (Stricanne et al., 1996; Colby, 1998; Cohen and Andersen, 2000). Accordingly, for multisensory perception of exteroceptive cues, no input from other modalities (if the eyes and head are fixed, see below) is needed, and integration is determined based on the described laws of space, time, and inverse efficiency. In the next section, we will review behavioral studies in humans showing that the integration of multisensory bodily signals requires the concurrent processing of several signals related not only to the stimuli themselves but also to proprioceptive signals encoding the subject's body position. It is worth noting that this also makes

studying the integration of multisensory bodily signals more difficult than for exteroceptive cues, because bodily-related inputs (e.g., signals about body-parts position) are always present and more difficult to manipulate.

Several studies have shown that the spatial determinants of the crossmodal interaction between tactile stimuli and visual targets depend on the participant's arm posture. For instance, Spence et al. (2004) compared CCE strength when tactile targets were delivered to the right or left hand, and visual cues were administered to the right or left visual space. Usually, same side visuo-tactile stimulation (e.g., visual cues on the left side with tactile stimuli on the left hand) induces stronger CCE. However, if participants cross their hands, the effects reverses (right visual cues interact more strongly with tactile stimulation on the left hand), showing that multisensory integration of bodily signals is re-referenced based on proprioceptive cues (spatial remapping of touch; Soto-Faraco and Deco, 2009; Heed et al., 2015); the prominent impact of proprioceptive signals for the perception of bodily signals is the first constraint for multisensory integration for BSC (see Figure 1A).

Other studies showed that multisensory integration of bodily inputs is determined not only by the physical position of the hand in space, as determined by proprioception, but also by

visual information related to the configuration of the body and its parts in space (body-related visual information) (Serino and Haggard, 2010). For instance, Pavani et al. (2000) showed that visual cues induced a stronger CCE over tactile targets (administered to the participants' hidden hands), when the cues were presented on fake hands, as compared to when they were presented exactly at the same spatial location, but without fake hands, or when presented at the same position on fake hands that were placed in a posture incompatible with the actual posture of participants' hands. Similar effects have been found using mirrors (Maravita et al., 2002) or hand shadows (Pavani and Castiello, 2004) to administer visual cues that, although being presented in a spatial location physically far from the place of tactile stimulation, were processed as occurring on the body, modulating tactile processing. Thus, top-down input related to the perceived visual configuration of the body in space is a second major constraint governing multisensory integration of bodily signals for BSC (see Figure 1B).

Thus, integration of multisensory stimuli requires that sensory inputs, originally processed in sensory-dependent reference frames (e.g., visual stimuli in eye-centered, auditory stimuli in head-centered, tactile stimuli in skin-centered reference frames), are realigned and integrated into a common reference frame. In the case of integration of exteroceptive inputs, such as audio-visual integration (e.g., the noise and the flashing of a fire alarm on the wall), multisensory integration is based on the spatial relationship between the source of the visual and the auditory cue, determined by the position of the visual stimulus on the retina, the location of the sound in the auditory space, and signals related to eye and head position. Thus, additional sensory signals (eye-head proprioception) only minimally concur with the integration process of exteroceptive stimuli under static conditions. Instead, in the case of bodily inputs (e.g., visuo-tactile or audio-tactile stimuli), the common reference frame of multisensory perception is the subject's body, and the transformation—or remapping process—involves processing and integration of additional proprioceptive and vestibular inputs signaling the location of a tactile cue on the body in space (first BSC constraint) and visual inputs related to the configuration of the body in space (second BSC constraint).

Multisensory Integration of Bodily Signals Occurs within a Limited Space around the Body: The PPS Constraint

Research in patients with crossmodal extinction following focal brain damage have confirmed the importance of both constraints in multisensory bodily perception (di Pellegrino et al., 1997; Farnè and Làdavas, 2002; Làdavas et al., 1998a; Farnè et al., 2000). These studies also showed that a visual or auditory stimulus more strongly interacts with tactile stimulation on the body when the visual or auditory event occurs close to the perceived location on the body, rather than farther away, within PPS. Serino and colleagues provided behavioral support that for healthy participants PPS is an additional critical factor for multisensory bodily perception. They reported that responses to a tactile stimulus delivered to the hand are enhanced if a concurrent, task-irrelevant sound is presented close to the stimulated hand (inside PPS) but not at larger distances (outside PPS) (Serino et al., 2007, 2011a). The border of PPS (i.e., the most distant position in space from the body where this audio-tactile interaction effect occurs)

was then defined by administering tactile targets coupled with dynamic sounds, originating from a far location and approaching the participant's stimulated hand (Canzoneri et al., 2012). By presenting tactile target stimuli at different delays from sound onset (simulating different sound distances from the body), reaction times to tactile targets became faster (compared to unimodal tactile stimulation) once the sound entered the participants' PPS. This facilitation effect was not linearly proportional to the spatial position of the sound, but occurred for sounds within a limited distance from the body (i.e., 40–50 cm for the hand), beyond which no space-dependent modulation of reaction times was found (Bassolino et al., 2015; Canzoneri et al., 2013a, 2013b; Serino et al., 2015; Teneggi et al., 2013). These data show that multisensory integration of bodily signals not only is governed by the metric distance of external stimuli from the body, but also depends on a third constraint of BSC that is absent for non-bodily multisensory perception: PPS. In the present paper, we define PPS as the part of space that surrounds the different body parts, which remains anchored to a given body part (arm, face, trunk) when that body part moves, and where information related to external stimuli (as signaled by visual or auditory inputs) interacts with the processing of somatosensory stimuli on the body. The extent or the boundaries of PPS are defined on the basis of multisensory responses, as captured by behavioral and neurophysiological measurements.

PPS has most often been linked to the arm reaching space, conceived as a sensory-motor interface for hand-object interactions (Brozzoli et al., 2012b; Makin et al., 2012; Maravita et al., 2003). However, data from patients and healthy volunteers also described a PPS around the head (Cléry et al., 2014; Farnè et al., 2005; Farnè and Làdavas, 2002; Làdavas et al., 1998b; Teneggi et al., 2013) and the trunk (Galli et al., 2015; Noel et al., 2014, 2015; A.S., unpublished data), suggesting that the extent of PPS should be defined by the (potential) interactions between stimuli on the body and objects in the space around it.

Prolonged Multisensory Stimulation Leads to Changes in Body Ownership, Self-Identification, and Self-Location: The Embodiment Constraint

Do multisensory stimulations within PPS that induce altered states of BSC also impact the constraints of multisensory perception? We propose that specific stimulation patterns, implemented during the different illusory own-body perceptions, change multisensory integration of bodily signals and shapes PPS representation, reflecting a fourth constraint for the neural mechanisms underlying BSC that we call “embodiment.” More specifically, the fourth constraint, which models of BSC need to account for, is how the synchronous and prolonged manipulation of multisensory stimulation impacts BSC. In the described experiments on BSC, subjects are exposed to synchronous visuo-tactile stimulations between their body and an artificial body, and these are generally applied for several minutes, inducing the different illusions (rubber-hand, enfacement, or full-body illusions), which are quantified by behavioral and brain imaging measurements. The prolonged synchronous stimulations related to the embodiment constraint temporally link stimuli from different modalities and from the physical body and another body or object. Embodiment applies when synchronous multisensory bodily signals are integrated over longer

periods of multisensory stimulation, thus inducing changes in BSC. Importantly, under normal conditions, embodiment applies for the physical parts of the biological body, which naturally and continuously receive prolonged and synchronous multisensory inputs. However, the reviewed bodily illusions (see [Makin et al., 2007](#); [Ehrsson, 2012](#); [Apps and Tsakiris, 2014](#); [Blanke, 2012](#) for revisions) and previous work on tool incorporation ([Maravita and Iriki, 2004](#)) show that embodiment can also apply to artificial objects and tools, whose features and position do not fully overlap with those of the biological body. In the rubber hand ([Makin et al., 2007](#); [Ehrsson, 2012](#)), enfacement ([Apps and Tsakiris, 2014](#)), and full-body illusion paradigms ([Blanke, 2012](#)), despite spatio-temporal conflicts in basic multisensory processing with respect to the three other BSC constraints, the embodiment constraint allows extending BSC to a different object or location than the biological body, if the period of multisensory stimulation is long enough. In the following sections, we will link specific changes in body ownership, self-identification, and self-location to mechanisms of plasticity in multisensory integration of bodily signals within the PPS, affecting embodiment.

Studies using the rubber hand illusion have consistently shown that the integration of visuo-tactile stimuli is determined by the same proprioceptive, visual, and spatial constraints determining multisensory bodily integration within PPS. No (or weaker) illusory hand ownership is induced if the rubber hand is presented far outside the participant's hand PPS ([Lloyd, 2007](#)), in a spatial position incompatible with the participants' posture ([Ehrsson et al., 2004](#); [Costantini and Haggard, 2007](#)), or for a visual stimulus whose shape does not resemble a hand ([Tsakiris et al., 2008, 2010](#)). Thus, visuo-tactile integration inducing the rubber hand illusion is subject to the constraints determining multisensory integration within the PPS (see [Figure 1C](#)). Illusory ownership can also be evoked for a very long virtual arm ([Kiltner et al., 2012](#); [Armel and Ramachandran, 2003](#)) or different arm colors ([Martini et al., 2013](#)), pending that the virtual limbs were perceived to be connected to the participant's body ([Perez-Marcos et al., 2012](#)). In addition, illusory hand ownership occurs not only when visuo-tactile stimulation on the participant's hand and on the virtual hand are perfectly synchronized, but also with a delay shorter than 300 ms, whereas at higher delays the strength of the illusion decays and vanishes for delays longer than 500 ms ([Shimada et al., 2009](#); see also [Aspell et al., 2010](#) and [Zopf et al., 2010](#) for temporal factors affecting multisensory interaction during the full-body illusion and the rubber hand illusion, respectively).

Other results show that once illusory ownership for the rubber hand is induced, the processing and integration of stimuli related to the real and the rubber hand is affected so that administering a threatening stimulus toward the rubber or virtual hand induces autonomic responses, as if the real hand was threatened ([Armel and Ramachandran, 2003](#)). Such effects have also been associated with physiological and perceptual changes in the participant's hand, such as reduction of hand temperature ([Moseley et al., 2008](#)), hand temperature sensitivity ([Llobera et al., 2013](#)), and change in immunological reactivity ([Barnsley et al., 2011](#)). Moreover, [Zopf et al. \(2010\)](#) showed the CCE magnitude reflected changes in BSC, since visual cues enhanced CCEs when applied on a rubber hand that was associated with illusory

hand ownership. This result reflects an alteration of multisensory integration within the PPS due to changes in BSC. Finally, [Ferri et al. \(2013\)](#) showed that the rubber hand illusion can be obtained even without touching the rubber hand by just presenting visual stimuli entering the rubber hand's PPS.

Less data are available for face ownership but are consistent in linking the enfacement illusion to multisensory integration within the face PPS. [Cardini et al. \(2013\)](#) showed that a visual stimulus occurring on another person's face (seen in front of the participant on a computer screen) impacted tactile stimulation on the participant's face more strongly after the two faces had received synchronous visuo-tactile stimulation to induce illusory face ownership. This effect was associated with a change in multisensory integration within the PPS: [Maister et al. \(2014\)](#) measured how a dynamic sound moving between the participant and the other person affected tactile processing of stimuli on the participant's face (as in [Canzoneri et al., 2012](#)) and how this depended on illusory face ownership with the other person's face. They found that a sound presented at a specific location far from the participant's face, but close to the other person's face, had a stronger effect on tactile processing, when the participants experienced illusory face ownership for the other person's face. To summarize, illusory ownership for a hand and face, due to prolonged stimulation, has been consistently linked to multisensory integration of bodily signals, based on proprioceptive, body-related visual information, PPS, and embodiment constraints. In case of ownership for specific body parts, we propose that such multisensory (mainly visuo-tactile) integration mechanisms concern body-part-specific (hand-centered, head-centered) representations. Multisensory stimulation involving larger body sectors, and in particular the trunk region, leads to alterations of global aspects of BSC, such as self-identification and self-location.

First experimental manipulations of self-location are reported by psychologist George Stratton, who performed self-experiments and described subjective changes in visuo-tactile perception using a portable system that consisted of two mirrors. One mirror was positioned horizontally above the head and another small mirror in front of the eyes (at an angle of 45°). The top mirror imaged the person as seen from above and was also reflected in the small mirror, leading to a projection of the image of Stratton's body in front-space. Prolonged usage of this device induced visuo-tactile sensations characterized by referral of touch to the visual locations and changes in self-location ([Stratton, 1899](#)). More systematic changes in self-location have been induced by recent studies employing different full-body illusion paradigms. By using questionnaires, behavioral tasks, mental imagery or skin conductance response, several studies proved that it is possible to make participants self-identify with an artificial body ([Lenggenhager et al., 2007, 2009, 2011](#); [Ehrsson, 2007](#); [Petkova and Ehrsson, 2008, 2011](#); [Guterstam et al., 2015](#); [Aspell et al., 2009, 2010, 2013](#); [Palluel et al., 2011](#); [Ionta et al., 2011](#); [Pfeiffer et al., 2013](#), [Pomés and Slater, 2013](#)) and also to induce changes in self-location. For instance, asking participants to walk to the position where they have been standing during the illusion induction (after displacing them), they place themselves not at the location of their physical body during the experiment, but either "in front" of or behind that position, depending on the

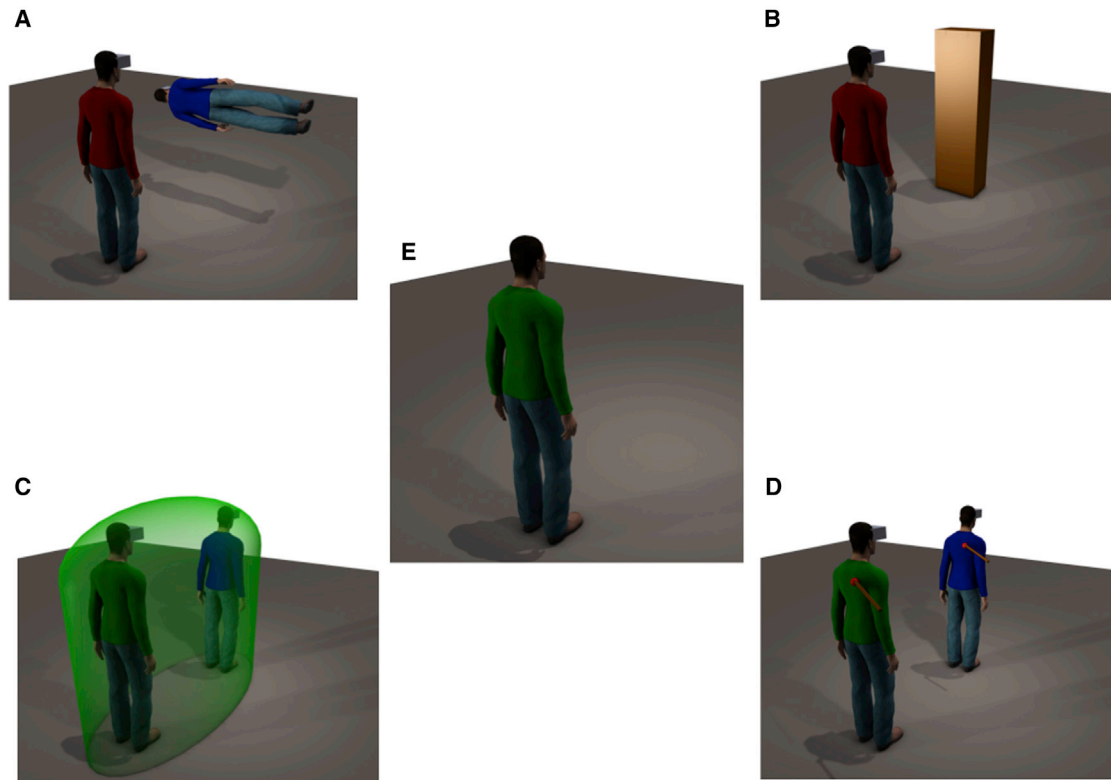


Figure 2. Four Constraints Determining Global Aspects of BSC (i.e., Self-Identification and Self-Location)

(A and B) Stimuli applied to an artificial body (with blue shirt) are integrated with stimuli on one's physical body (with red or green shirt), if the artificial body is placed coherently with the posture of the physical body. This change in global BSC does not occur if proprioceptive (and vestibular) information from one's own and the artificial body does not match ([A], proprioceptive constraint), or if an object with non-bodily shape is shown ([B], body-related visual information constraint). (C–E) Prolonged synchronous visuo-tactile stimulation applied to one's physical body and to the artificial body induces changes in global BSC, extends one's own PPS ([C], PPS constraint), and induces self-identification for, and a shift of self-location toward, the artificial body ([D], embodiment constraint). These four constraints normally determine integration of multisensory body signals for one's whole body, thus underlying self-identification with the body and normal self-location at the location of the physical body, within the PPS (E). Red and green body of the participant indicates, respectively, absence or presence of global aspects of BSC.

location of the artificial body during the manipulation. [Aspell et al. \(2009\)](#) studied changes in multisensory integration of bodily signals (CCE) associated to these experimentally induced changes in BSC. Stronger CCEs were found in the synchronous condition—inducing self-identification with the avatar and a drift in self-location toward the avatar's location. Proprioceptive constraints of multisensory integration of bodily signals were also found to modulate BSC, as investigated in the full-body illusion, since the magnitude of the CCE, as well as self-identification with the virtual body, were modulated consistently by leg muscle vibration (inducing proprioceptive noise), but not by arm muscle vibration ([Palluel et al., 2012](#)). Body-related visual information also impacts on such changes in BSC, as the administration of visuo-tactile synchronous stroking with a non-bodily object induces no or minimal changes in self-identification and self-location ([Figure 2B](#)) ([Lenggenhager et al., 2007](#); [Salomon et al., 2012](#); [Aspell et al., 2009](#); [Romano et al., 2014](#)). Thus, the embodiment constraint of BSC—based on the prolonged synchronous visuo-tactile stimulation—is also present and is associated with illusory changes in self-identification and self-location. Critically, such changes have been directly linked with a modulation of trunk-

centered PPS. [Noel et al. \(2015\)](#) measured the PPS size and the location of PPS boundaries adapted to the full body (while participants were exposed to synchronous visuo-tactile stroking to induce the full-body illusion). The PPS was found to extend in the front-space, toward the avatar's body, for which illusory self-identification was experienced. The opposite effect (a contraction of the PPS) was found in the back-space (and no such changes were observed in the asynchronous control condition in front- or back-space). These data show that the boundaries of PPS during the full-body illusion shift toward the avatar, suggesting that the reshaping of PPS representation mirrored the experimentally induced changes in BSC and further suggest that the trunk-centered, whole-body, PPS is referenced to the experienced location of the self, rather at the location of the physical body (see [Figure 2C](#)). These data show that although multisensory integration for the body occurs under normal conditions within the PPS, prolonged temporally synchronized stimulation of the body and of a virtual or physical replacement of it (embodiment, see [Figure 2D](#)) alters the constraints of multisensory bodily integration, reshapes PPS, and induces BSC for an artificial body.

Box 1. Current Status of the Field

BSC depends on the integration of bodily signals from different sensory modalities. As compared to other forms of multisensory integration involving purely exteroceptive stimuli, multisensory processing of bodily signals for BSC is determined by four computational constraints.

- It depends on proprioceptive and vestibular inputs signaling the location of body parts and of the whole body in space (proprioceptive constraint).
- It depends on visual information about the shape and the structure of the body (body-related visual information constraint).
- Normally it occurs within a limited space surrounding the body, termed PPS (PPS constraint).
- Prolonged multisensory stimulation manipulating the spatio-temporal coherence of bodily signals alters BSC, by reshaping the PPS boundaries and inducing BSC for non-corporeal objects (embodiment constraint).

Multisensory Integration for Partial versus Global Aspects of BSC

We summarize what is known about the constraints determining multisensory mechanisms of BSC in [Box 1](#). We note that, although the four constraints of BSC (proprioception, visual body-related information, PPS, and embodiment) are present for hand, face, and trunk, the mechanisms of multisensory perception of stimuli at the trunk and head are based on different mechanisms that are not present for hand-related perception and hand-related aspects of BSC. These differences are reflected in differences in tactile properties; for instance, the tactile spatial resolution at the fingers and hand is very high, whereas it is very low for the trunk, since the size of tactile receptive fields is small at finger/hand and large at the trunk (see next section). Moreover, the impact of vestibular cues is much more important for head-related processing than for arm-related processing, where proprioceptive cues are more relevant. Other differences are the limited direct visual access we have to our face and back as compared to the highly visible limbs and the differences in movement properties for hand and trunk (i.e., hand movements versus head or full-body movements) ([Kannape and Blanke, 2012](#); [Kannape et al., 2010](#)).

The importance of these distinct bodily signals for global aspects of BSC are prominent for self-identification and self-location, as distinguished from body-part ownership. Thus, while it has been shown that body ownership relies on multisensory signals from smaller circumscribed body regions (hand, face), self-identification relies on more global multisensory signals, encompassing large parts of the body (or the entire body). Accordingly, the mechanisms involved in self-identification and self-location rely heavily on proprioceptive and vestibular signals, and related multisensory bodily processes are referenced to the trunk. Finally, while illusory hand ownership occurs only when the hand is within the PPS, illusory self-identification and a shift of self-location can be induced for an artificial body presented farther away, to which the participant's PPS extends. Thus, we propose that neural processes of global BSC related to the trunk are fundamental for self-identification and self-location and are different from neural processes encoding BSC for circumscribed body parts. Only the former lead to the experience of an organism to be located within a particular portion of space in the world (self-location) and to identify with that portion of space. Most of the time, that position of space coincides with the organism's physical body (self-identification), because multisensory bodily inputs, under normal conditions, are all coherently related to the same physical object, the

body—"the same old body, always there" to use William James' words ([James, 1890](#))—which is then experienced as one's own body and where the PPS representation is centered. However, if multisensory bodily inputs are manipulated, using specific conflicts under specific constraints, it is possible to induce states of BSC for other objects or spatial locations, reshaping PPS representation and altering self-identification and self-location.

Major Neurophysiological Properties of BSC Bimodal and Multimodal Neurons

Next we focus on a particular set of neurons, bimodal and multimodal neurons, located in posterior parietal cortex, posterior insula, and premotor cortex (PMC) of non-human primates and highlight their main neurophysiological properties related to multisensory bodily perception and BSC. The key feature of bimodal neurons is that they respond not only to stimuli in one modality, such as tactile cues, but also to visual, auditory, and proprioceptive signals. Following seminal work by Vernon Mountcastle ([Mountcastle et al., 1975, 1995](#)), subsequent single unit studies in awake, behaving monkeys have consistently described several populations of bimodal and trimodal neurons processing multisensory bodily inputs. These neurons are mainly located in the posterior parietal cortex, in particular in a region ranging from the postcentral sulcus (at the junction between the superior parietal and the inferior parietal lobules) to more posterior regions along the intraparietal sulcus (IPS), and involve area 5, area 7, and area VIP. Frontal cortex, in particular ventral PMC (area 6), also harbors bimodal and trimodal neurons processing multisensory inputs (see [Figure 3](#)). These fronto-parietal areas are strongly interconnected, directly or indirectly project to the cortico-spinal tracts, and together are considered to form a fronto-parietal multisensory-motor network supporting sensory-motor functions ([Rizzolatti et al., 1997, 2002](#); [Colby, 1998](#); [Grefkes and Fink, 2005](#); [Andersen, 1997](#)).

Typically, these neurons have a tactile receptive field (RF) covering a relatively large part of the skin that is centered on a specific body part. Importantly, these neurons also respond to visual stimulation ([Duhamel et al., 1998](#); [Fogassi et al., 1996](#); [Graziano et al., 1994, 1997](#); [Rizzolatti et al., 1981](#); [Avillac et al., 2005](#)) or auditory stimulation ([Graziano et al., 1999](#); [Schlack et al., 2005](#)) (bimodal neurons), and still others respond to all three modalities (trimodal neurons). Many of them receive proprioceptive inputs, and some of them are active during body movements. The neuronal responses (i.e., spike discharge rate) are enhanced (or depressed) when bimodal stimuli

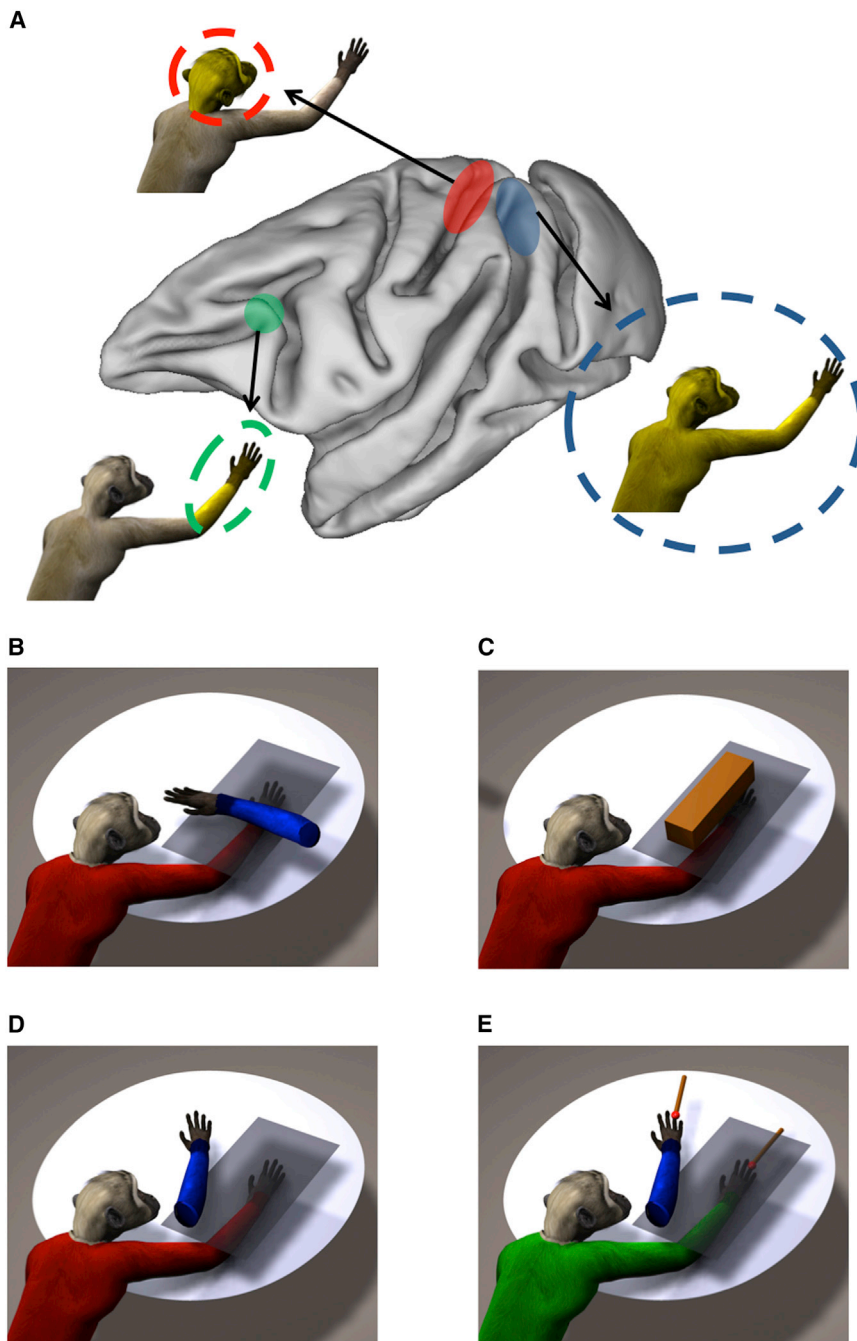


Figure 3. Neurophysiological Mechanisms of BSC in the Macaque

(A–C) Upper panel: main brain regions, dimensions, and location of multisensory receptive fields of multimodal neurons integrating body-related multisensory inputs within the PPS in the macaque ([A], PPS constraint). Lower panel: multisensory neurons may respond to stimulation related to an artificial arm, but this effect depends on whether the artificial hand is placed coherently or not with the posture of the physical hand ([B], proprioceptive constraint) and on whether a visual stimulus with bodily or non-bodily shape is shown ([C], body-related visual information constraint).

(D and E) Some multisensory neurons originally respond only to stimuli related to the real arm (D) and not to an artificial arm; however, prolonged synchronous visuo-tactile of the real and the artificial arm makes these neurons responding also to the artificial arm ([E], embodiment constraint).

Stein and Stanford, 2008). Frontal and parietal bimodal neurons are particularly sensitive to dynamic stimuli, as their firing rate increases in response to external (visual or auditory) cues approaching the body (Graziano et al., 1997; Graziano, 1999) and are sensitive to the velocity of looming stimuli (the boundaries of their receptive fields extend in space when presented with fast, as compared to slow, visual stimuli; Fogassi et al., 1996).

Receptive Field Properties of Bimodal and Multimodal Neurons

At least four distinct fronto-parietal functional networks have been described, based on their anatomical and functional properties, compatible with their involvement in specific sensory-motor functions (see Rizzolatti et al., 1997, 2002; Colby, 1998). Here we will focus on area F4 in the ventral-PMC and on the fundus of the IPS (ventral intraparietal area [VIP]), which, together with neighboring parietal areas 5 and 7b, host multisensory neurons whose multisensory properties have been most directly linked to bodily processing and BSC.

Compared to tactile receptive fields in lower-tier parietal regions such as S1,

(e.g., visuo-tactile) are presented simultaneously, as compared to non-stimulation trials (baseline neuronal discharge rate) or to unimodal conditions (unimodal visual or unimodal tactile stimulation). Different nonlinear sub-, super-, or additive mechanisms have been described (Avillac et al., 2007), and these neural activity modulations are a prominent feature of multisensory integration (i.e., Stein and Stanford, 2008). Integration is usually optimal when stimuli are in temporal synchrony and spatially congruent, similarly as for cortical regions processing auditory-visual stimuli (in superior temporal sulcus regions or superior colliculus; see

the size of the tactile receptive fields of bimodal neurons is large and may cover an entire hand/arm, the head or trunk, or an entire body half. Some may cover bilateral body regions. The size of the visual or auditory receptive fields typically matches that of the tactile receptive field, and the different receptive fields overlap spatially and extend from the body for varying distances. For instance, in ventral PMC, most neurons have a tactile receptive field covering the arm, but can also cover the shoulder, upper trunk, or face. Visual receptive fields (Fogassi et al., 1996; Graziano et al., 1997) of such PMC neurons also have variable

dimensions (from 5 cm to 1 m), and auditory receptive fields may extend into space by approximately 30 cm (Graziano et al., 1999). In most VIP neurons, the tactile receptive fields are usually centered on the head (Duhamel et al., 1998; Avillac et al., 2005), but have also been reported for the upper trunk (chest), shoulder, or arm (Iriki et al., 1996). Visual (Duhamel et al., 1998; Bremmer et al., 2001a) and auditory (Schlack et al., 2005) receptive fields in area VIP are usually limited to the upper part of visual or auditory space and cover a distance of 10–60 cm from the body surface, almost always on the same side of space as the tactile receptive field. Most bimodal neurons in area 7b have even larger tactile receptive fields and may cover the arm, the head, and the trunk, and sometimes even the whole body bilaterally. Again, the size and location of their visual (or auditory) receptive fields are congruent with the dimensions of the tactile receptive field and also extend bilaterally over large regions of the visual field, sometimes covering more than 1 m (Leinonen, 1980; Leinonen et al., 1979, 1980; Leinonen and Nyman, 1979; Hyvärinen, 1981; Graziano and Gross, 1995; Jiang et al., 2013). Thus, the receptive fields of these bi- and tri-modal neurons cover body-parts or larger parts of the body surface extending over portions of PPS and are proportional in size. At the anatomical level, upper extremities are represented mainly in PMC, the face in VIP, and the trunk in area 7b (Figure 3A).

Body-Part-Centered Multisensory Properties

Next to their sensitivity to tactile, visual, and auditory signals, these neurons also integrate proprioceptive and sometimes vestibular signals, which are important inputs allowing to anchor their multisensory receptive fields to the different body parts and to maintain spatial congruency between visual, auditory, and tactile receptive fields. Indeed, a critical feature of these neurons is that their visual (and auditory) receptive fields remain in spatial alignment with the tactile receptive field, despite active or passive movements of the arm, head, or trunk. If the body part (e.g., the arm) to which the tactile receptive field is anchored moves, the spatial location of the visual or auditory receptive field shifts congruently from the initial spatial position to its new location (Fogassi et al., 1996; Graziano et al., 1997), compatible with the importance of proprioceptive signals highlighted in behavioral studies of multisensory bodily processing in humans (Làdavias et al., 1998a; Spence et al., 2004; Serino et al., 2011a). Thus, multimodal neurons encode multisensory bodily stimuli in body-centered reference frames (i.e., arm-centered, head-centered, trunk-centered) by anchoring the different receptive fields to a given body part. In order to study the relative contribution of proprioceptive and visual inputs to arm-centered neurons, Graziano (1999) recorded the activity of ventral PMC neurons with multisensory arm-centered receptive fields and exposed a monkey to the following conflicting visuo-proprioceptive conditions: the monkey saw a visual stimulus that approached either its real arm or a fake arm, which was placed either congruently or incongruently with the real arm posture. The firing rates of the neurons to approaching stimuli varied as a function of the position not only of the monkey's real arm but also of the fake arm (see also Graziano et al., 2000 for similar coding by parietal neurons). Thus, body-related visual information, as signaled by the fake arm, in addition to proprioception of the real arm, modulates the location of multisensory receptive fields of these neurons in a similar way

as shown for multisensory perception in healthy (Pavani et al., 2000) and brain-damaged (Farnè and Làdavias, 2002) individuals.

Since sensory stimuli coming from an external object are initially processed in sensory-dependent reference frames (e.g., visual stimuli in eye-centered, auditory stimuli in head-centered, tactile stimuli in body-centered frames), their coordinates need to be aligned for integration. To this aim, the same stimuli are coded, or remapped, with respect to different body-centered reference frames (Colby, 1998; Andersen, 1997; Rizzolatti et al., 1997; Sereno and Huang 2014; see also Deneve and Pouget, 2004; Ma et al., 2006; Pouget et al., 2002). The computations necessary for coding stimuli from different modalities in body-centered reference frames differ depending on the concerned body parts to which external stimuli are referenced to (Andersen and Buneo, 2002; Cohen and Andersen, 2002; Pouget et al., 2002), compatible with the proprioceptive constraint of BSC and the differences between hand- and trunk-related aspects of BSC. Thus, in order to construct a visual receptive field that is anchored to the arm, it is necessary to take into account the position of the arm relative to the eye and the head, as well as the position of the arm relative to the trunk. Accordingly, fronto-parietal multisensory neurons mapping the peri-hand space show responses that are modulated by eye position, head position, and arm position (Graziano et al., 1997; Fogassi et al., 1996). In contrast, in order to construct a visual receptive field that is anchored to the head, it is necessary to take into account the position of the eye relative to the head and that of the head with respect to the trunk (while the position of the arm with respect to the trunk is irrelevant in this context). Most neurons in VIP, mapping the peri-head PPS, have been shown to modulate their responses depending on the position of the eyes and the head, but not of the arm (see Duhamel et al., 1998; Avillac et al., 2005; Graziano and Gross, 1995). Finally, for a trunk-centered spatial representation, head position and arm position are irrelevant. In fact, responses of area 7b or VIP neurons, mapping the trunk or the whole body, are not modulated by arm and head movements (Leinonen and Nyman, 1979; Leinonen et al., 1979; Hyvärinen, 1981; Graziano and Gross, 1995; Jiang et al., 2013) (see Figure 3A).

Multisensory Integration in PPS and Its Relevance for BSC at the Level of Single Neurons: Body Ownership and Self-Identification

In a series of elegant neurophysiological experiments, Graziano and Gross described multimodal neurons in area 5 that come closest of being the neurophysiological basis of BSC in animals (Graziano et al., 2000). These authors applied conditions of multisensory stimulation (similar to those of the rubber hand illusion in humans) and tested the response properties in monkey area 5. Presenting the animal either with a fake hand or the animal's hand (placed either on the right or the left side of space), several neurons responded preferentially when the arm occupied one side of space; bimodal visuo-proprioceptive neurons coded either the location of the physical arm (proprioception), the position of the fake arm (vision), or both (visuo-proprioceptive integration) (see also Graziano, 1999). Moreover, visuo-proprioceptive coding in area 5 neurons depended on whether a fake arm was seen or not (i.e., a box did not affect the cell's responses; body-related visual constraint of BSC; Figure 3C) and on whether the fake hand was shown in a physically possible

position (i.e., an inverted arm was not effective; proprioception constraint of BSC; Figure 3B). Most importantly, Graziano et al. (2000) showed that prolonged visuo-tactile stroking—similarly as that used to induce the rubber hand illusion—affected the tuning properties of these neurons. Selecting neurons whose response preference depended on the location of the real (proprioceptive), but not of the fake (visual information), arm, they applied synchronous visuo-tactile stroking repeatedly to the monkey's hidden real and visible fake arm. Re-evaluating the visual tuning of the same neurons immediately afterward, these neurons were now tuned to the visual location of the fake arm (a coding which was absent before visuo-tactile stimulation; embodiment constraint of BSC; see Figure 3E). As in the rubber hand illusion in healthy humans, such neuronal tuning changes were absent after asynchronous visuo-tactile stroking. We argue that changes in body ownership that are induced by synchronized visuo-tactile stroking during the rubber hand illusion involve comparable neurophysiological changes and shifts in the spatial characteristics of hand-centered multimodal neurons in human parietal or PMC areas (see Makin et al., 2008). Analogously, we argue that changes in self-identification and self-location induced in the full-body illusion (i.e., Lenggenhager et al., 2007) that are associated with changes in the boundary of trunk PPS (Noel et al., 2015) rely on similar neurophysiological tuning changes, but for trunk- and not hand-centered neurons, especially in areas VIP or area 7b. We thus speculate that the visuo-tactile stroking procedures described for the arm, face, and trunk and affecting BSC change the neural responses of multimodal neurons, resulting in a displacement or enlargement of their visual or auditory receptive fields, so that they also encode the seen hand, face, or whole body, even if presented at spatial location beyond the body's boundaries (see Iriki et al., 2001). In other words, appropriate manipulations, implementing specific spatio-temporal conflicts in multisensory signals, might alter the standard constraints typically ruling multisensory integration of bodily inputs, thus re-shaping PPS representation and inducing specific and predicted changes in BSC.

Similar links between multisensory integration, body perception, and BSC in animals can be proposed for face perception (Chang et al., 2015). These authors assessed self-face recognition in monkeys by means of the mirror-mark test (Gallop, 1970). Usually, monkeys fail to pass the test, indicating a potential lack of self-awareness (at least as tested by this procedure; see Suddendorf and Butler, 2013 and RoCHAT and Zahavi, 2011 or discussions). However, Chang and colleagues observed that monkeys passed the test after exposure to multisensory bodily stimulation, which consisted in projecting a laser light of mildly irritating facial tactile stimulation, the monkey could observe through a mirror. Such facial somatosensory stimulation was coupled with synchronous visual stimulation of the face (seen in the mirror), mimicking the enfacement illusion in humans (Tsakiris, 2008; Sforza et al., 2010). Crucially, after prolonged visuo-tactile training in front of the mirror, the trained monkeys showed behavioral evidence of self-recognition and exhibited spontaneous untrained behaviors that were directed toward their body (potential behavioral evidence for BSC). We speculate that such synchronous visuo-tactile stimulation during the training may have activated face-selective PPS neurons in VIP and that

changes in the tuning of these neurons may have resulted in successful self-face recognition (Chang et al., 2015). Ishida et al. (2010) reported that VIP bimodal face-centered neurons, which responded to tactile and visual stimulation approaching the monkey's face, also discharged when a visual stimulus approached the experimenter's face. As the latter condition is comparable to looking into a mirror, it is possible that the systematic and prolonged activation of such bimodal neurons due to the mirror visuo-tactile training as used by Chang and colleagues may establish new systematic links between the seen face (mirror) and the monkey's own face. By repeating comparable experiments as described by Chang et al. (2015) for the face and by Graziano et al. (2000) for the hand, but by exposing monkeys to conditions of multisensory stimulation of the full-body illusion while recording neural activities from multisensory areas in different animal species, one may reveal the detailed neural machinery of self-identification and self-location not only in monkeys but also in lower species such as cats (Wallace and Stein, 2007) or rodents (Raposo et al., 2012; Olcese et al., 2013); even in *Drosophila* the investigation of multisensory signals that are of relevance for BSC is possible (see e.g., Gepner et al., 2015).

Major Brain Regions of BSC in Humans

In the following section, we present neuroimaging data suggesting how multisensory integration of bodily signals in PPS, relevant for BSC, is implemented in the human brain.

Hand Ownership

Many studies have focused on the processing of hand-centered multisensory bodily signals. Makin et al. (2007) showed that regions along the IPS, in the lateral occipital complex (LOC), and the ventral PMC were activated more strongly when a stimulus approached the participants' hand (near condition) as compared to the same visual stimulation presented at a distance of 70 cm from the hand (far condition). This differential activation was further modulated by proprioceptive hand position signals as well as body-related visual information, compatible with coding in a hand-centered reference frame. Differential near-far activation (i.e., within or outside the hand PPS) in IPS was also present when viewing a fake hand at the near location (even if the participant's real hand was retracted), but was absent in LOC and ventral PMC, if participants positioned their hand far from the location of the near stimulus. These activation patterns, especially in IPS (dependence on visual information as occurring near versus far from the hand and dependence on proprioceptive and visual bodily information), are compatible with the proprioceptive and body-related visual constraints highlighted by behavioral and neurophysiological studies. Gentile et al. (2011) further showed that these areas do not only process signals that are on or close to the arm but also preferentially integrate multisensory stimuli, when occurring within the arm-centered PPS. They compared neural activity associated with unimodal tactile stimulation of the hand, unimodal visual stimulation near the hand, and bimodal (visuo-tactile) stimulation within the PPS. Moreover, areas in posterior and inferior parietal cortex and PMC showed additive response to bimodal, as compared to unimodal stimulation (see also Makin et al., 2007). Other regions in the anterior IPS, dorsal PMC, insula, and putamen showed non-linear, super-additive responses, similarly to

multisensory integration regions in animals (Avillac et al., 2005; Stein and Stanford, 2008).

Such multisensory integration effects further depend on the spatial and temporal coherence between visuo-tactile inputs. Gentile et al. (2013) joined tactile stimulation of the participant's real hand with the visual presentation of a virtual hand while manipulating spatial congruency (i.e., manipulating the direction of visual and tactile stimulation along the proximo-distal or medio-lateral hand axis) and temporal synchrony of stimulation (i.e., with synchronous or asynchronous visuo-tactile stimulation): activation in IPS, in ventral and dorsal PMC, in LOC, and in the cerebellum varied as a function of the spatial and temporal congruency of visuo-tactile hand stimulation and were modulated by proprioceptive and visual signals related to the hand, reflecting the spatio-temporal constraints of multisensory bodily integration. (Brozzoli et al., 2011) used fMRI adaption to identify multisensory arm-related neuronal activations responding to stimulation within the PPS; they found that IPS, the inferior parietal lobe (supramarginal gyrus), the dorsal and ventral PMC, the cerebellum, and the putamen show reduced activation (adaptation) to consecutive visual stimulation near the hand, but not for consecutive far stimuli, compatible with their role in multisensory perception within PPS. Taken together, these neuroimaging studies highlight a network of premotor and parietal areas (as well as the putamen and the cerebellum) associated with the integration of tactile hand-centered stimulation with visual stimuli occurring within the hand PPS, depending on the first three constraints of BSC (i.e., proprioceptive, body-related visual information, and PPS constraints).

Further neuroimaging studies linked this PPS hand-centered system to arm-related BSC, and to hand ownership, in particular. Prolonged synchronous visuo-tactile stroking of the real and a fake hand (placed in a plausible posture), inducing illusory hand ownership, was found to activate ventral PMC (Ehrsson et al., 2004), IPS, and the cerebellum (Ehrsson et al., 2004, 2005) (i.e., the same areas showing de-activation in case of incongruent visuo-tactile hand stimulation and decreased hand ownership) (Gentile et al. (2013). Others described ownership-related activation in the supplementary motor area (Ehrsson, 2007) and posterior parietal regions, including the inferior parietal and superior parietal lobule (Lloyd et al., 2006), by showing that those areas responded to threatening stimuli directed to the fake hand. Moreover, the strength of hand ownership (as measured by questionnaire ratings) was found to correlate with activity in anterior insular, anterior cingulate cortices (Ehrsson, 2007), PMC, and cerebellum (Ehrsson et al., 2004). These findings were extended by Tsakiris et al. (2007), who reported that activity in right posterior insula and sensorimotor cortices (pre-central and postcentral gyri) was associated with illusory hand ownership and that activity in the right insula and left somatosensory cortex correlated with proprioceptive drift. We note that hand ownership has also been manipulated by applying finger-specific stimulations (i.e., numbness illusion) and has been associated with circumscribed activity in sub-regions of primary somatosensory cortex (Dieguez et al., 2009; Martuzzi et al., 2015).

Inducing illusory ownership for a fake hand through prolonged synchronous visuo-tactile stimulation recodes the space around the rubber hand as peri-hand space. While bilateral IPS and PMC

activations normally show an adaptation effect for consecutive visual stimuli presented close to the participant's real hand (Brozzoli et al., 2011), this effect was not obtained if repeated visual stimulations were presented close to a fake hand that was positioned in contralateral space. Yet, adaptation effects in IPS and PMC were evoked by stimuli near the fake hand when additional visuo-tactile stroking was used to induce illusory hand ownership for the contralateral fake hand (Brozzoli et al., 2012a). This suggests that both areas, normally representing the participant's PPS, also coded the space surrounding the illusory own fake hand, extending earlier single cell responses in area 5 and PMC (Graziano et al., 1999, 2000) to subjective hand ownership.

Taken together, these human neuroimaging studies highlight two main regions (PMC and PPC), within a larger network of cortical areas (including insula, primary somatosensory cortex, LOC, TPJ, supplementary motor area, anterior cingulate cortex, and cerebellum), involved in the integration of multisensory arm-related signals (see Figure 4A). Human PMC and IPS have been consistently found to integrate multisensory stimuli within the hand PPS, based on the spatial and temporal laws of multisensory perception as well as the four constraints of BSC (proprioception, hand-related visual signals, PPS, and embodiment). Activity in these regions depends on the spatio-temporal congruency between the processing of these hand-related multisensory inputs and is consistent with the reviewed behavioral data in humans and the neurophysiological data in PMC and area 5 in non-human primates. These data support the hypothesis that the tuning properties of bi- or tri-modal neurons, mapping the peri-hand space, in the PMC-IPS network (Graziano et al., 1999, 2000; see also Makin et al., 2008) define ownership for one's own hand, or for an artificial replacement of it (embodiment), by integrating multiple hand-related signals within the PPS on the basis of proprioceptive and visual constraints (see Figure 4B).

Self-Face Perception and Face Ownership

An early study on humans showed that neural activity associated with tactile stimulation on one's face overlapped with activity evoked by visual or auditory stimuli approaching the face in three cortical regions: IPS, ventral PMC, and lateral inferior parts of the postcentral gyrus (Bremmer et al., 2001b). Based on this response profile, Bremmer and colleagues proposed that the IPS region was the human homolog of monkey area VIP, a proposal further corroborated by (Serenó and Huang, 2006), who found that the same anatomical IPS region contained aligned maps of tactile and visual stimuli in the peri-face region and that this activity encoded stimuli in a face-centered reference frame. More recently, Cardini et al. (2011) showed that the IPS/VIP region was activated when participants received tactile stimulation on their face, while viewing another face being touched. Visuo-tactile evoked IPS/VIP activity in this study did not differ if participants viewed their own face being touched (as in the mirror) or another person's face. Ventral PMC was also activated by visuo-tactile face stimulation and was found to encode face identity.

Concerning BSC and the particular case of the enfacement illusion (Tsakiris et al., 2008; Sforza et al., 2010; Apps et al., 2015), it was shown that prolonged synchronous visuo-tactile stimulation of the face, as compared to asynchronous stimulation, significantly activated ventral IPS, temporo-parietal junction (TPJ), and an extrastriate visual face region in the inferior

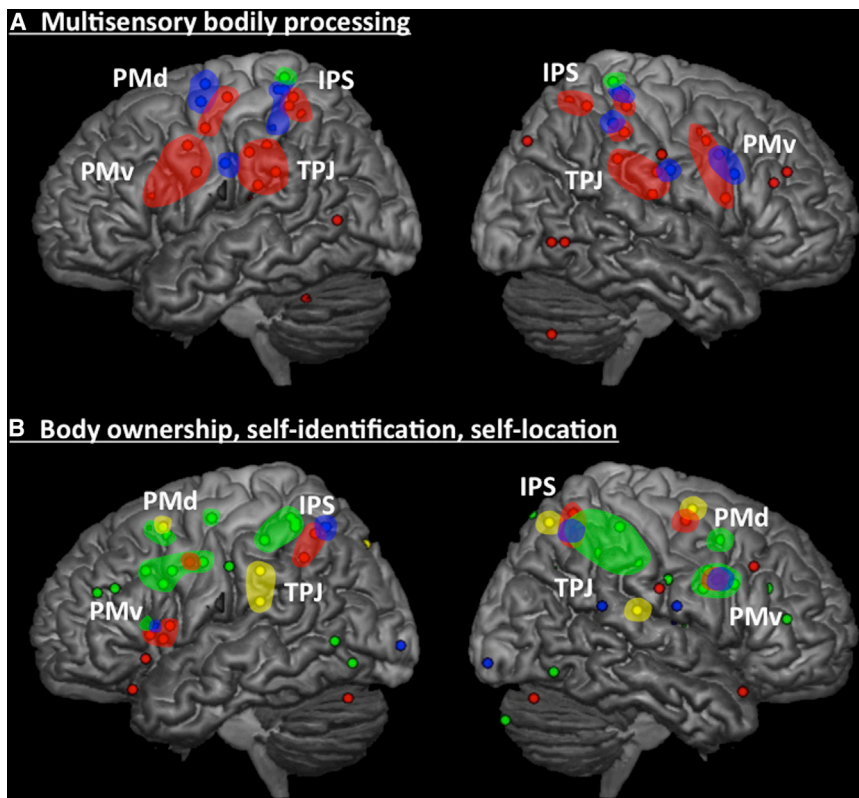


Figure 4. Brain Regions Integrating Multisensory Bodily Inputs and Implied in BSC in the Human Brain

(A) Brain areas selectively responding to multisensory inputs within the PPS around the hand (red), face (blue) or trunk (green).

(B) Brain areas active during manipulations of BSC, underlying ownership for the hand (red) or face (blue), self-identification (green), or self-location (yellow). Each dot represents an activation site as identified by the studies reviewed in section 4. The colored shadows highlight clusters of activations.

occipital gyrus (occipital face area; (Kanwisher et al., 1997; Apps et al., 2012). Activation in all three regions was further correlated with the strength of the enfacement illusion. The data from these studies converge on a key role for posterior parietal cortex (IPS/VIP) within a larger network of cortical regions, including PMC, inferior postcentral gyrus, TPJ, and occipital face area, in the integration of multisensory face-related signals (see Figure 4A). In posterior parietal cortex within IPS, especially area VIP contains bimodal and trimodal neurons mapping the face PPS as described in animal studies (Duhamel et al., 1998; Avillac et al., 2005; Schlack et al., 2005). This area both in humans and in monkeys preferentially responds not only to tactile stimulation on the face and visual (or auditory) stimulation approaching one's own face but also to the face of other individuals (Ishida et al., 2010; Cardini et al., 2011). Moreover, activation patterns in area VIP change after prolonged visuo-tactile stimulation of one's own and another person's face inducing face-related changes in BSC (Apps et al., 2015) (see Figure 4B).

This face-related IPS/VIP region likely overlaps with the hand-related areas (see Figures 3 and 4). We note, however, that less information is available on how multisensory responses in face-specific areas is modulated by proprioceptive and visual inputs related to the face, as shown for hand-centered areas. This might be the case because face and hand rely on different anatomical and functional constraints. Direct visual signals from the own face are absent or rare (i.e., not available without a mirror or related technology), whereas the arm and hand are often in our visual fields. Moreover, proprioceptive input is also different, given the axial head system involved in neck proprioception

(head and face), the strongly lateralized hand proprioception system for arm and hand position, and the different degrees of freedom in movements for both different body parts. Accordingly, vestibular inputs are strongly recruited for face-related multisensory processing, and indeed, monkey VIP regions representing the face process not only visual, tactile, or auditory stimuli in face PPS but also vestibular inputs signaling head motion (Bremmer et al., 2002). We argue that the tuning properties of multimodal neurons in VIP and other face-encoding IPS regions define face ownership, accordingly with the four major constraints of

BSC described before. However, the role of the different sensory inputs and constraints vary between hand and face representation and ownership. In the latter case, vestibular inputs have a strong role in determining face orientation (in addition to proprioceptive signals that are of importance for hand and face). Furthermore, visual inputs are prominently related to process visual features about the face—as a stronger hallmark of self-identity—than signaling face orientation.

Self-Identification and Self-Location

Human brain regions integrating multisensory signals concerning the trunk have also been investigated. Huang et al. (2012) administered tactile stimulation on the face, shoulders, hands, legs, and toes while concurrently stimulating different sectors of the visual field and found a general overlap of activity induced by tactile stimulation of each body part and the visual stimulation of spatially congruent sectors of the visual field (i.e., head tactile stimulation with upper visual field; leg tactile stimulation with lower visual field). Visuo-tactile maps of different body parts were identified in the superior posterior parietal cortex: the face representation was located within the IPS/VIP region described in the previous section, whereas the representation of the lower body parts was located more medially and posteriorly, and the finger and hand representations more laterally and anteriorly see Figure 4A).

In order to study the brain mechanisms of self-identification, Petkova et al. (2011) combined fMRI with the body-swap illusion, whereby participants receive prolonged tactile stimulation on their abdomen while viewing a mannequin through an HMD being touched at the same body location. This stimulation induces

illusory body ownership for a virtual body, if it is seen from the viewpoint of a camera mounted on the head of the virtual body (third-person viewpoint; [Petkova and Ehrsson, 2008](#); see also [Slater et al., 2010](#); [Maselli and Slater, 2013](#) for effects of changes in viewpoint during full-body illusions). fMRI data revealed IPS and ventral PMC activations when tactile information applied to the participant's body was spatially congruent and temporally synchronous with the seen stimulation of the virtual body, and activity modulation in ventral PMC (but not IPS) was correlated with the strength of illusory ownership for the virtual body (assessed by post-scan questionnaires). In a series of follow-up experiments, Ehrsson and colleagues investigated whether and how such illusory body ownership differs in its underlying neural mechanisms from ownership for body parts ([Gentile et al., 2015](#); [Petkova et al., 2011](#)). To this aim, visuo-tactile stimulation was applied to different parts (abdomen, chest, or legs) of the participant's body and to the seen virtual body. During prolonged synchronous visuo-tactile stimulation, illusory touch was perceived as arising from the mannequin's body, regardless of the stimulated body part, with no difference in the strength of the illusion, suggesting that illusory bodily feelings could be obtained by co-stimulating different body parts of the participant and the virtual body ([Gentile et al., 2015](#)). Such effects were not obtained by stimulating a rubber hand detached from the mannequin and placed in an implausible posture. By using multivoxel pattern analysis, the authors found that ventral PMC activity discriminated between prolonged synchronous and asynchronous visuo-tactile stimulation (independently from the stimulated body part), and it was not activated for a detached rubber hand ([Petkova et al., 2011](#); [Gentile et al., 2015](#)). Other portions of the ventral PMC, IPS, LOC, and putamen showed more selective responses for synchronous visuo-tactile stimulation of specific body parts.

Another fMRI study used the full-body illusion ([Ionta et al., 2011](#)) to study global changes in BSC, and found that self-identification with a virtual body is associated with activation of the TPJ (see below) and the middle-inferior temporal cortex. The latter activation in middle-inferior temporal cortex partially overlapped with the extrastriate body area ([Astafiev et al., 2004](#); [Downing et al., 2001](#); [Grossman and Blake, 2002](#)), a region involved in the multisensory processing of human bodies ([Orlov et al., 2010](#)). No activations related to body ownership were observed in PMC and IPS in the study performed by [Ionta et al., \(2011\)](#). Differently from the standard body-swap illusion, the full-body illusion has also been shown to induce changes in self-location ([Lenggenhager et al., 2007, 2009](#); [Serino et al., 2013](#)), which were found to be associated with gamma band oscillations in the right TPJ and alpha band oscillations in the medial prefrontal cortex ([Lenggenhager et al., 2011](#)) (see [Figure 4B](#)). Interestingly, if the prolonged stimulation used to induce the full-body illusion is performed while participants are lying, as during fMRI, and view a virtual body that was filmed from an elevated position, changes in self-location are associated to changes in the experienced direction of participants' first-person perspective (see also [Pfeiffer et al., 2013](#)). Critically, activity at the TPJ, peaking in the posterior superior temporal gyri, the parietal operculum, and the posterior insula, was associated with changes in self-location and in the experienced direction of first-person perspective induced by the full-body illu-

sion at individual-subject level. In particular, despite identical prolonged visuo-tactile stimulation, half of the participants experienced looking upward toward the virtual body (up-looking first-person perspective), and half experienced looking down on the virtual body (down-looking first-person perspective). These subjective perspectival changes in the experienced direction of the first-person perspective were associated with consistent changes in self-location: up-looking participants reported an elevation (drift) in self-location during synchronous stroking, from an initially lower initial self-location; down-looking participants reported the opposite downward drift from an initially higher self-location. TPJ activity reflected these differential changes during synchronous versus asynchronous visuo-tactile stimulation, suggesting that TPJ processing reflects self-location and depends on the experienced direction of the first-person perspective, compatible with clinical data ([Blanke et al., 2002](#); [Heydrich and Blanke, 2013](#); [De Ridder et al., 2007](#)).

Additional functional connectivity analysis by [Ionta et al. \(2014\)](#) showed that the TPJ regions are bilaterally connected to other regions integrating multisensory inputs within the PPS, such as the IPS/VIP, the ventral PMC, extrastriate visual regions (extrastriate body area), the supplementary motor area, and the insula. Interestingly, the pattern of functional connectivity from the TPJ to the insula and the supplementary motor area varied during visuo-tactile stimulation, and reflected experimentally-induced changes in self-location and first-person perspective. The involvement of the insula in BSC and self-location is in line with the prominent involvement of the insula neurons in the processing of bodily multisensory signals ([Craig, 2002, 2009](#); [Critchley, 2004](#); [Critchley et al., 2004](#)), including vestibular signals ([Indovina et al., 2005](#); [Mazzola et al., 2014](#)). The insula is also the primary region processing interoceptive signals ([Craig, 2002](#); [Critchley et al., 2004](#)) and has recently been shown to mediate changes in self-identification and self-location based on cardio-visual stimulation in the full-body illusion ([Aspell et al., 2013](#); [Ronchi et al., 2015](#)), illusory own-body perceptions due to interoceptive-exteroceptive disintegration in neurological patients ([Heydrich and Blanke, 2013](#)) and hand ownership ([Tsakiris et al., 2007](#)). Thus this brain region, by processing and integrating multisensory signals from the outside and the inside of the body, may play a primary role in self-consciousness, as suggested by recent reviews ([Craig, 2002, 2009](#); [Seth, 2013](#)).

Finally, in a recent study, [Guterstam et al. \(2015\)](#) used the body-swap illusion and combined visuo-tactile stimulation (of the participant's abdomen) with different visual viewpoints from where the mannequin's body and the room were seen. This was done to induce changes in self-location (and self-identification). Participants experienced illusory self-location at different places in the scanner room, depending on the mannequin's viewpoint (as assessed by questionnaires), and this was reflected by hippocampal, posterior cingulate, and IPS activations (further modulated by visuo-tactile synchrony). Moreover, functional connectivity between posterior cingulate cortex and IPS correlated with the experienced self-location.

To conclude, neuroimaging studies in humans suggest that self-identification recruits a network of multisensory brain areas located in the posterior parietal cortex (IPS/VIP region) and PMC. These areas in IPS and PMC, which contain bimodal and

trimodal neurons underlying PPS representation, are widely connected with more lateral, temporo-occipital regions (LOC; processing high-level visual and multisensory information related to the body), with the insular cortex (processing interoceptive bodily signals), and with more lateral regions at the TPJ, including posterior insula and parietal operculum (receiving important projections from the vestibular system). We argue that these trunk-centered activations related to self-identification are based on neuronal populations and regions that partially overlap, but are anatomically and functionally distinct from arm-related aspects of BSC (hand ownership), containing neurons with multisensory receptive fields that are anchored to large body regions, encompassing the right or left hemibody, the upper or lower body half, or in some cases the entire body surface (Graziano and Gross, 1995; Duhamel et al., 1998; Leinonen et al., 1979; Hyvärinen, 1981). Face ownership activations are likely an intermediate case between hand- and trunk-centered activations, overlapping with hand, but particularly with trunk- and body-related ownership regions. Importantly, the reviewed neuroimaging data show that activations in these regions depend on the four constraints of BSC.

Next to the degree of separation between hand, face, and body ownership regions, there remain fascinating open questions for BSC, especially in relation to the brain mechanisms related to the global components of BSC; future research should aim at identifying the differences between the neural bases of self-identification, self-location, and first-person perspective. For instance, different brain activations have been reported during prolonged visuo-tactile stimulation when the virtual trunk is seen from an embodied viewpoint (looking down your own body; viewing a virtual body as employed in the Body-swap illusion) as compared to when the trunk (back) of a virtual body is seen from a more distant viewpoint (as in the full-body illusion), suggesting different neural and functional mechanisms for self-identification and self-location (e.g., Ionta et al., 2011; Pfeiffer et al., 2013). We argue that the key regions for self-identification are within the PMC-IPS network, whereas key areas for self-location are located in more lateral temporo-parietal regions, encompassing parietal operculum, supramarginal gyrus, posterior superior temporal gyrus, and posterior insula, (Ionta et al., 2011, 2014), as well as posterior cingulate cortex (Guterstam et al., 2015). Systematic human studies are needed to differentiate the self-identification PMC/IPS system from the self-location TPC/PCC system, ideally using automatized and robotically-controlled experimental approaches.

Models of Multisensory Integration and BSC

Computational models have focused on how inputs from two or more senses are combined to improve perception based on the principles of optimal integration and Bayesian computations. These models have been applied to visuo-tactile integration (Ernst and Banks, 2002; Ernst and Bühlhoff, 2004) to explain object perception during haptic manipulation and to audio-visual integration to explain phenomena such as the ventriloquism effect or sound-induced visual illusions (Alais and Burr, 2004; Magnotti et al., 2013; Wozny et al., 2010; Wozny and Shams, 2011). The integration of visuo-vestibular stimuli for translational and rotational self-motion perception has also been studied by several investigators (Fetsch et al., 2012,

2013; Prsa et al., 2012, 2015). In all these cases, it has been shown that inputs from different modalities are combined accordingly to maximum-likelihood estimation models: multisensory estimate is the weighted sum of unisensory signals, where signals from the less noisy modality (i.e., with lower variance and higher reliability) are weighted more strongly during the integration process. This integration rule minimizes error so that the perceptual precision of the multisensory estimate is always higher than the individual estimates.

Other models focused on neural mechanisms of multisensory integration, and some were developed to explain the non-linear properties of audio-visual integration by implementing the temporal, spatial, and inverse effectiveness laws in neural structures like the superior colliculus (Cuppini et al., 2010, 2011; Stein et al., 2014; Xu et al., 2015). Other research investigated how signals from different sensory modalities are aligned into common reference frames for integration. Early studies focused on visuo-motor transformations, necessary to re-map visual inputs, originally coded in eye-centered reference frames, into body-part centered reference frames, such as an arm-centered reference frame for reaching movements toward a seen object (Andersen et al., 1985; Cohen and Andersen, 2002; Colby and Goldberg, 1999; Salinas and Thier, 2000). These reference frame transformations have been proposed to be implemented at the level of individual neurons, so that a single cell's response to a visual stimulus occurring within their receptive field is rescaled as a function of eye, head, or arm posture (a mechanism known as gain fields). Neurons with gain field properties have been extensively described in parietal cortex and fronto-parietal networks supporting body-object interactions (for reviews, see Colby, 1998; Grefkes and Fink, 2005). Others extended these reference frame transformation models to the population level and implicated not only visuo-motor neurons, but also auditory, somatosensory, as well as vestibular and proprioceptive neurons in multisensory integration processes. In particular, Pouget and colleagues (Deneve and Pouget, 2004; Ma et al., 2006; Pouget et al., 2002) proposed an influential computational framework based on neural network dynamics, consisting of multiple layers ranging from layers coding unisensory inputs to multisensory layers. Following this approach, unisensory layers are interconnected with different multisensory layers, containing so-called basis function units, which, due to attractor dynamics, code multisensory stimuli in mixed reference frames, consistent with partially shifting receptive fields. Such models are supported by neurophysiological data showing that multimodal neurons have not only eye-centered or head-centered receptive fields but also mixed or combined receptive fields (e.g., combining eye-centered and head-centered reference frames), especially in regions of the posterior parietal cortex (i.e., area LIP, VIP and MIP), which are known to integrate multisensory inputs (Duhamel et al., 1998; Avillac et al., 2005, 2007) and enable sensorimotor transformations (Andersen and Buneo, 2002).

Sabes and colleagues tested the dynamics of neural network models for reference frame transformations and multisensory integration based on multiple neuronal layers, proposing that the computations implemented to combine inputs from unisensory layers into multisensory layers are learned and depend on sensory experience. Using machine learning, they proposed to

conceptualize reference frame transformations and multisensory integration in terms of a density estimation model, whereby the distribution of observed data (the activity of unisensory neurons) is encoded by a set of latent variables (the activity of neurons in multisensory layers) and a set of parameters (the synaptic connections between unisensory and multisensory layers) (Dadarlat et al., 2015; Makin et al., 2013). The network is trained (by changing the synaptic weights) so to generate the same distribution of unisensory activities when they are driven by the multisensory neurons as when they are driven by their true “hidden” causes in the world. This requires that the latent variables encode the “hidden causes” of the data and their relationships, learning a range of neural computations, such as optimal integration of signals with a common cause, separation of signals with different causes, and coordinate transformations.

Magosso and Serino also used a multilayer architecture to design a neural network of the arm PPS representation (Magosso et al., 2010a, 2010b; Serino et al., 2015). The model includes a series of unisensory layers (representing tactile, auditory, and visual areas) connected to a multisensory layer. In this model, the strength of the synapses from unisensory to multisensory neurons is set to reproduce the response tuning that has been observed for near-body stimuli of the PPS system. Thus, the weight of the synapses from unisensory neurons with tactile, visual, or auditory receptive fields on the body or at short distances from the body is strong, whereas the synaptic weight from unisensory neurons with receptive fields covering far space is weak. The model reproduced behavioral data showing enhanced tactile processing when dynamic visual and auditory stimuli enter the boundaries of the PPS (Serino et al., 2015; Canzoneri et al., 2012). By implementing feedback projections from multisensory to unisensory neurons and inhibitory interhemispheric projections, the model also explained behavioral data from brain-damaged patients suffering from crossmodal extinction (Magosso et al., 2010b). In addition, the model proposes a mechanism to account for PPS-related plasticity. The weights of the model connections, indeed, are continuously defined through experience due to Hebbian learning aimed at simulating everyday life hand-objects integration. Hand stimulation activates the tactile unisensory layers, which in turn activates the multisensory layer. Usually, tactile stimulation is coupled with visual or auditory stimulation occurring within the PPS, thus activating visual or auditory unisensory neurons with receptive fields close to the body. Instead, neurons with receptive fields covering far space are not, or much less frequently, activated. In this way, the synaptic weights from unimodal visual or auditory neurons with receptive fields close to the body continuously strengthen due to the concurrent firing of the post-synaptic multisensory neurons (activated by tactile stimulation), while the synaptic weights from unimodal visual or auditory neurons with far receptive fields decay. However, such stimulation patterns may vary, for instance, if people use tools to reach far objects, as many studies in multisensory integration have shown (see Maravita and Iriki, 2002, for a well-known review). During tool use, people receive a tactile stimulation on their hand from the tool-extended body, synchronously coupled with visual and/or auditory stimulation from far space, where the tool exerts its function. Thus, tool-use, inducing a synchronous near-far

stimulation, might result in a strengthening of the synapses between unisensory neurons with far receptive fields and multisensory neurons. Serino et al. (2015) recently provided the computational demonstration of this prediction and also showed, in a behavioral experiment, that administering synchronous tactile stimulation on the participants' hand and auditory stimulation at a far location, even without any tool use, resulted in an extension of PPS boundaries, which reproduced the effect obtained after actual tool use (Canzoneri et al., 2013b).

We note that the patterns of stimulation used to investigate model performance in the case of extending the PPS via tool use (Serino et al., 2015) resembles that used to induce the rubber hand illusion. In the latter illusion, participants receive tactile stimulation on their hand that is coupled with synchronous visual stimulation of the rubber hand, placed at a distance, whereas in the former case auditory stimulation at the tip of the tool is coupled with tactile stimulation of the hand. We speculate that a similar model can account for the changes in multisensory bodily perception and the shift of the arm-related PPS boundary toward an artificial replacement of the body during the rubber hand illusion (see Brozzoli et al., 2012a; Graziano et al., 2000) and tool use (Serino et al., 2015). In case this hypothesis is confirmed by computational and experimental work, it would be possible to link mechanisms of plasticity in PPS representation with changes in BSC induced by multisensory bodily stimulations.

Closely related to this point, Samad et al. (2015) recently modeled proprioceptive drifts during the rubber hand illusion as the result of a multisensory integration based on Bayesian causal inferences. Based on tactile and proprioceptive cues from the real hand and visual cues from the rubber hand, Bayesian computation was used to determine whether these multiple sensory inputs relate to the same object (illusory ownership and proprioceptive drift) or to two different objects, depending on the temporal and the spatial coherence between the multiple bodily signals. The model also predicts that no multisensory integration nor proprioceptive drift occur if the rubber hand is placed at distance of more than 30 cm from the real hand; this is compatible with behavioral data (Lloyd, 2007), the size of the arm-centered PPS in humans (Canzoneri et al., 2012), the size of visuo-tactile receptive fields of arm-centered PPS neurons in monkeys (Graziano and Cooke, 2006), and the distance-dependent activation patterns observed in human PMC and IPS (Makin et al., 2007; Gentile et al., 2011; Brozzoli et al., 2011). These data confirm that multisensory integration of bodily signals is constrained by the dimensions of PPS and that such constraints likely impact BSC.

We note, however, that a Bayesian model based only on bottom-up inputs cannot explain why hand ownership is absent or weaker when the stroking is applied over a non-bodily visual stimulus (Ehrsson et al., 2004; Tsakiris, 2010) or on a rubber hand placed in an incompatible body posture (Tsakiris and Haggard, 2005). Bottom-up integration of multisensory inputs is necessary, but not sufficient, for these effects. Additional signals about the body from visual and proprioceptive inputs regulate the degree of multisensory integration and determine illusory hand ownership. The interaction between bottom-up inputs and top-down modulation in generating the rubber hand illusion has been recently formalized into Bayesian models incorporating predictive coding (Clark, 2013) and the free energy principle (Friston, 2010).

In general, such models conceptualize brain function as the interaction between bottom-up neural processes, coding sensory information, and top-down processes, generating predictions about the incoming sensory inputs. Information travels continuously in feedforward and feedback directions between bottom-up and top-down levels, with the main regulating principle of minimizing the differences between the generated predictions and the incoming sensory inputs. This architecture is repeated hierarchically at successively more complex stages of neural information processing. These models have been recently applied to describe bodily illusions such as the rubber hand illusion as the result of different unisensory inputs (touch and proprioception from the real hand and vision of the rubber hand), initially processed in unisensory areas, and then integrated in multisensory areas, depending on a series of predictions based on prior experience (Apps and Tsakiris, 2014; Hohwy and Paton, 2010; Limanowski and Blankenburg, 2013). If a mismatch arises from incoming sensory inputs and predictions, the prior is updated to minimize error predictions. In everyday life, tactile stimulation on the hand and visual information within the PPS about a hand being synchronously touched are integrated because the standard prediction is that those inputs derive from the same object (one's own hand). During the rubber hand illusion, however, the incongruence between tactile and visual inputs (due to the proprioceptive mismatch between the position of the real and the rubber hand, or by the appearance of the rubber hand) generates a strong prediction error, which needs to be minimized. This is done by changing predictions and modulating sensory inputs so that the proprioceptive mismatch (proprioceptive drift) and the perceptual difference between the real and the rubber hand is reduced, resulting in the new prediction that "the rubber hand is my hand," thus supporting embodiment (see Limanowski and Blankenburg, 2015 for recent neuroimaging data supporting this model).

It has also been argued that similar models based on Bayesian computation, predictive coding, and free energy principle may also account for changes in face ownership during the enface-ment illusion and face perception (Apps and Tsakiris, 2013, 2014) and to BSC and the different kinds of bodily illusions, including the full-body and the body-swap illusion (Limanowski and Blankenburg, 2013; Hohwy and Paton, 2010; Apps and Tsakiris, 2014). These models may also explain why bodily illusions can be easily obtained in virtual reality contexts. Thus, whenever individuals throughout their entire life look toward their body they of course see their own body. Hence when in immersive virtual reality contexts they control a virtual body while receiving sensory stimulation and carrying out movements, the simplest hypothesis for the brain to adopt is that what they are seeing is their own body. Thus, in order to minimize prediction errors, sensory information signaling that the seen body does not look like the real body and that "virtual reality isn't real" is discounted at the perceptual and subjective level. This is emphasized by another manipulation that many bodily illusions based on immersive virtual reality carried out by Slater and colleagues included: the participant sees a reflection in a virtual mirror of a virtual body. The reflection they see is a virtual body rather than their real one, while in their entire life individuals have seen their own body reflected back when looking in a mirror. Nevertheless, people self-identify with the virtual body, suggesting that the "prior

probability" that what they see in a mirror is their body is overwhelming (Sanchez-Vives and Slater, 2005; Slater, 2009).

Although there is a wealth of computational models on multisensory integration, multisensory illusions, and reference frame transformations, we currently lack models on the integration of multisensory bodily stimuli within PPS underlying BSC. We argue that models related to arm-centered multisensory PPS and hand ownership, if adapted to the reviewed trunk-related processing principles, are likely to also account for self-identification and self-location during the full-body and body-swap illusions. Thus, more computational work is needed to compute the mechanisms of the integration of multisensory bodily inputs that are of relevance for trunk-centered aspects of BSC, accounting for the constraints of vestibular and proprioceptive signals, body-related visual signals, and PPS. In addition, none of the available models, at the moment, seems able to convincingly account for the subjective BSC components induced by the body-swap and full-body illusions, including self-location and first-person perspective.

Conclusion and Outlook

We reviewed the brain mechanisms of multisensory integration of bodily stimuli underlying BSC. We highlighted four different constraints for designing neurocomputational models of BSC and showed how the integration of multisensory bodily stimuli for BSC depends on (1) proprioception, (2) body-related visual information, (3) PPS, and (4) embodiment (see Box 1). These constraints were highlighted in the reviewed data from human behavior, animal neurophysiology, human neuroimaging, and computational models, suggesting the presence of two distributed and partially overlapping cortical networks of BSC: one in frontoparietal cortex (IPS and PMC) processing signals for hand and face ownership (i.e., ownership for circumscribed body parts) and a second in more posterior temporo-parietal cortex (supramarginal gyrus, insula, superior temporal gyrus) processing signals for such global aspects of BSC, such as self-identification and self-location. Both networks are densely interconnected and partially overlapping, forming the neural substrate for the multisensory integration of bodily stimuli underlying BSC.

Such knowledge is starting to impact engineering and in particular virtual reality technology. Over the last 30 years, technological developments in virtual reality have struggled to modulate and control, substitute, and enhance human experience. Recent advances in digital technologies, such as communication, personal computing, and wearable technologies, now offer powerful tools to manipulate bodily and environmental information to study first-person perspective (Petkova and Ehrsson, 2008; Ionta et al., 2011; Slater et al., 2010; Maselli and Slater, 2013). Detailed descriptions of the brain mechanisms of BSC might inform the exploitation of such technologies to produce or enhance the experience of being in other places and to control and perceive multiple artificial bodies, or body parts, and robots (see Blanke, 2012; Sanchez-Vives and Slater, 2005) for more extensive discussion). Moreover, these methods are currently applied in the field of social psychology to study and potentially reduce implicit racial and other social biases, by inducing implicit self-identification for out-group members (in terms of race, age, or gender; Banakou et al., 2013; Peck et al., 2013; Maister et al., 2014, 2015).

Box 2. Future Directions

Most of the data about integration of multisensory bodily signals for BSC focus on single body-part representations. Thus, we lack information about global aspect of BSC. In particular:

- More single unit data, imaging data, and computational models are needed about trunk-centered mechanisms of multisensory integration within PPS, critical for global aspects of BSC.
- We do not know which computational mechanisms distinguish body-parts versus trunk-centered, global coding of BSC.
- While mechanisms of body ownership and self-identification have been explored, more work is needed on self-location and, even more, on 1PP.
- More animal research in model simpler than primates (e.g., rodents especially, but also insects) might contribute to unveil the biological and genetic basis of BSC.

There are several outstanding issues that need to be solved in order to design neurocomputational models of BSC, which are summarized in [Box 2](#). First, while some of the necessary conditions of multisensory stimulation inducing specific changes in BSC are known (based on four constraints reviewed in this paper), many of the parameters for manipulating BSC are currently less well specified (e.g., the minimal duration of multisensory stimulation affecting BSC, the precise features of stimulation inducing stronger effects). The integration of psychophysical studies, with computational models and animal neurophysiology, might contribute to provide such information. Second, most currently available data describe the mechanisms of visuo-tactile integration for hand-related inputs, hand-centered spatial representations, and hand ownership. For the more relevant aspects of BSC, such as self-identification and self-location (and first-person perspective; not reviewed here), behavioral, animal, and neuroimaging data, as well as computational descriptions, are currently missing. As a simple thought experiment shows, finger or limb amputation would likely induce some alterations of limb ownership and phantom limb experiences in most patients ([Ramachandran and Hirstein, 1998](#)), but it does not radically alter BSC, as amputees maintain normal self-identification with the body, normal self-location, and normal first-person perspective. Conversely, consider the case of neurological patients suffering from out-of-body experiences due to damage to temporo-parietal cortex. These patients suffer strong BSC alterations with altered self-identification, self-location, and first-person perspective, as they report to feel abnormally elevated self-location, self-identify with this elevated position, and experience to perceive the world from a disembodied perspective ([Blanke et al., 2002](#); [Ionta et al., 2011](#); [Blanke, 2012](#); [Heydrich and Blanke, 2013](#)). None of the reviewed models can currently account for these clinical alterations of BSC that could be described not as phantom limb but as phantom body experiences. However, the existing trunk-related behavioral and neuroscientific data suggest that neurocomputational accounts of BSC are possible and should extend models proposed for hand-centered BSC (e.g., [Makin et al., 2008](#); [Samad et al., 2015](#)) and other multisensory effects to the study of global components of self-experience.

More animal, neuroimaging, and modeling work on trunk-centered multisensory bodily processing is needed to understand and describe how global components of BSC underlying subjective experience are implemented in the mammalian brain. A clear definition of BSC, as in the present study, that is based on neural mechanisms of integration of multisensory bodily signals may

allow to build powerful bridges with biology. Highly independent from human language, memory, and other cognitive functions, the mechanisms of BSC have already been studied in monkey; we argue that they can also be studied in rodents and *Drosophila*, targeting the neural, genetic, and molecular origins of BSC. In mice, for example, we argue that the trunk-centered multisensory BSC system likely relates to other neural systems involved in generating spatial maps of the environment such as place and grid cells ([Moser et al., 2008](#)), calibrating the coordinates of the subject of conscious experience not only with respect to the subject's body but also to egocentric and allocentric maps of the external world. This work needs to investigate multisensory integration of bodily stimuli relying on the processing of axial cues in trunk- and head-centered coordinates instead of the visuo-tactile hand-related cues that have been studied in innumerable investigations. We note that the morphology of the trunk is particularly well preserved across animal species. We also suggest that inputs from the vestibular system to this trunk-centered BSC system are not only fundamental to determine the orientation and motion of the body in space, but also for BSC, especially self-location, self-motion, and the first-person perspective.

ACKNOWLEDGMENTS

The authors would like to thank Petr Grivaz for help with the figures and Nathan Faivre for his comments on a previous version of the manuscript. O.B. and A.S. are supported by grants from the Swiss National Science Foundation, the European Science Foundation (EU FP7 FET Integrated Project VERE #257695; the FP7/2007-2013 (grant agreement no. 604102; Human Brain Project), and the Bertarelli Foundation. M.S. is supported by the EU FP7 FET Integrated Project VERE #257695; the FP7/2007-2013 (grant agreement no. 604102; Human Brain Project).

REFERENCES

- Alais, D., and Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Curr. Biol.* 14, 257–262.
- Andersen, R.A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 352, 1421–1428.
- Andersen, R.A., and Buneo, C.A. (2002). Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.* 25, 189–220.
- Andersen, R.A., Essick, G.K., and Siegel, R.M. (1985). Encoding of spatial location by posterior parietal neurons. *Science* 230, 456–458.
- Apps, M.A., and Tsakiris, M. (2013). Predictive codes of familiarity and context during the perceptual learning of facial identities. *Nat. Commun.* 4, 2698.

- Apps, M.A., and Tsakiris, M. (2014). The free-energy self: a predictive coding account of self-recognition. *Neurosci. Biobehav. Rev.* *41*, 85–97.
- Apps, M.A., Tajadura-Jiménez, A., Turley, G., and Tsakiris, M. (2012). The different faces of one's self: an fMRI study into the recognition of current and past self-facial appearances. *Neuroimage* *63*, 1720–1729.
- Apps, M.A., Tajadura-Jiménez, A., Sereno, M., Blanke, O., and Tsakiris, M. (2015). Plasticity in unimodal and multimodal brain areas reflects multisensory changes in self-face identification. *Cereb. Cortex* *25*, 46–55.
- Armel, K.C., and Ramachandran, V.S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proc. Biol. Sci.* *270*, 1499–1506.
- Aspell, J.E., Lenggenhager, B., and Blanke, O. (2009). Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *PLoS ONE* *4*, e6488.
- Aspell, J.E., Lavanchy, T., Lenggenhager, B., and Blanke, O. (2010). Seeing the body modulates audiotactile integration. *Eur. J. Neurosci.* *31*, 1868–1873.
- Aspell, J.E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., and Blanke, O. (2013). Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychol. Sci.* *24*, 2445–2453.
- Astafiev, S.V., Stanley, C.M., Shulman, G.L., and Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat. Neurosci.* *7*, 542–548.
- Avillac, M., Denève, S., Olivier, E., Pouget, A., and Duhamel, J.R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nat. Neurosci.* *8*, 941–949.
- Avillac, M., Ben Hamed, S., and Duhamel, J.R. (2007). Multisensory integration in the ventral intraparietal area of the macaque monkey. *J. Neurosci.* *27*, 1922–1932.
- Barnsley, N., McAuley, J.H., Mohan, R., Dey, A., Thomas, P., and Moseley, G.L. (2011). The rubber hand illusion increases histamine reactivity in the real arm. *Curr. Biol.* *21*, R945–R946.
- Bassolino, M., Finisguerra, A., Canzoneri, E., Serino, A., and Pozzo, T. (2015). Dissociating effect of upper limb non-use and overuse on space and body representations. *Neuropsychologia* *70*, 385–392.
- Bertelson, P. (1999). Ventriloquism: A case of crossmodal perceptual grouping. *Adv. Psychol.* *129*, 347–362.
- Bisiach, E., Luzzatti, C., and Perani, D. (1979). Unilateral neglect, representational schema and consciousness. *Brain* *102*, 609–618.
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nat. Rev. Neurosci.* *13*, 556–571.
- Blanke, O., and Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends Cogn. Sci.* *13*, 7–13.
- Blanke, O., Ortigue, S., Landis, T., and Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature* *419*, 269–270.
- Blanke, O., Arzy, S., and Landis, T. (2008). Illusory reduplications of the human body and self. *Handb. Clin. Neurol.* *88*, 429–458.
- Botvinick, M., and Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature* *391*, 756–756.
- Bremmer, F., Schlack, A., Duhamel, J.R., Graf, W., and Fink, G.R. (2001a). Space coding in primate posterior parietal cortex. *Neuroimage* *14*, S46–S51.
- Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K., Zilles, K., and Fink, G.R. (2001b). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* *29*, 287–296.
- Bremmer, F., Klam, F., Duhamel, J.R., Ben Hamed, S., and Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *Eur. J. Neurosci.* *16*, 1569–1586.
- Brozzoli, C., Gentile, G., Petkova, V.I., and Ehrsson, H.H. (2011). FMRI adaptation reveals a cortical mechanism for the coding of space near the hand. *J. Neurosci.* *31*, 9023–9031.
- Brozzoli, C., Gentile, G., and Ehrsson, H.H. (2012a). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *J. Neurosci.* *32*, 14573–14582.
- Brozzoli, C., Makin, T.R., Cardinali, L., Holmes, N.P., and Farne, A. (2012b). Peripersonal Space: A Multisensory Interface for Body-Object Interactions. In *The Neural Bases of Multisensory Processes*, M.M. Murray and M.T. Wallace, eds. (CRC Press).
- Brugger, P., Regard, M., and Landis, T. (1997). Illusory reduplication of one's own body: phenomenology and classification of autoscopic phenomena. *Cogn. Neuropsychiatry* *2*, 19–38.
- Calvert, G., Spence, C., and Stein, B.E. (2004). *The handbook of multisensory processes* (MIT press).
- Canzoneri, E., Magosso, E., and Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS ONE* *7*, e44306.
- Canzoneri, E., Marzolla, M., Amoresano, A., Verni, G., and Serino, A. (2013a). Amputation and prosthesis implantation shape body and peripersonal space representations. *Sci. Rep.* *3*, 2844.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., and Serino, A. (2013b). Tool-use reshapes the boundaries of body and peripersonal space representations. *Exp. Brain Res.* *228*, 25–42.
- Cardini, F., Costantini, M., Galati, G., Romani, G.L., Làdavas, E., and Serino, A. (2011). Viewing one's own face being touched modulates tactile perception: an fMRI study. *J. Cogn. Neurosci.* *23*, 503–513.
- Cardini, F., Tajadura-Jiménez, A., Serino, A., and Tsakiris, M. (2013). It feels like it's me: interpersonal multisensory stimulation enhances visual remapping of touch from other to self. *J. Exp. Psychol. Hum. Percept. Perform.* *39*, 630–637.
- Chang, L., Fang, Q., Zhang, S., Poo, M.M., and Gong, N. (2015). Mirror-induced self-directed behaviors in rhesus monkeys after visual-somatosensory training. *Curr. Biol.* *25*, 212–217.
- Christoff, K., Cosmelli, D., Legrand, D., and Thompson, E. (2011). Specifying the self for cognitive neuroscience. *Trends Cogn. Sci.* *15*, 104–112.
- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* *36*, 181–204.
- Cléry, J., Guipponi, O., Wardak, C., and Hamed, S.B. (2014). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: Knowns and unknowns. *Neuropsychologia* *70*, 313–326.
- Cohen, Y.E., and Andersen, R.A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nat. Rev. Neurosci.* *3*, 553–562.
- Colby, C.L. (1998). Action-oriented spatial reference frames in cortex. *Neuron* *20*, 15–24.
- Colby, C.L., and Goldberg, M.E. (1999). Space and attention in parietal cortex. *Annu. Rev. Neurosci.* *22*, 319–349.
- Cohen, Y.E., and Andersen, R.A. (2000). Reaches to sounds encoded in an eye-centered reference frame. *Neuron* *27*, 647–652.
- Costantini, M., and Haggard, P. (2007). The rubber hand illusion: sensitivity and reference frame for body ownership. *Conscious. Cogn.* *16*, 229–240.
- Craig, A.D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nat. Rev. Neurosci.* *3*, 655–666.
- Craig, A.D. (2009). How do you feel—now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* *10*, 59–70.
- Critchley, H.D. (2004). The human cortex responds to an interoceptive challenge. *Proc. Natl. Acad. Sci. USA* *101*, 6333–6334.
- Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., and Dolan, R.J. (2004). Neural systems supporting interoceptive awareness. *Nat. Neurosci.* *7*, 189–195.
- Cuppini, C., Ursino, M., Magosso, E., Rowland, B.A., and Stein, B.E. (2010). An emergent model of multisensory integration in superior colliculus neurons. *Front. Integr. Neurosci.* *4*, 6.

- Cuppini, C., Stein, B.E., Rowland, B.A., Magosso, E., and Ursino, M. (2011). A computational study of multisensory maturation in the superior colliculus (SC). *Exp. Brain Res.* 213, 341–349.
- Dadarlat, M.C., O'Doherty, J.E., and Sabes, P.N. (2015). A learning-based approach to artificial sensory feedback leads to optimal integration. *Nat. Neurosci.* 18, 138–144.
- Damasio, A., Meyer, K., Laureys, S., and Tononi, G. (2009). Consciousness: An overview of the phenomenon and of its possible neural basis. In *The Neurology of Consciousness: Cognitive Neuroscience and Neuropathology*, S. Laureys and G. Tononi, eds. (Associated Press), pp. 3–14.
- De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., and Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *N. Engl. J. Med.* 357, 1829–1833.
- de Vignemont, F. (2011). Embodiment, ownership and disownership. *Conscious. Cogn.* 20, 82–93.
- Dehaene, S., and Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron* 70, 200–227.
- Deneve, S., and Pouget, A. (2004). Bayesian multisensory integration and cross-modal spatial links. *J. Physiol. Paris* 98, 249–258.
- Deroy, O., Chen, Y.C., and Spence, C. (2014). Multisensory constraints on awareness. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 369, 20130207.
- di Pellegrino, G., Làdavas, E., and Farné, A. (1997). Seeing where your hands are. *Nature* 388, 730.
- Dieguez, S., Mercier, M.R., Newby, N., and Blanke, O. (2009). Feeling numbness for someone else's finger. *Curr. Biol.* 19, R1108–R1109.
- Downing, P.E., Jiang, Y., Shuman, M., and Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473.
- Duhamel, J.R., Colby, C.L., and Goldberg, M.E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *J. Neurophysiol.* 79, 126–136.
- Ehrsson, H.H. (2007). The experimental induction of out-of-body experiences. *Science* 317, 1048.
- Ehrsson, H.H. (2012). The concept of body ownership and its relation to multisensory integration. In *The New Handbook of Multisensory Processing*, B.E. Stein, ed. (MIT Press), pp. 775–792.
- Ehrsson, H.H., Spence, C., and Passingham, R.E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305, 875–877.
- Ehrsson, H.H., Holmes, N.P., and Passingham, R.E. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *J. Neurosci.* 25, 10564–10573.
- Ernst, M.O., and Banks, M.S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415, 429–433.
- Ernst, M.O., and Bühlhoff, H.H. (2004). Merging the senses into a robust percept. *Trends Cogn. Sci.* 8, 162–169.
- Evans, N., and Blanke, O. (2013). Shared electrophysiology mechanisms of body ownership and motor imagery. *Neuroimage* 64, 216–228.
- Faivre, N., Mudrik, L., Schwartz, N., and Koch, C. (2014). Multisensory integration in complete unawareness: evidence from audiovisual congruency priming. *Psychol. Sci.* 25, 2006–2016.
- Faivre, N., Salomon, R., and Blanke, O. (2015). Visual consciousness and bodily self-consciousness. *Curr. Opin. Neurol.* 28, 23–28.
- Farné, A., and Làdavas, E. (2002). Auditory peripersonal space in humans. *J. Cogn. Neurosci.* 14, 1030–1043.
- Farné, A., Pavani, F., Meneghelo, F., and Làdavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain* 123, 2350–2360.
- Farné, A., Demattè, M.L., and Làdavas, E. (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology* 65, 1754–1758.
- Ferri, F., Chiarelli, A.M., Merla, A., Gallese, V., and Costantini, M. (2013). The body beyond the body: expectation of a sensory event is enough to induce ownership over a fake hand. *Proc. Biol. Sci.* 280, 20131140.
- Fetsch, C.R., Pouget, A., DeAngelis, G.C., and Angelaki, D.E. (2012). Neural correlates of reliability-based cue weighting during multisensory integration. *Nat. Neurosci.* 15, 146–154.
- Fetsch, C.R., DeAngelis, G.C., and Angelaki, D.E. (2013). Bridging the gap between theories of sensory cue integration and the physiology of multisensory neurons. *Nat. Rev. Neurosci.* 14, 429–442.
- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., and Rizzolatti, G. (1996). Coding of peripersonal space in inferior premotor cortex (area F4). *J. Neurophysiol.* 76, 141–157.
- Frassinetti, F., Bolognini, N., and Làdavas, E. (2002). Enhancement of visual perception by crossmodal visuo-auditory interaction. *Exp. Brain Res.* 147, 332–343.
- Friston, K. (2010). The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* 11, 127–138.
- Gallagher, I. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* 4, 14–21.
- Gallese, V., and Sinigaglia, C. (2010). The bodily self as power for action. *Neuropsychologia* 48, 746–755.
- Galli, G., Noel, J.P., Canzoneri, E., Blanke, O., and Serino, A. (2015). The wheelchair as a full-body tool extending the peripersonal space. *Front. Psychol.* 6, 639.
- Gallop, G.G., Jr. (1970). Chimpanzees: self-recognition. *Science* 167, 86–87.
- Gentile, G., Petkova, V.I., and Ehrsson, H.H. (2011). Integration of visual and tactile signals from the hand in the human brain: an fMRI study. *J. Neurophysiol.* 105, 910–922.
- Gentile, G., Guterstam, A., Brozzoli, C., and Ehrsson, H.H. (2013). Disintegration of multisensory signals from the real hand reduces default limb self-attribution: an fMRI study. *J. Neurosci.* 33, 13350–13366.
- Gentile, G., Björnsson, M., Petkova, V.I., Abdulkarim, Z., and Ehrsson, H.H. (2015). Patterns of neural activity in the human ventral premotor cortex reflect a whole-body multisensory percept. *Neuroimage* 109, 328–340.
- Gepner, R., Mihovilovic Skanata, M., Bernat, N.M., Kaplow, M., and Gershow, M. (2015). Computations underlying *Drosophila* photo-taxis, odor-taxis, and multi-sensory integration. *eLife* 4, <http://dx.doi.org/10.7554/eLife.06229>.
- Goldberg, I.I., Harel, M., and Malach, R. (2006). When the brain loses its self: prefrontal inactivation during sensorimotor processing. *Neuron* 50, 329–339.
- Graziano, M.S.A. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc. Natl. Acad. Sci. USA* 96, 10418–10421.
- Graziano, M.S.A., and Gross, C.G. (1995). The representation of extrapersonal space: A possible role for bimodal, visual-tactile neurons. In *The cognitive neurosciences*, M.S. Gazzaniga, ed. (MIT Press), pp. 1021–1034.
- Graziano, M.S., and Cooke, D.F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia* 44, 845–859.
- Graziano, M.S., Yap, G.S., and Gross, C.G. (1994). Coding of visual space by premotor neurons. *Science* 266, 1054–1057.
- Graziano, M.S., Hu, X.T., and Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* 77, 2268–2292.
- Graziano, M.S., Reiss, L.A., and Gross, C.G. (1999). A neuronal representation of the location of nearby sounds. *Nature* 397, 428–430.
- Graziano, M.S., Cooke, D.F., and Taylor, C.S. (2000). Coding the location of the arm by sight. *Science* 290, 1782–1786.
- Grefkes, C., and Fink, G.R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *J. Anat.* 207, 3–17.
- Grossman, E.D., and Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron* 35, 1167–1175.

- Guterstam, A., Björnsdotter, M., Gentile, G., and Ehrsson, H.H. (2015). Posterior cingulate cortex integrates the senses of self-location and body ownership. *Curr. Biol.* **25**, 1416–1425.
- Haggard, P., and Chambon, V. (2012). Sense of agency. *Curr. Biol.* **22**, R390–R392.
- Heatherton, T.F., Wyland, C.L., Macrae, C.N., Demos, K.E., Denny, B.T., and Kelley, W.M. (2006). Medial prefrontal activity differentiates self from close others. *Soc. Cogn. Affect. Neurosci.* **1**, 18–25.
- Heed, T., Buchholz, V.N., Engel, A.K., and Röder, B. (2015). Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends Cogn. Sci.* **19**, 251–258.
- Heydrich, L., and Blanke, O. (2013). Distinct illusory own-body perceptions caused by damage to posterior insula and extrastriate cortex. *Brain* **136**, 790–803.
- Hohwy, J., and Paton, B. (2010). Explaining away the body: experiences of supernaturally caused touch and touch on non-hand objects within the rubber hand illusion. *PLoS ONE* **5**, e9416.
- Huang, R.S., Chen, C.F., Tran, A.T., Holstein, K.L., and Sereno, M.I. (2012). Mapping multisensory parietal face and body areas in humans. *Proc. Natl. Acad. Sci. USA* **109**, 18114–18119.
- Hyvärinen, J. (1981). Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res.* **206**, 287–303.
- Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., and Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science* **308**, 416–419.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., Gassert, R., and Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron* **70**, 363–374.
- Ionta, S., Martuzzi, R., Salomon, R., and Blanke, O. (2014). The brain network reflecting bodily self-consciousness: a functional connectivity study. *Soc. Cogn. Affect. Neurosci.* **9**, 1904–1913.
- Iriki, A., Tanaka, M., and Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* **7**, 2325–2330.
- Iriki, A., Tanaka, M., Obayashi, S., and Iwamura, Y. (2001). Self-images in the video monitor coded by monkey intraparietal neurons. *Neurosci. Res.* **40**, 163–173.
- Ishida, H., Nakajima, K., Inase, M., and Murata, A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J. Cogn. Neurosci.* **22**, 83–96.
- James, W. (1890). *The principles of psychology*, Volume 1 (Holt).
- Jeannerod, M. (2003). The mechanism of self-recognition in humans. *Behav. Brain Res.* **142**, 1–15.
- Jiang, H.H., Hu, Y.Z., Wang, J.H., Ma, Y.Y., and Hu, X.T. (2013). Visuospatial properties of caudal area 7b in *Macaca fascicularis*. *Zool. Res.* **34** (E2), E50–E61.
- Kannape, O.A., and Blanke, O. (2012). Agency, gait and self-consciousness. *Int. J. Psychophysiol.* **83**, 191–199.
- Kannape, O.A., and Blanke, O. (2013). Self in motion: sensorimotor and cognitive mechanisms in gait agency. *J. Neurophysiol.* **110**, 1837–1847.
- Kannape, O.A., Schwabe, L., Tadi, T., and Blanke, O. (2010). The limits of agency in walking humans. *Neuropsychologia* **48**, 1628–1636.
- Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311.
- Kilteni, K., Normand, J.M., Sanchez-Vives, M.V., and Slater, M. (2012). Extending body space in immersive virtual reality: a very long arm illusion. *PLoS ONE* **7**, e40867.
- Kim, C.-Y., and Blake, R. (2005). Psychophysical magic: rendering the visible 'invisible'. *Trends Cogn. Sci.* **9**, 381–388.
- Knoblich, G. (2002). Self-recognition: body and action. *Trends Cogn. Sci.* **6**, 447–449.
- Koch, C. (2004). *The quest for consciousness* (New York).
- Làdavas, E., di Pellegrino, G., Farnè, A., and Zeleni, G. (1998a). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *J. Cogn. Neurosci.* **10**, 581–589.
- Làdavas, E., Zeleni, G., and Farnè, A. (1998b). Visual peripersonal space centred on the face in humans. *Brain* **121**, 2317–2326.
- Legrand, D. (2007). Subjectivity and the body: introducing basic forms of self-consciousness. *Conscious. Cogn.* **16**, 577–582.
- Legrand, D., and Ruby, P. (2009). What is self-specific? Theoretical investigation and critical review of neuroimaging results. *Psychol. Rev.* **116**, 252–282.
- Leinonen, L. (1980). Functional properties of neurones in the posterior part of area 7 in awake monkey. *Acta Physiol. Scand.* **108**, 301–308.
- Leinonen, L., and Nyman, G. (1979). II. Functional properties of cells in antero-lateral part of area 7 associative face area of awake monkeys. *Exp. Brain Res.* **34**, 321–333.
- Leinonen, L., Hyvärinen, J., Nyman, G., and Linnankoski, I. (1979). I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Exp. Brain Res.* **34**, 299–320.
- Leinonen, L., Hyvärinen, J., and Sovijärvi, A.R. (1980). Functional properties of neurons in the temporo-parietal association cortex of awake monkey. *Exp. Brain Res.* **39**, 203–215.
- Lenggenhager, B., Tadi, T., Metzinger, T., and Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science* **317**, 1096–1099.
- Lenggenhager, B., Mouthon, M., and Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Conscious. Cogn.* **18**, 110–117.
- Lenggenhager, B., Halje, P., and Blanke, O. (2011). Alpha band oscillations correlate with illusory self-location induced by virtual reality. *Eur. J. Neurosci.* **33**, 1935–1943.
- Limanowski, J., and Blankenburg, F. (2013). Minimal self-models and the free energy principle. *Front. Hum. Neurosci.* **7**, 547.
- Limanowski, J., and Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. *Hum. Brain Mapp.* **36**, 2284–2304.
- Llobera, J., Sanchez-Vives, M.V., and Slater, M. (2013). The relationship between virtual body ownership and temperature sensitivity. *J. R. Soc. Interface* **10**, 20130300.
- Lloyd, D.M. (2007). Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain Cogn.* **64**, 104–109.
- Lloyd, D., Morrison, I., and Roberts, N. (2006). Role for human posterior parietal cortex in visual processing of aversive objects in peripersonal space. *J. Neurophysiol.* **95**, 205–214.
- Ma, W.J., Beck, J.M., Latham, P.E., and Pouget, A. (2006). Bayesian inference with probabilistic population codes. *Nat. Neurosci.* **9**, 1432–1438.
- Macaluso, E., and Driver, J. (2005). Multisensory spatial interactions: a window onto functional integration in the human brain. *Trends Neurosci.* **28**, 264–271.
- Macaluso, E., and Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia* **48**, 782–795.
- Magnotti, J.F., Ma, W.J., and Beauchamp, M.S. (2013). Causal inference of asynchronous audiovisual speech. *Front. Psychol.* **4**, 798.
- Magosso, E., Ursino, M., di Pellegrino, G., Làdavas, E., and Serino, A. (2010a). Neural bases of peri-hand space plasticity through tool-use: insights from a combined computational-experimental approach. *Neuropsychologia* **48**, 812–830.
- Magosso, E., Zavaglia, M., Serino, A., di Pellegrino, G., and Ursino, M. (2010b). Visuotactile representation of peripersonal space: a neural network study. *Neural Comput.* **22**, 190–243.

- Maister, L., Cardini, F., Zamariola, G., Serino, A., and Tsakiris, M. (2014). Your place or mine: Shared sensory experiences elicit a remapping of peripersonal space. *Neuropsychologia* 70, 455–461.
- Maister, L., Slater, M., Sanchez-Vives, M.V., and Tsakiris, M. (2015). Changing bodies changes minds: owning another body affects social cognition. *Trends Cogn. Sci.* 19, 6–12.
- Makin, T.R., Holmes, N.P., and Zohary, E. (2007). Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *J Neurosci.* 27, 731–740.
- Makin, T.R., Holmes, N.P., and Ehrsson, H.H. (2008). On the other hand: dummy hands and peripersonal space. *Behav. Brain Res.* 191, 1–10.
- Makin, T.R., Holmes, N.P., Brozzoli, C., and Farnè, A. (2012). Keeping the world at hand: rapid visuomotor processing for hand-object interactions. *Exp. Brain Res.* 219, 421–428.
- Makin, J.G., Fellows, M.R., and Sabes, P.N. (2013). Learning multisensory integration and coordinate transformation via density estimation. *PLoS Comput. Biol.* 9, e1003035.
- Maravita, A., and Irlki, A. (2004). Tools for the body (schema). *Trends Cogn. Sci.* 8, 79–86.
- Maravita, A., Spence, C., Sergent, C., and Driver, J. (2002). Seeing your own touched hands in a mirror modulates cross-modal interactions. *Psychol. Sci.* 13, 350–355.
- Maravita, A., Spence, C., and Driver, J. (2003). Multisensory integration and the body schema: close to hand and within reach. *Curr. Biol.* 13, R531–R539.
- Marcel, A. (2003). The sense of agency: Awareness and ownership of action. In *Agency and Self-Awareness*, J. Roessler and N. Eilan, eds. (Oxford University Press), pp. 48–93.
- Martini, M., Perez-Marcos, D., and Sanchez-Vives, M.V. (2013). What color is my arm? Changes in skin color of an embodied virtual arm modulates pain threshold. *Front. Hum. Neurosci.* 7, 438.
- Martuzzi, R., van der Zwaag, W., Dieguez, S., Serino, A., Gruetter, R., and Blanke, O. (2015). Distinct contributions of Brodmann areas 1 and 2 to body ownership. *Soc. Cogn. Affect. Neurosci.* Published online March 25, 2015.
- Maselli, A., and Slater, M. (2013). The building blocks of the full body ownership illusion. *Front. Hum. Neurosci.* 7, <http://dx.doi.org/10.3389/fnhum.2013.00083>.
- Mazzola, L., Lopez, C., Faillenot, I., Chouchou, F., Mauguière, F., and Isnard, J. (2014). Vestibular responses to direct stimulation of the human insular cortex. *Ann. Neurol.* 76, 609–619.
- McGurk, H., and MacDonald, J. (1976). Hearing lips and seeing voices. *Nature* 264, 746–748.
- Metzinger, T. (2004). *Being no one: The self-model theory of subjectivity* (MIT Press).
- Mitchell, J.P., Banaji, M.R., and Macrae, C.N. (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. *J. Cogn. Neurosci.* 17, 1306–1315.
- Moseley, G.L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., and Spence, C. (2008). Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proc. Natl. Acad. Sci. USA* 105, 13169–13173.
- Moser, E.I., Kropff, E., and Moser, M.-B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annu. Rev. Neurosci.* 31, 69–89.
- Mountcastle, V.B. (1995). The parietal system and some higher brain functions. *Cereb. Cortex* 5, 377–390.
- Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., and Acuna, C. (1975). Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J. Neurophysiol.* 38, 871–908.
- Noel, J.P., Grivaz, P., Marmaroli, P., Lissek, H., Blanke, O., and Serino, A. (2014). Full body action remapping of peripersonal space: the case of walking. *Neuropsychologia* 70, 375–384.
- Noel, J.P., Pfeiffer, C., Blanke, O., and Serino, A. (2015). Peripersonal space as the space of the bodily self. *Cognition* 144, 49–57.
- Ocelli, V., Spence, C., and Zampini, M. (2011). Audiotactile interactions in front and rear space. *Neurosci. Biobehav. Rev.* 35, 589–598.
- Olcese, U., Iurilli, G., and Medini, P. (2013). Cellular and synaptic architecture of multisensory integration in the mouse neocortex. *Neuron* 79, 579–593.
- Orlov, T., Makin, T.R., and Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron* 68, 586–600.
- Palluel, E., Aspell, J.E., and Blanke, O. (2011). Leg muscle vibration modulates bodily self-consciousness: integration of proprioceptive, visual, and tactile signals. *J. Neurophysiol.* 105, 2239–2247.
- Palluel, E., Aspell, J.E., Lavanchy, T., and Blanke, O. (2012). Experimental changes in bodily self-consciousness are tuned to the frequency sensitivity of proprioceptive fibres. *Neuroreport* 23, 354–359.
- Pavani, F., and Castiello, U. (2004). Binding personal and extrapersonal space through body shadows. *Nat. Neurosci.* 7, 14–16.
- Pavani, F., Spence, C., and Driver, J. (2000). Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychol. Sci.* 11, 353–359.
- Perez-Marcos, D., Sanchez-Vives, M.V., and Slater, M. (2012). Is my hand connected to my body? The impact of body continuity and arm alignment on the virtual hand illusion. *Cogn Neurodyn* 6, 295–305.
- Petkova, V.I., and Ehrsson, H.H. (2008). If I were you: perceptual illusion of body swapping. *PLoS ONE* 3, e3832.
- Petkova, V.I., Björnsson, M., Gentile, G., Jonsson, T., Li, T.Q., and Ehrsson, H.H. (2011). From part- to whole-body ownership in the multisensory brain. *Curr. Biol.* 21, 1118–1122.
- Pfeiffer, C., Lopez, C., Schmutz, V., Duenas, J.A., Martuzzi, R., and Blanke, O. (2013). Multisensory origin of the subjective first-person perspective: visual, tactile, and vestibular mechanisms. *PLoS One* 8, <http://dx.doi.org/10.1371/journal.pone.0061751>.
- Pomés, A., and Slater, M. (2013). Drift and ownership toward a distant virtual body. *Front. Hum. Neurosci.* 7, 908.
- Poppel, E., Held, R., and Frost, D. (1973). Leter: Residual visual function after brain wounds involving the central visual pathways in man. *Nature* 243, 295–296.
- Pouget, A., Deneve, S., and Duhamel, J.R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nat. Rev. Neurosci.* 3, 741–747.
- Prsa, M., Gale, S., and Blanke, O. (2012). Self-motion leads to mandatory cue fusion across sensory modalities. *J. Neurophysiol.* 108, 2282–2291.
- Prsa, M., Jimenez-Rezende, D., and Blanke, O. (2015). Inference of perceptual priors from path dynamics of passive self-motion. *J. Neurophysiol.* 113, 1400–1413.
- Ramachandran, V.S., and Hirstein, W. (1998). The perception of phantom limbs. The D. O. Hebb lecture. *Brain* 121, 1603–1630.
- Raposo, D., Sheppard, J.P., Schrater, P.R., and Churchland, A.K. (2012). Multisensory decision-making in rats and humans. *J. Neurosci.* 32, 3726–3735.
- Rizzolatti, G., Scandolara, C., Matelli, M., and Gentilucci, M. (1981). Afferent properties of periacuate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2, 147–163.
- Rizzolatti, G., Fogassi, L., and Gallese, V. (1997). Parietal cortex: from sight to action. *Curr. Opin. Neurobiol.* 7, 562–567.
- Rizzolatti, G., Fogassi, L., and Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Curr. Opin. Neurobiol.* 12, 149–154.
- Rochat, P., and Zahavi, D. (2011). The uncanny mirror: a re-framing of mirror self-experience. *Conscious. Cogn.* 20, 204–213.

- Romano, D., Pfeiffer, C., Maravita, A., and Blanke, O. (2014). Illusory self-identification with an avatar reduces arousal responses to painful stimuli. *Behav. Brain Res.* 267, 275–281.
- Ronchi, R., Bello-Ruiz, J., Lukowska, M., Herbelin, B., Cabrilo, I., Schaller, K., and Blanke, O. (2015). Right insular damage decreases heartbeat awareness and alters cardio-visual effects on bodily self-consciousness. *Neuropsychologia* 70, 11–20.
- Salinas, E., and Thier, P. (2000). Gain modulation: a major computational principle of the central nervous system. *Neuron* 27, 15–21.
- Salomon, R., van Elk, M., Aspell, J.E., and Blanke, O. (2012). I feel who I see: visual body identity affects visual-tactile integration in peripersonal space. *Conscious. Cogn.* 21, 1355–1364.
- Samad, M., Chung, A.J., and Shams, L. (2015). Perception of body ownership is driven by Bayesian sensory inference. *PLoS ONE* 10, e0117178.
- Sanchez-Vives, M.V., and Slater, M. (2005). From presence to consciousness through virtual reality. *Nat. Rev. Neurosci.* 6, 332–339.
- Schlack, A., Sterbing-D'Angelo, S.J., Hartung, K., Hoffmann, K.P., and Bremner, F. (2005). Multisensory space representations in the macaque ventral intraparietal area. *J. Neurosci.* 25, 4616–4625.
- Sereno, M.I., and Huang, R.S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. *Nat. Neurosci.* 9, 1337–1343.
- Sereno, M.I., and Huang, R.S. (2014). Multisensory maps in parietal cortex. *Curr. Opin. Neurobiol.* 24, 39–46.
- Sergent, C., and Dehaene, S. (2004). Neural processes underlying conscious perception: experimental findings and a global neuronal workspace framework. *J. Physiol. Paris* 98, 374–384.
- Serino, A., and Haggard, P. (2010). Touch and the body. *Neurosci. Biobehav. Rev.* 34, 224–236.
- Serino, A., Bassolino, M., Farnè, A., and Làdavas, E. (2007). Extended multisensory space in blind cane users. *Psychol. Sci.* 18, 642–648.
- Serino, A., Canzoneri, E., and Avenanti, A. (2011a). Fronto-parietal areas necessary for a multisensory representation of peripersonal space in humans: an rTMS study. *J. Cogn. Neurosci.* 23, 2956–2967.
- Serino, A., Alsmith, A., Costantini, M., Mandrigin, A., Tajadura-Jimenez, A., and Lopez, C. (2013). Bodily ownership and self-location: components of bodily self-consciousness. *Conscious Cogn.* 22, 1239–1252.
- Serino, A., Canzoneri, E., Marzolla, M., di Pellegrino, G., and Magozzo, E. (2015). Extending peripersonal space representation without tool-use: evidence from a combined behavioral-computational approach. *Front. Behav. Neurosci.* 9, 4.
- Seth, A.K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends Cogn. Sci.* 17, 565–573.
- Sforza, A., Bufalari, I., Haggard, P., and Aglioti, S.M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Soc. Neurosci.* 5, 148–162.
- Shimada, S., Fukuda, K., and Hiraki, K. (2009). Rubber hand illusion under delayed visual feedback. *PLoS ONE* 4, e6185.
- Slater, M. (2009). Place illusion and plausibility can lead to realistic behaviour in immersive virtual environments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 3549–3557.
- Slater, M., Spanlang, B., Sanchez-Vives, M.V., and Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS One* 5, <http://dx.doi.org/10.1371/journal.pone.0010564>.
- Soto-Faraco, S., and Deco, G. (2009). Multisensory contributions to the perception of vibrotactile events. *Behav. Brain Res.* 196, 145–154.
- Spence, C., and Driver, J. (2004). *Crossmodal space and crossmodal attention* (Oxford University Press).
- Spence, C., Pavani, F., and Driver, J. (2000). Crossmodal links between vision and touch in covert endogenous spatial attention. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 1298–1319.
- Spence, C., Pavani, F., and Driver, J. (2004). Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cogn. Affect. Behav. Neurosci.* 4, 148–169.
- Stein, B.E., and Stanford, T.R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nat. Rev. Neurosci.* 9, 255–266.
- Stein, B., Meredith, M., Huneycutt, W., and McDade, L. (1989). Behavioral indices of multisensory integration: orientation to visual cues is affected by auditory stimuli. *Cognitive Neuroscience. Journalism* 1, 12–24.
- Stein, B.E., Stanford, T.R., and Rowland, B.A. (2014). Development of multisensory integration from the perspective of the individual neuron. *Nat. Rev. Neurosci.* 15, 520–535.
- Stratton, G.M. (1899). The spatial harmony of touch and sight. *Mind* 8, 492–505.
- Striccanne, B., Andersen, R.A., and Mazzoni, P. (1996). Eye-centered, head-centered, and intermediate coding of remembered sound locations in area LIP. *J. Neurophysiol* 76, 2071–2076.
- Suddendorf, T., and Butler, D.L. (2013). The nature of visual self-recognition. *Trends Cogn. Sci.* 17, 121–127.
- Teneggi, C., Canzoneri, E., di Pellegrino, G., and Serino, A. (2013). Social modulation of peripersonal space boundaries. *Curr. Biol.* 23, 406–411.
- Tsakiris, M. (2008). Looking for myself: current multisensory input alters self-face recognition. *PLoS ONE* 3, e4040.
- Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. *Neuropsychologia* 48, 703–712.
- Tsakiris, M., and Haggard, P. (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *J. Exp. Psychol. Hum. Percept. Perform.* 31, 80–91.
- Tsakiris, M., Hesse, M.D., Boy, C., Haggard, P., and Fink, G.R. (2007). Neural signatures of body ownership: a sensory network for bodily self-consciousness. *Cereb. Cortex* 17, 2235–2244.
- Tsakiris, M., Costantini, M., and Haggard, P. (2008). The role of the right temporo-parietal junction in maintaining a coherent sense of one's body. *Neuropsychologia* 46, 3014–3018.
- Tsakiris, M., Carpenter, L., James, D., and Fotopoulou, A. (2010). Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Exp. Brain Res.* 204, 343–352.
- Van der Stoep, N., Nijboer, T.C., Van der Stigchel, S., and Spence, C. (2015). Multisensory interactions in the depth plane in front and rear space: a review. *Neuropsychologia* 70, 335–349.
- Wallace, M.T., and Stein, B.E. (2007). Early experience determines how the senses will interact. *J. Neurophysiol.* 97, 921–926.
- Weiskrantz, L., Warrington, E.K., Sanders, M.D., and Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain* 97, 709–728.
- Wozny, D.R., and Shams, L. (2011). Recalibration of auditory space following milliseconds of cross-modal discrepancy. *J. Neurosci.* 31, 4607–4612.
- Wozny, D.R., Beierholm, U.R., and Shams, L. (2010). Probability matching as a computational strategy used in perception. *PLoS Comput. Biol.* 6, e1000871.
- Xu, J., Yu, L., Stanford, T.R., Rowland, B.A., and Stein, B.E. (2015). What does a neuron learn from multisensory experience? *J. Neurophysiol.* 113, 883–889.
- Zampini, M., Torresan, D., Spence, C., and Murray, M.M. (2007). Auditory-somatosensory multisensory interactions in front and rear space. *Neuropsychologia* 45, 1869–1877.
- Zopf, R., Savage, G., and Williams, M.A. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia* 48, 713–725.