Multisensory processing in full-body illusions

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MULTISENSORY PROCESSING IN FULL-BODY ILLUSIONS

MULTISENSORY PROCESSING IN FULL-BODY ILLUSIONS

DISSERTATION

to obtain the degree of Doctor at Maastricht University
Department of Cognitive Neuroscience
Faculty of Psychology and Neuroscience
Maastricht University

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by
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CHAPTER 1

INTRODUCTION

Our own bodies are unique objects of perception. This uniqueness is rooted in two main aspects. First, the perception of our body pervades our all existence: sensations from our bodies are ubiquitous and omnipresent, as they cannot be switched off at will. Second, the perception of our own bodies exceeds in complexity other forms of perceptual experiences in what concerns the related multisensory dimension. In fact, beside the sensory channels typically available for exploring the external world, when it comes to building up a representation of our own bodies, we have access to additional information from proprioception, interoception and vestibular sensations.

The ubiquity and complexity that characterize the own body as an object of perception, when considered one beside the other, pose an interesting conundrum. The ubiquitous perception of our own bodies needs to be extremely effortless and almost transparent to our consciousness so to not interfere with our daily activities of whatever sort. At the same time, it needs to be informative enough so to allow us to optimally explore and act within the environment. The non-trivial question arising is therefore “How comes that the massive sensory processing involved in creating a stable and down-to-earth representation of our bodies does happen so effortlessly that we are only occasionally conscious about it?”. The answer to this question is far from being obvious and in the last decades a large community of philosophers, neurologists and cognitive neuroscientists devoted their work to shed some light on this problem. This collective effort has highlighted the multisensory and dynamic nature of the body percept, and established evidences for its neural correlates to be spread in a network of cortical and subcortical brain areas. The work presented in this thesis aimed at providing a contribution to this collective effort.

Bringing own body perception under scientific scrutiny is arduous. As a form of self-perception, it can be inspected either through descriptions of subjective experiences, or indirectly through behavioural and/or neurophysiological assessments, which should be nevertheless correlated to some extent with subjective accounts. In addition, the classical experimental approaches adopted in multisensory integration research are not easily applicable in the context of own body perception because the temporal and spatial dissociation of bodily signals is not trivial to achieve. In fact, the visual, somatosensory, motor and haptic sensations related to whatever bodily experience are locked in an intrinsic spatiotemporal “synchrony” dictated by physical laws. These difficulties have confined for long time the study of the multisensory mechanisms involved in own body perception to the domain of neuropsychology, in which the study of conditions characterized by impaired self-body perception (for example, the misattribution of one’s own arm to someone else), provided the first important insights. Only recently, the scientific inquire about the multisensory basis of self-perception could be extended to the normotypical population thanks to the introductions of novel experimental approaches, mainly relying on bodily illusions and prompted by new technological advances such as immersive virtual reality devices (de Gelder et al., 2018; Sanchez-Vives and Slater, 2005).

Various experimental paradigms have been established in the last decades that can alter the perception of one’s own body in a predictable and systematic manner. These paradigms are based

on the manipulation of sensory stimuli so that, by delivering conflicting information about the body, illusory experiences arise as the brain “looks for” an explanatory solution to the conflict. In this way, it is possible to let people experience their noses elongating, or experience a fake rubber as one’s own to the point of engaging in gross defensive reactions when the fake hand is threatened. The Pinocchio and the Rubber Hand Illusions are just two examples from a battery of body illusions that, because of their reproducibility and the concurrent possibility to monitor their behavioural and physiological correlates in controlled experimental environment, have been proven powerful tools for the investigation of the neural and cognitive mechanisms underlying self-body perception and corporeal awareness.

The works presented in this dissertation capitalize on the established use of bodily illusions as research tools, with the aim of advancing our understanding of the multisensory mechanisms underlying the perception of our bodies. Making use of Immersive Virtual Reality (IVR) technology, four experimental studies have been carried out to tackle issues related with the multisensory processing underlying the sense of body ownership, namely the feeling that the our body and its parts belong to the self, and the sense of self-location, i.e., the feeling of where the self is located in space. More specifically, the first study was tailored for identifying the “building blocks” of the sense of body ownership in terms of the major multisensory components involved and of their interaction. Two other studies focused on the impact of illusory ownership experience in the subsequent processing of sensory stimuli, i.e. visuotactile integration and pain. The fourth experimental study aimed at disentangling the multisensory mechanisms that can selectively affect body-ownership and self-location. In the other two review studies presented in this dissertation, results from the experiments performed are placed and discussed in the context of the relevant literature. Concurrently, proposals for common frameworks have been advanced that could account for the plethora of results, sometimes controversial, presented and discussed in the literature.

I. BACKGROUD

1.1 ALTERED BODY PERCEPTIONS OF NEUROLOGICAL ORIGIN

Bizarre conditions in which people experience abnormal perceptions of their own bodies have been the first inquiring tool for scientifically approaching the problem of how the information conveyed into the brain through different sensory channels is merged and integrated into the own-body percept. Because of their recurrence, phantom limbs have been the most documented and studied of these phenomena. Virtually all amputees report having phantom limbs experiences, which consist in vivid sensations that closely resemble somatosensory perceptions of the removed real limb, and that in some case are extremely painful (Ramachandran and Hirstein, 1998). Based on the vast phenomenology of phantom limbs sensations, it was early suggested that explanations for these phenomena must be sought in the “same brain processes that underlie the experience of the body when it is intact” (Melzack, 1990). Melzack further proposed that these brain processes should occur in a neural network encompassing several brain areas (the “neuromatrix”), which is at first genetically wired and later shaped through experience. In his proposal, Melzack also advanced the idea that “the feeling that all the parts of the body are uniquely one’s own” – a.k.a. the sense of body ownership – is generated by activity in the neuromatrix, as all the perceptual experiences “that are felt to originate from the body”.

Several other neurological disorders that involve the impairment of different aspects of own-body perception have contributed in gathering knowledge about the complex brain processes underlying own-body perception (Berlucchi and Aglioti, 1997; Head and Holmes, 1911). Particularly relevant for the work presented in this dissertation, are the cases of disturbed sensations of body ownership (DSO), in which patients do not recognize one of their limbs as part of their body, and the case of out-of-body experiences (OBEs), involving the feeling of floating outside one’s own body and seeing it from an elevated perspective. The contribution that these conditions have given to the current understanding of own-body perception is briefly reviewed in the following sections.

1.1.1 DISTURBED SENSATIONS OF LIMB OWNERSHIP (DSO)

Neurological conditions characterized by abnormal experiences of the body or of a body part, are typically associated with damage in a rich set of cortical and subcortical structures in the right hemisphere (Berlucchi and Aglioti, 1997, 2010). Among numerous interesting conditions, a prime example is the cases of asomatognosia and somatoparaphrenia (Feinberg, 2010). Asomatognosia literally means “lack of knowledge of the body”. It was first described as a condition in which patients are not aware of their disease “in parts or side of the body, with forgetting or not recognition of their possession” (Gerstmann, 1942). In somatoparaphrenia, these symptoms are associated with some forms of delusion and confabulation, often consisting in the misattribution of one of the limb contralateral to the lesion to someone else (Critchley, 1955).

Group studies on patients affected by these “disturbed sensations of limb ownership” (DSO) (Baier and Karnath, 2008) have revealed consistent damages in the temporoparietal cortex, the posterior insula, and in several subcortical areas (Feinberg et al., 2010; Gandola et al., 2012; Romano et

al., 2014). Interestingly, a consistent reduction in the insula cortical volume was also shown in individuals suffering from xenomelia, the obsessing desire of amputating one's own limb (Hilti et al., 2013). Instead, lesions in the right frontal cortex have been consistently observed only in somatoparaphrenic patients (Feinberg and Roane, 2005; Gandola et al., 2012; Invernizzi et al., 2013). Crucially, these DSO syndromes are rare and most often associated with a number of other conditions, from hemiplegia to spatial neglect (Gerstmann 1942; Vallar & Ronchi 2009), which makes it practically unfeasible to pin-point specific areas that are potentially responsible for shaping the experience of the body as part of the self. Despite this, the fact that the implicated brain areas are involved with multisensory integration and high-order cognitive processes provided the first evidence for the tight link between the sense of body ownership and multisensory integration (Bisiach et al., 1991; Vallar and Ronchi, 2009). Furthermore, this link pushed forward the idea that the sense of body ownership emerges as the result of distributed activity processing of massive amount of information in an extensive fronto-temporo-parietal network (Feinberg and Venneri, 2014; Vallar and Ronchi, 2009).

1.1.2 OUT-OF-BODY EXPERIENCES (OBE)

OBEs are another type of altered body perception that provided interesting insights into the brain processes underlying corporeal awareness. OBEs consist in transitory episodes in which the self, intended as "the centre of awareness", is experienced as dislocated from the physical body, which is typically seen from an elevated perspective (Blackmore, 1982; Brugger et al., 1997). OBEs are therefore associated with abnormal perception of self-location, in which the spatial unity between the self and the body is broken.

These illusory experiences have been associated with neurological conditions, such as migraine (Lippman, 1953), traumatic and vascular brain damage (Todd and Dewhurst, 1955), focal epilepsy (Devinsky et al., 1989) and, more recently, to dizziness (Lopez and Elzière, 2017). The first neurological accounts of OBEs reported about associated brain damages mainly in the temporal, parietal and occipital areas, with a predominance of the right hemisphere (see Blanke & Mohr 2005 for a review). Later group lesion studies showed a consistent implication of the right temporo-parietal junction, with particular implication of the anterior angular gyrus and the posterior part of the superior temporal gyrus (Blanke and Arzy, 2005). It was further shown that focal electrical stimulation of the temporo-parietal junction (TPJ) could systematically trigger OBEs (Blanke et al., 2002). Interestingly, a positron-emission tomographic (PET) scanning recorded during experiences of disembodiment, without autoscopia, showed specific brain activation in the TPJ and interconnected subcortical regions (De Ridder et al., 2007).

Because of the associated sensation of flying and floating, most of the early authors attributed OBEs to a dysfunction of the vestibular system and its interaction with other senses. This view has been confirmed in later studies, which identified disrupted activity in the TPJ to be associated with OBEs (Arzy et al., 2006; Blanke et al., 2002). The TPJ incorporates information from subcortical areas, like the thalamus and the limbic system, receives afferent from the visual, auditory and somatosensory system, and hosts the angular gyrus, a core region for the processing of vestibular signals and the coding of body orientation in space (Bottini et al., 1994; Brandt and Dieterich, 1999; Lopez et al., 2012). This is consistent with the established view that OBEs results from a failure to

integrate somatosensory, visual and vestibular information into a coherent body representation (Blanke, 2012; Blanke and Mohr, 2005).

1.2 BODY ILLUSIONS: EXPERIMENTAL TOOLS TO STUDY SELF-BODY PERCEPTION

During bodily illusions healthy subjects are induced to experience altered body perceptions, which significantly deviates from the configuration of the real body and which could be very similar to the abnormal perceptions experienced in some of the neurological conditions involving dysfunctions of own-body perception. Several experimental paradigms have been developed and established in the last decades, which allow eliciting these illusions in controlled and reproducible experimental setups through the systematic manipulations of bodily stimuli. The consistency and reproducibility of the induced perceptual experiences, unachievable in neuropsychology, leveraged bodily illusions to be among the most powerful research tools in the study of own-body perception and its neural correlates.

In the following sections, a brief overview is given on the main experimental paradigms used in the scientific community for eliciting body illusions, and on the contribution that experimental studies utilizing body illusions have provided to the current understanding of how different bodily signals are processed and integrated to generate a unitary and stable own-body percept.

1.2.1 EXPERIMENTAL PARADIGMS TO ALTER OWN-BODY PERCEPTIONS

Body illusions can be systematically induced in healthy subjects by manipulating multisensory bodily stimuli. The underlying principle is that, when presented with conflicting information about the body the brain generates abnormal body perceptions in the attempt to “make sense” of all incoming information. Depending on the nature of the conflict, different illusory experiences may arise, including illusory displacements of body parts or entire bodies, limb distortions, and ownership felt over fake objects resembling bodies or body parts.

Illusory body part displacements can be induced by dissociating visual and proprioceptive information about the location of a limb, by using prisms or mirrors to present a non veridical limb position (Hay et al., 1965). In these cases, vision dominates on proprioception as subjects typically misperceive their limb to be misplaced in the direction of the visual stimulus, an effect known as visual capture of proprioception (van Beers et al., 1999). In absence of vision, the illusory movement of a static limb can be elicited by applying tendon vibration and results in a misperceived position of the limb (Goodwin et al., 1972). Illusory displacement of body parts, when combined with self-touch could elicit body distortion illusions. Touching one’s own nose while experiencing an illusory extension of the elbow results in the sensation of an elongating Pinocchio-like nose (Lackner, 1988). In a similar fashion, touching one’s own wrist while experiencing an illusory flexion of the wrist results in the striking sensation of a shrinking wrist (Ehrsson et al., 2005b).

Body ownership illusions pertain to a different class of bodily illusions and consist in the temporary attribution of external objects to the own-body. Sixty year after Tastevin (1937) described how an object protruding by one’s clothes could be misperceived as one’s own finger, Botvinick and Cohen (1998) introduced the Rubber Hand Illusion (RHI), highlighting its tight link with the multisensory

processing of bodily stimuli and its great potential as an experimental tool. In the classic RHI, a rubber hand is placed on a table in front of the subject, while the real corresponding hand is hidden from view, and two paintbrushes are used to stroke simultaneously the real and the rubber hands. Under this simple, yet ingenious combination of conflictive sensory stimuli, most subjects report the feeling that the rubber hand is their own and that they feel touch as if generated by the paintbrush stroking it. Later studies introduced alternative setups to induce ownership illusions of hand shaped objects. The visual input from the non-corporeal hand (the rubber hand surrogate) could be given via mirrors (Longo et al., 2008), videos (Tsakiris et al., 2006) or virtual reality screens (Sanchez-Vives et al., 2010). These setups further allowed replacing the visuotactile stimulation, used in the classic RHI as the illusion trigger, with congruent visuomotor stimuli. Videos and virtual reality based setups allow in fact to display the non-corporeal hand replicating in real-time the movements performed by the real hand, which can be filmed or tracked. It has been extensively shown that, besides these bottom-up multisensory components, other factors can modulate the illusory experiences in a top-down fashion. The visual appearance of the surrogate body with its level of realism (Maselli and Slater, 2013; Tsakiris et al., 2010), and the exposure to emotional or threatening stimuli during the illusion (Engelen et al., 2017) are representative examples. All these different setups, and many others, have been developed and adopted by a large number of research groups to selectively manipulate and explore the different factors potentially contributing to the experience of an external object as being part of one's own body and their impact on self-perception. An extensive review is given in Chapter 5.

The introduction of immersive head mounted displays (HMD) has been decisive for extending the research work based on bodily illusions to encompass full body illusions and therefore to address issues related to self-consciousness (Blanke and Metzinger, 2009). In fact, the use of HMD entails the possibility –unworkable otherwise– to gather visual information from virtually all and every perspectives. These include disembodied perspectives, in which when looking down the space normally occupied by the own body is seen empty, and first-person perspectives on different bodies. These particular configurations of the visual perspective, in combination with specific multisensory stimulations, have been adopted for eliciting Full Body Ownership Illusions (FBOI) as well as illusory OBEs in healthy subjects.

The first FBOI study reported how healthy subjects could be induced to feel the body of a plastic mannequin as being their own body (Petkova and Ehrsson, 2008). Subjects were fitted with a HMD, completely occluding their own body, while streaming in real-time the video recorded from two cameras arranged at the eyes position of a plastic mannequin, pointing downward. The setup resulted in subjects having a static stereo view on the mannequin body, which visually replaced the real one. In analogy with the classic RHI protocol, experimenters were then able to induce a FBOI by stroking the real and the mannequin's chests simultaneously and with similar spatial patterns, while asynchronous stimulations resulted in no illusory experience. Few years later, a study based on immersive virtual reality technology showed how a similar FBOI could be induced over a virtual body, which could differ importantly from the participants body in both gender and age (Slater et al., 2010). In this study, participants could perform head movements that were tracked and used to accordingly render the scene in real time. Later studies showed how FBOIs towards virtual bodies seen from a 1PP could be induced through visuomotor congruent stimuli, which is when participants are allowed to move and see the virtual body moving accordingly (González-Franco et al., 2010;

Kokkinara and Slater, 2014; Spanlang et al., 2014). In the study presented in Chapter 2, it was further shown that, when the appearance of the virtual body is realistic, static visuoproprioceptive congruent stimuli (i.e., seeing the virtual body collocated with the real body) are sufficient to elicit FBOI (Maselli and Slater, 2013).

Illusory OBEs are another important class of full body illusions, in which illusory changes in self-location are experienced. In this case, a HMD is used to occlude from view the real body and display it—or alternatively a virtual body—from a third person perspective (3PP) in the extra-personal space. The illusion is then triggered by applying visuotactile stimulation, analogously to the classic RHI and FBOI. Two different experimental manipulations have been introduced that can temporarily alter the perceived self-location. Remarkably, the first reports of both types of experimentally induced OBE were published in the same issue of the prestigious journal *Science*. In both cases, participants were fitted with a HMD streaming in stereo-view a video of their own body, captured by a video-camera placed two meters behind. In one case, a rod was used to stroke the real chest, while a similar rod was moved in the empty space right in front of the cameras, so that through the HMD the rod was seen moving in a congruent spatial location with respect to the felt touch, but from a disembodied 1PP perspective (Ehrsson, 2007b). In the second study, a rod was used to touch the back of the participant, who therefore felt it on the back while seeing moving on the back seen at in the extra-personal space from a 3PP (Lenggenhager et al., 2007). In the following, I will refer to these two variants as front-stroking and back-stroking experimentally induced OBE. The illusory experiences elicited with the two protocols differ from each other. While they both entail an illusory shift of the perceived self-location, they are characterized by different modulations of the sense of ownership. In front-stroking OBEs, an explicit sense of disownership with respect to the body seen in front is consistently reported (Ehrsson, 2007a; Guterstam and Ehrsson, 2012), while in back-stroking OBEs subjects tend to report a sense of self identification with the seen body (Aspell et al., 2009; Ionta et al., 2011; Lenggenhager, 2007). However, it should be stressed that self-identification with a seen body is not necessarily equivalent to experiencing a sense of ownership of the same body (Maselli, 2015; Petkova and Ehrsson, 2008). The differences among the two types of illusory OBEs are extensively discussed in Chapters 6 and 7. Later studies have introduced alternative protocols to elicit illusory experiences similar to back-stroking OBEs. For example, it was recently shown that illusory OBEs can be induced experimentally with synchronous visuotactile stimuli delivered below detection threshold and therefore processed outside of awareness (Salomon et al., 2017).

1.2.2 EXPERIMENTAL ASSESSMENTS AND MEASURES

Measuring and quantifying subjective illusory experiences is not trivial. This is particularly true when dealing with illusory experiences like the feeling of ownership towards an external object, or the feeling of drifting in space away from the physical body. At first, characteristics of the qualitative experience of the illusion can be gathered through subjective reports. The use of questionnaires is the established practice to collect this kind of qualitative information in the form of ordinal data suited for comparison tests. However, explicit questionnaire items, such as “I felt as if the rubber hand were my hand”, at interplay with the common tendency for task compliance, could result in biased and not reliable responses (Holtgraves, 2004; Slater, 2004). For this reason, questionnaire assessments should be complemented with other quantitative, although implicit, measurements. In fact, most of the research work on bodily illusions includes implicit assessments based on the monitoring of

behavioural, physiological and/or neural correlates of the illusion.

Behavioural assessments of bodily illusions include implicit measurements of the spatial coding of body parts or of the whole body, responses to threats addressed to the fake body (part) and performances in psychophysics tasks, specifically designed to test the perceived spatiotemporal alignment of multisensory stimuli. In the case of the classic RHI, a blindfolded self-pointing task was used to show how subjects experiencing the illusion typically recode the position of their “substituted” hand towards the position of the rubber hand (Botvinick and Cohen, 1998). This effect, known as “proprioceptive drift”, has been measured alternatively by asking participants to verbally report the perceived position of the hand with respect to hallmarks in the environment (Tsakiris and Haggard, 2005), and could alternatively be tested through reaching tasks (Holmes et al., 2004; Rossetti et al., 1995; Zopf et al., 2011b). Analogously, several methods have been introduced to measure illusory displacements of the whole body during OBE. These include the “walking task” in which participants had to reach their initial position after a random displacement guided by the experimenter (Lenggenhager, 2007), and a “ball dropping” task in which participants had to estimate the time for a ball held in their hand to reach the floor (Ionta et al., 2011). These tasks were designed for measuring changes in the perceived self-location in a participant-centred egocentric reference frame. Other tasks were instead designed for assessing allocentric recordings of self-location, as for example asking participants to indicate their perceived location in a map of the experimental room (Guterstam and Ehrsson, 2012).

Alternative assessments of illusory changes in self-location, for both body parts and whole bodies, are based on experimental evaluations of the spatial structure of the peripersonal space (PPS). The PPS is classically defined as the “reachable” portion of space surrounding the body, in which object can be grasped and manipulated (Rizzolatti et al., 1981a, 1981b). This portion of space is represented by frontoparietal brain structures that integrate visual and auditory stimuli presented near the body with somatosensory information (di Pellegrino and Ladavas, 2015; Serino et al., 2015). The visual (or auditory) receptive fields of neurons in these areas are anchored to the corresponding part of the body encoded in the tactile domain. For example, a hand-encoding neuron of this type selectively responds to visual stimuli presented at different locations, depending on whether the hand is nearby (Graziano and Cooke, 2006). A standard tool to estimate the spatial extent of the PPS and its dynamic representation is the cross-modal congruency task (CCT), a psychophysics task designed to measure the effects of multisensory integration of independent stimuli presented through different sensory channels (Spence et al., 2008). In brief, the CCT efficacy as a tool for estimating the PPS extent in space in the visuotactile domain, is based on the evidence that reactions times to tactile target stimuli are modulated by the distance at which task-irrelevant visual stimuli are presented. In this way, it was shown how the felt position of the “replaced” hand(s) in the RHI shifts towards the location of the fake hand(s) (Pavani et al., 2000; Zopf et al., 2010). Similarly, CCT have been adopted to assess shifts in the perceived location of the full-body during illusory OBEs (Aspell et al., 2009; Maselli and Slater, 2014). A complementary audio-tactile paradigms, developed to infer the PPS extent through audio-tactile interactions (Canzoneri et al., 2012), was further adopted to reveal changes in the perceived self-location during OBEs illusions (Noel et al., 2015).

Another quantitative measure of the illusory sense of ownership toward a rubber hand or a full fake body, consists in presenting an event threatening the fake body and in monitoring how the illusion modulates the evoked behavioural and physiological responses. During an ownership illusion, threatening events (e.g., suddenly bending back the rubber fingers in a painful posture or stabbing the rubber hand with a knife) elicit enhanced responses in skin conductance (Armel and Ramachandran, 2003) and enhanced activations of brain areas associated with anxiety (Ehrsson et al., 2007), which are not observed when the illusion is not experienced. Analogously, stabbing the chest of a mannequin triggers higher SCRs when a full body ownership illusion is experienced toward the mannequin, but not otherwise (Petkova and Ehrsson, 2008). Similarly, during the “front-stroking” induced OBEs illusions enhanced SCRs were recorded when hitting with a hammer the space of the illusory disembodied self (Ehrsson, 2007b).

A novel alternative measure for the sense of ownership towards a virtual body is based on behavioral assessments of the visuo-proprioceptive coupling that is established during a FBOI, and was introduced in the study presented in Chapter 6 (Maselli and Slater, 2014). The assessment consists in a behavioral measurement of the perceived body posture performed right after the posture of the surrogate body is virtually manipulated while the physical body stays still. The posture (visual) manipulation induces changes in the perceived posture of the own body when ownership is experience toward the virtual body, but not otherwise.

Physiological and neural correlates of bodily illusions have been explored in a large number of studies. Beside addressing the main goal of characterizing the origin and the neural mechanisms underlying bodily illusions, these works further served the function of providing objective and quantitative measures of illusory experiences. The illusory feeling of ownership over a rubber hand has several physiological effects measurable on the corresponding real hand, including cooling (Moseley et al., 2008a), reduced tactile (Zeller et al., 2015; Zopf et al., 2011a) and temperature (Llobera and Slater, 2013) sensitivity, and increased histamine reactivity (Barnsley et al., 2011). Brain imaging studies further revealed selective activation of distributed brain areas corresponding to specific aspects of bodily illusory experiences (see Section 1.2.3 for a detailed review). These selective patterns of activation could in turn, be regarded as objective markers of the specific illusory experience. Importantly, all the objective measures reviewed above were shown to significantly correlate with the subjective ratings assessing the vividness of the illusory experience (Barnsley et al., 2011; Ehrsson et al., 2004; Ionta et al., 2011; Limanowski and Blankenburg, 2015; Llobera and Slater, 2013; Moseley et al., 2008a). This quantitative link between the subjective quantification of illusory experiences, reflected in questionnaire ratings, and objective behavioural, physiological and neural measurements provides a strong evidence of the validity and robustness of bodily illusions as tools for quantitative research.

1.2.3 NEURAL CORRELATES OF BODILY ILLUSIONS

Neuroimaging studies have shown how the patterns of brain activity engaged during bodily illusions depend on the specific aspects of the ongoing illusory experience. In all cases, imaging studies from different groups highlighted how bodily illusory experiences involve spread networks of brain activity, always including high-order multisensory areas known to encode the peripersonal space. The involvement of additional areas have been shown instead to reflect the specificity of the ongoing

illusion, differentiating for example the illusory self-attribution of a body-part with respect to that of an entire artificial body, or illusory changes in body ownership (as in FBOI) from illusory changes in self-location (as in OBE illusions).

Neural correlates of peripersonal space (PPS)

The consistent engagement of multisensory areas associated with the encoding of peripersonal space (PPS) during bodily illusions is not surprising. In fact, the standard experimental paradigms used to trigger bodily illusions are based on the exposure to ambiguous multisensory bodily stimuli, which are eventually integrated giving rise to the illusory experience (Blanke, 2012; Ehrsson, 2011; Hohwy and Paton, 2010). Imaging fMRI studies in humans have revealed a set of multimodal areas integrating somatosensory information with external visual and auditory stimuli, homologous to those revealed by neurophysiological recordings in non-human primates (di Pellegrino and Làdavas, 2015). A set of interconnected areas encompassing the posterior parietal and premotor cortex was shown to encode the location of visual stimuli near the body in hand-centered coordinates (Brozzoli et al., 2011; Makin et al., 2007). Multisensory integration of touch on the hand with visual stimuli presented close to the hand were found to occur in a set of parietal (inferior posterior), frontal (dorsal and ventral premotor) and subcortical (cerebellum) regions (Gentile et al., 2011, 2013). Multisensory areas encoding different body parts in the visuotactile domain have been further detailed in a “higher-level” homunculus map within the posterior parietal cortex (Huang et al., 2012). So, while it is not surprising that activity in these areas is consistently implicated across different types of bodily illusions, specific combinations of co-activations and the involvement of additional areas were found to be specific of the nature of the illusory experience. In the follow, the neural correlates that have been identified for different types of bodily illusions are summarized.

Self-attribution of body parts (RHI)

The illusory self-attribution of a body part, as in the RHI, has been initially associated with enhanced activity in the ventral premotor cortex (vPM), which was found to correlate positively with the subjective ratings of the illusion (Ehrsson et al., 2004). In their seminal work, Ehrsson and colleagues further showed how other multisensory cortical (intraparietal sulcus and dorsal premotor – IPS and dPM) and subcortical (cerebellum and putamen) regions show enhanced activity in experimental conditions leading to the illusion, but only in the early phase of the stimulation, i.e., before the illusion onset. Because of its specific temporal course, this activity –spread in various regions known to encode the PPS– was suggested to reflect the integration of (truly independent) sensory information and the related recalibration of the hand position. These conclusions were supported by later studies. Activity in the the vPM cortex was found to correlate with the rated strength of the illusion also in the somatic RHI (Ehrsson et al., 2005a), ruling out the possible confound that such activity was associated with the view of an object moving near the hand (Botvinick, 2004). This view of distinctive activities reflecting the recalibration of the hand location and the illusory sense of ownership of the rubber hand, is consistent with other following studies (Brozzoli et al., 2012; Tsakiris et al., 2007). By introducing an automatized device to deliver tactile stimuli that allows removing the view of another human (the experimenter), Limanowski and colleagues found that also the extrastriate body area (EBA) reflects the strength of the illusory experience (Limanowski et al., 2013; Limanowski and Blankenburg, 2015). Interestingly, these later studies further explored how brain activity is modulate at a network level. An increase in connectivity reflecting the illusory

experience was observed between the EBA and multisensory parietal regions (IPC) as well as between EBA and unisensory regions (primary and secondary somatosensory cortex – SI and SII). The same group has next shown that activity in a similar set of brain areas (vPM, PPC and EBA) is enhanced also during the self-attribution of a rubber hand resulting by visuo-proprioceptive congruent information only, this time with an increased strength in the connection between EBA and the primary visual cortex (V1) (Limanowski and Blankenburg, 2016).

Self attribution of entire bodies (FBOI)

The self-attribution of entire bodies, as in FBOIs, has been shown to involve the same multisensory areas implicated in the self-attribution of body parts, but with some specificity. Petkova and colleagues first reported enhanced activity in bilateral vPM, left IPC and left putamen during the illusion of owning an entire mannequin body (Petkova et al., 2011). Crucially, it was shown that activity in vPM cortex was independent on the specific body part exposed to the visuotactile stimulation and was correlated to the strength of the subjective illusory experience. Furthermore, activity in vPM was stronger if the body part receiving the visuotactile stimulation was seen attached to the body, a result the author interpreted as an evidence for the role of vPM in integrating multisensory information across body segments. However, it must be noticed that in the detached condition, the “detached” hand was shown isolated, with the rest of the body absent, so it is possible that the illusion was inhibited by the strong visuo-proprioceptive incongruence of seeing empty the space occupied by the physical body. Few years later, the same group showed how activity in the left vPM reflected the illusion of owning the whole body irrespectively of the site of the visuotactile stimulation (legs, hand or abdomen), while other implicated multisensory areas (putamen, IPC, PM and lateral occipital cortex) were selectively implicated depending on the site of the stimulation (Gentile et al., 2015). These results support the established view that the feeling of owning an entire body, the whole-body percept, is mediated by neuronal populations that are hosted in the vPM and are characterized by visuo-somatic receptive fields encompassing different body segments.

Illusory out-of-body experiences (OBEs)

The neural correlates of experimentally induced OBEs have been investigated in a series of studies, carried out independently mainly by two groups. These studies have revealed how different brain networks underlie the illusory experiences elicited during front-stroking and back-stroking OBEs. In the back-stroking paradigm, the illusory shifts in the perceived self-location towards the virtual body have been mainly associated with modulations in the TPJ and middle-inferior cortex activity, while the sense of self-identification with the virtual body have been associated with activity in the EBA (Ionta et al., 2011). Interestingly levels of TPJ's activities were found to correlate with the perceived elevation of the body, when the back-stroking paradigm was applied to participants laying in the scanner and resulted in illusory shifts of self-location downward or upwards (Ionta et al., 2011). Functional connectivity analysis revealed that illusory changes in the perceived self-location corresponded to enhanced connectivity patterns of the TPJ with a right-hemispheric networks including the insula and supplementary motor areas (Ionta et al., 2014). EEGs recordings during standing back-stroking induced OBEs showed instead no major involvement of the TPJ, but revealed a positive correlation of the strength illusory shifts in self-location with the power of alpha-band oscillations in the medio-dorsal prefrontal cortex (Lenggenhager et al., 2011).

The neural correlates of front-stroking induced OBEs includes different sets of brain areas. fMRI recordings revealed indeed the major involvement of hippocampus, posterior cingulate cortex (PCC), retrosplenial cortex (RSC) and intraparietal sulcus (IPS) (Guterstam et al., 2015). These regions are known to be relevant for spatial cognition, navigation (Vann et al., 2009) and mnemonic allocentric representations (Hassabis et al., 2009). The radical differences found in the brain activity monitored during front-stroking and back-stroking OBEs corroborates the differences emerging from subjective reports and behavioural correlates. The different nature of the two illusory experiences is discussed extensively in Chapter 7.

In summary, a consistent number of studies have demonstrated how extended network of multisensory brain areas underlie various aspects of own-body perception, with different subsets of brain areas selectively implicated in different types of bodily illusions. The fronto-parietal network corresponding to the multisensory representation of the space close to the body, i.e. the PPS, is always engaged, independently on the specific illusion under analysis. This is not surprising as the experimental protocols used to elicit bodily illusions rely on presenting multisensory bodily related stimuli as triggers of the illusory experience. Activations of different sets of brain areas specific to the type of illusion elicited, point instead to the multidimensional nature of the own-body percept.

1.2.4 IMPACT OF BODY ILLUSIONS ON PERCEPTION AND COGNITION

Body illusions, even when transiently induced in the laboratory, are associated with a wide spectrum of perceptual and cognitive correlates. Profound implications of body change illusions have been demonstrated in a plethora of experimental studies, and encompass altered states that range from the processing of low-level sensory stimuli to cognitive processing and social behavior.

The illusory self-attribution of a body part, as experienced during a RHI, has an important impact on the ongoing processing of perceptual stimuli. It engenders a reduction of tactile sensitivity, demonstrated by increased reaction times (Folegatti et al., 2009), increased detection thresholds (Zopf et al., 2011a), and reduced amplitudes of somatosensory evoked potentials (Zeller et al., 2014), observed when tactile stimuli are delivered to participants undergoing a RHI, with respect to a non-illusory control condition. These effects are in line with complementary observations showing that the “substituted” hand’s cools down during RHIs (Hohwy and Paton, 2010; Moseley et al., 2008a). This altered processing is compatible with the view that, during the illusion, the real hand is no longer processed as a part of the self. These observations are in line with the predictive coding models of multisensory integration, in that they may be explained as a way of minimizing sensory conflict (Seth et al., 2011; Zeller et al., 2015). In the study presented in Chapter 3, we showed how the impact of ownership illusions on perceptual processing extends to the domain of multisensory integration. The study demonstrated how, while undergoing a FBOI over a virtual body, the temporal constraints for multisensory integration of visuotactile stimuli are relaxed. This was interpreted as the result of the causal binding effect driven by the assumption that the visual and the tactile stimuli (seen on the virtual and felt on the physical body) have the same origin, i.e. the own-body (Maselli et al., 2016). Recently, it was shown how the sense of body ownership over a fake arm further involves the updating of the own-body representation used to plan actions and to predict their sensory consequences (Kilteni and Ehrsson, 2017).

The effects of body ownership illusions on the processing of afferent sensory signals extends to

the perception of nociceptive stimuli. The studies that investigated the way ownership illusion could modulate pain perception mostly relied on the possibility to alter the physical properties of the fake body (part) that substitutes its real counterparts. These studies were in fact inspired by previous evidences showing that having view of one's own body when receiving a painful stimulus is analgesic (Longo et al., 2009), and that the pain sensitivity is further modulated by the perceived size of the body part affected (Mancini et al., 2011; Moseley et al., 2008b; Romano and Maravita, 2014). Along these lines, it was shown that analgesic effects (similar to those associated with viewing the real body part) are induced when viewing the surrogate hand during a RHI (Hegedüs et al., 2014; Martini et al., 2014), but only if the surrogate and the real hands are collocated (Nierula et al., 2017). It was further shown that pain thresholds could be modulated by manipulating the appearance of the fake arm. In particular, negative body image cues in the surrogate arm appearance – e.g., a reddened (Martini et al., 2013) or an injured arm (Osumi et al., 2014b) – were found to enhance pain sensitivity. An experimental study presented in Chapter 4, explored the possibility to modulate pain perception by varying the degree of transparency of a virtual body during FBOs, showing how pain thresholds increased with the level of ownership experienced toward semi-transparent virtual bodies (Martini et al., 2015). Beside paving the way to interesting clinical applications for pain treatments, these results provide further evidence for the complex interplay among the multisensory representation of the self-body, pain perception, and higher-order cognitive and emotional aspects associated with body appearance (Martini, 2016; Moseley et al., 2012; Romano and Maravita, 2014).

The use of immersive virtual reality has been crucial for exploring the impact of owning an artificial body, differing from one's own in terms of age, sex and race, on cognition and social aspects of behaviour. Several experiments have shown, for example, how white people undergoing the illusory experience of owning a black body, tend to reduce their implicit racial bias (Farmer et al., 2012; Maister et al., 2013; Peck et al., 2013). Experiencing embodiment over a child body has been shown to have important effects on both perception and behaviour. After embodying a child body, adults typically overestimate object sizes, enhance the implicit association of themselves with child-like attributes, and report positive changes in their emotional state (Banakou et al., 2013; Tajadura-Jiménez et al., 2017). Other studies have further demonstrated that body ownership illusions could further modulate the engagement and the actual performance on a given task, depending on the perceived appropriateness of the surrogate body for the task (Kiltner et al., 2013; Osimo et al., 2015). Finally, a recent work showed how being embodied in a female body while receiving a verbal domestic abuse by a male avatar could improve the ability of male offenders to properly process fearful faces (Seinfeld et al., 2018). Interestingly, it was further showed that the experience of full body ownership illusion can have significant after-effects on the way threatening stimuli are processed. In particular, a recent study showed that experiencing an ownership illusion over a female character modulates the activation of defensive and emotional processing, in fronto-parietal networks encoding human peripersonal space, during the subsequent exposure to a verbal aggression by a virtual male offender (de Borst et al., 2018).

The results reviewed in this section provide just a rough overview of the profound impact that illusory experience of body ownership over fake bodies can have on perception, behaviour and cognition, over time scales of few tens of seconds. Nevertheless, it appears evident from this overview that, beside providing a powerful tool for scientific research, bodily illusions proved to have a great

potential for application in the clinical, therapeutic and educational applications.

2. STRUCTURE AND CONTRIBUTION OF THESIS

The works presented in this thesis focus on the study of the multisensory mechanisms underlying the perception of our own bodies. By making use of Immersive Virtual Reality and established experimental paradigms for eliciting bodily illusions, the multisensory basis of two main components of self-perception, the sense of body ownership and *self-location*, have been identified. In addition, some implications of manipulating *ownership* under controlled experimental settings have been explored. The first part of the thesis (Chapters 2-5) deals with sense of *ownership* experienced in full body ownership illusions (FBOIs). The second part (Chapters 6 and 7) explores how the sense of *ownership* and *self-location* differ from each other, how they can be selectively altered during bodily illusions, and how they are differently characterized in terms of subjective perceptual experience and multisensory mechanisms involved.

The aim of the study presented in **Chapter 2** was to identify the perceptual “building blocks” of the sense of body ownership in terms of the major multisensory components involved and of their mutual interaction. The study was initially planned for disambiguating earlier reports about whether or not congruent visuotactile stimulation is a necessary trigger for eliciting a FBOI (Petkova and Ehrsson 2007 vs Slater et al. 2010), but eventually it was designed to more generally pinpoint the minimal combinations of multisensory stimuli that could elicit a FBOI. More specifically, we explored the role and mutual interaction of different perceptual components that have been manipulated in previous experimental studies on FBOIs. These were: (i) the degree of realism of the surrogate body (mannequin vs realistic gender-matched human body), (ii) the visual perspective over the surrogate body (1PP vs 3PP), (iii) the congruency of visuotactile stimuli (synchronous vs asynchronous) and (iv) the availability of visuo-vestibular signals associated to head movements (present or absent). By manipulating these components while monitoring the level of the induced FBOI in healthy participants via subjective reports and physiological correlates, we could achieve several novel insights into the mechanisms that allow to swap the sense of body ownership from our physical one to a virtual one. These results, presented and discussed in Chapter 2, provided the bases for the Bayesian inference formulation for describing the mechanisms that determine whether or not an external object is experienced as belonging to the own-body, which was formulated and presented in a following study (Chapter 5).

The study presented in **Chapter 3** tested the following hypothesis: when undergoing an ownership illusion the temporal constraints for visuotactile integration are relaxed as a result of the causal binding between the real and the fake bodies established by the illusion. This hypothesis stemmed from a serendipitous finding from our previous study, in which we found that when the FBOI was established, asynchronous visuotactile stimuli were not perceived as “wrong”, which is otherwise the case (presented in Chapter 2). Indeed this seemed to suggest that during ownership illusions participants are more tolerant to visuotactile incongruences. To test this idea, we designed an experimental protocol combining the triggering of a FBOI and a temporal order judgment (TOJ)

task. The latter allowed psychophysical quantification of the temporal window for visuotactile integration to occur (Vroomen and Keetels, 2010). Participants in this experiment performed the same TOJ task in three different conditions in which we manipulated the sense of ownership and the visual information providing, or not, hints for the visual and tactile stimuli in the TOJ to be causally related. We found that the temporal window for visuotactile integration was significantly larger when participants experienced an ownership illusion and the visual stimuli were consistent with an object touching the virtual body, with respect to other conditions. Crucially, the temporal window for visuotactile integration was positively correlated with the strength of the ownership illusions measured through questionnaire ratings.

In **Chapter 4** a study is presented that, taking advantage of the possibility to arbitrarily manipulate the appearance of a virtual body, investigated how the level of transparency of a virtual body affects the sense of body ownership and pain perception in healthy participants. The study was motivated by a set of previous experimental evidences. Having direct view of one's own body while receiving painful stimuli was shown to have an analgesic effect (Longo et al., 2009), an effect that holds true when looking at a collocated virtual body during ownership illusions (Martini et al., 2014; Nierula et al., 2017). Complementary evidence showed that perception of painful stimuli on the hand is modulated when manipulating the appearance of the hand, either in size (Mancini et al., 2011) or skin colour (Martini et al., 2013). In line with our previous study showing how the level of realism of the virtual body modulates the strength of FBOs (Maselli and Slater, 2013), we expected that by gradually decreasing the visibility of the virtual body the experienced sense of *ownership* would fade away. On the other hand, we could not make straightforward predictions about the impact on pain perception. Would the analgesic effect fade away together with the vision of the body that in normal condition produce it? Or otherwise, would the analgesic effect be modulated by the cognitive value of having a transparent body? The results from our experiment showed that, as expected the strength of perceived *ownership* over the collocated virtual body seen from 1PP diminished progressively for increasing levels of body transparency. On the other hand, we found that the level of transparency does not directly modulate pain perception. Nevertheless, we found that in the conditions where the body was semi-transparent, higher levels of *ownership* resulted in an increased pain sensitivity. Different interpretations for these finding have been thoroughly discussed.

Chapter 5 presents a general overview of “*how and why*” body ownership illusions (BOIs) occur. The perspective taken was to address the following question: how does our brain distinguish its own body from others' bodies and objects in the environment? To tackle this question, we first undertook a broad review of experimental findings concerning the spatial, temporal, and semantic principles of crossmodal stimuli used to trigger BOIs, presenting them in a coherent and unified scheme. We did so by analysing the semantic and spatiotemporal constraints that different multimodal triggers (visuotactile, visuomotor and visuoproprioceptive) need to satisfy for eliciting BOIs. We further reviewed the theoretical frameworks that have been proposed to describe the underlying mechanism of BOIs. Next, based on the schematic arrangement we proposed for the available experimental evidences, we introduced a conceptual model for how our nervous system infers whether an object belongs to the body, giving rise in some cases to BOIs. The model is worked out in the Bayesian inference framework for the representative case of the classic RHI. After presenting our formulation, we discussed how it can account for several experimental findings. Finally, we discussed how neural

network models already developed in the literature for multisensory integration can be taken as implementational frameworks within which the computational problem behind BOIs could be addressed in the future.

The last two chapters of this thesis explore how, while intrinsically interlaced in normal body perception, the sense of *ownership* and the sense of *self-location* can be selectively altered during FBOIs.

Chapter 6 presents an experimental study in which the aim was to test to what extent changes in *self-location* entail changes in *ownership*. The lack of consensus about this issue in previous works from different groups was the main motivation for conducting the study. In fact, on the one hand in our previous study we confirmed that illusory *ownership* over a fake body required having a first person perspective (1PP) on it and an established visuoproprioceptive coupling between the real and fake bodies (Maselli and Slater, 2013). On the other, independent works consistently reported that *ownership* towards a filmed or virtual body was experienced together with changes in *self-location* during illusory back-stroking OBEs (Blanke, 2012; Ionta et al., 2011; Lenggenhager, 2007). However, in these latter studies *ownership* was assessed only through questionnaire scores that, as we reasoned, could reflect a sense of self-identification rather than actual ownership. We therefore designed a set of experiments in which FBOIs were triggered from different visual perspectives, each corresponding to different degree of overlap between real and virtual bodies. Concurrently both *ownership* and *self-location* were measured using a combination of questionnaire, psychophysical and behavioural assessments. A novel self-posture task was introduced to measure *ownership* by assessing the strength of visuoproprioceptive coupling, while an adaptation of the cross-modal congruency task was adopted to indirectly measure *self-location*. We found that, despite their strong coupling, *self-location* and *ownership* were selectively altered depending on the perspective. The results demonstrated that illusory OBEs are mainly associated with alterations in the perceived sense of *self-location*, and do not necessarily involve alterations in the sense of body ownership. When discussing our results in the context of the relevant literature, we argued that changes in the perceived *self-location* are associated to the dynamical representation of peripersonal space encoded by visuotactile neurons, while illusory *ownership* entails the implication of visuoproprioceptive populations.

Finally, **Chapter 7** provides a closer look into the nuances of different illusory experiences affecting the sense of *self-location* and their relation to *ownership*. The ideas developed in Chapter 6 have been extended and complemented to further disentangle how *self-location* is differently modulated in front-stroking and back-stroking OBEs. The profound differences between the two illusory experiences that a number of studies had previously highlighted, at the level of subjective experience and of behavioural and neural correlates, have been attentively described. Based on these, it was proposed that the sense of *self-location* may be regarded as the blending of two parallel representations: the abstract allocentric coding of the position occupied in the environment, and the egocentric mapping of somatosensory sensations into the external space. While the first is mainly associated with visual-perspective, the second is tightly linked to peripersonal space.

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CHAPTER 2

THE BUILDING BLOCKS OF THE FULL BODY OWNERSHIP ILLUSION

Related publication:

The building blocks of the full body ownership illusion.

Maselli, A., and Slater, M.

Front. Hum. Neurosci. 7, 83, 2013

ABSTRACT

Previous work has reported that it is not difficult to give people the illusion of ownership over an artificial body, providing a powerful tool for the investigation of the neural and cognitive mechanisms underlying body perception and self consciousness. We present an experimental study that uses immersive virtual reality focused on identifying the perceptual building blocks of this illusion. We systematically manipulated visuotactile and visual sensorimotor contingencies, visual perspective, and the appearance of the virtual body in order to assess their relative role and mutual interaction. Consistent results from subjective reports and physiological measures showed that a first person perspective over a fake humanoid body is essential for eliciting a body ownership illusion. We found that the level of realism of the virtual body, in particular the realism of skin tone, plays a critical role: when high enough, the illusion can be triggered by the sole effect of the spatial overlap between the real and virtual bodies, providing congruent visuoproprioceptive information, with no need for the additional contribution of congruent visuotactile and/or visual sensorimotor cues. Additionally, we found that the processing of incongruent perceptual cues can be modulated by the level of the illusion: when the illusion is strong, incongruent cues are not experienced as incorrect. Participants exposed to asynchronous visuotactile stimulation can experience the ownership illusion and perceive touch as originating from an object seen to contact the virtual body. Analogously, when the level of realism of the virtual body and/or the spatial overlap of the two bodies is not high enough, the contribution of congruent multisensory and/or sensorimotor cues is required for evoking the illusion. On the basis of these results and inspired by findings from neurophysiological recordings in the monkey, we propose a model that accounts for many of the results reported in the literature.

I. INTRODUCTION

The experience of our body results from the complex interplay of various perceptual streams involving vision, touch, proprioception, interoception, motor control, and vestibular sensations. Strong evidence supporting this statement comes from a number of neurological conditions where the sense of the body becomes altered as a consequence of focal brain lesions, limb amputation or deafferentation. Examples of such conditions are somatoparaphrenia and associated anosognosia (Berlucchi and Aglioti, 1997, 2010; Vallar and Ronchi, 2009), phantom limb sensations (Giummarra et al., 2007), and out-of-body experiences (OBEs) (Blanke and Mohr, 2005).

Altered body perceptions analogous to those experienced in lesioned patients, can be temporally induced in healthy subjects in controlled experimental settings, where the delivery of anomalous sensory stimuli is systematically manipulated. These altered perceptual states are usually referred to as bodily illusions and have been extensively used for studying body perception, self-consciousness and their underlying neural correlates. In particular, experimentally controlled bodily illusions allow, to some extent, the isolation of the various components that converge in the holistic experience of our bodies.

In this paper we present a study that investigates the main perceptual components of the full body ownership illusion, a specific type of bodily illusion in which healthy subjects experience an artificial body as if it were their own physical body. This illusion is particularly interesting for the study of self-consciousness as it relies on an altered representation of the entire body (Blanke and Metzinger, 2009; Blanke, 2012) and, as such, it is complementary to the “rubber hand illusion” (RHI) paradigm in the study of body perception.

In the original version of the RHI (Botvinick and Cohen, 1998), participants see a rubber hand located in front of them in a similar posture to their corresponding but hidden real hand. Both rubber and real hands are stroked by the experimenter. When the strokes on the real and rubber hands are delivered synchronously and in the corresponding spatial locations, most participants experience the rubber hand as if it were their own and feel the touch as originating from the rubber hand itself; the same does not happen, or to a much lesser extent, when the stroking is asynchronous, or when there are other inconsistencies (such as spatial) between the stroking on both hands. A large number of studies have adapted and extended this classical set-up providing experimental evidence about the different perceptual components that contribute to the RHI. These include the spatial configuration and appearance of the artificial hand and the delivery of multisensory and/or sensorimotor stimulation. The spatial configuration of the artificial hand with respect to the real body affects the illusion. For example, the illusion does not occur when anatomical constraints are violated: when the rubber hand is located outside the participant’s peripersonal space (e.g., Lloyd, 2007), when it is in impossible postures (e.g., Ehrsson et al., 2004; Tsakiris and Haggard, 2005), or when it does not represent the main topological features of a hand (Tsakiris and Haggard, 2005). In terms of perceptual cues, the spatial configuration component corresponds to a stream of visuoproprioceptive information in which the spatial location encoded by vision is compared with the one encoded by proprioception. The body’s spatial location encoded by proprioception can be

altered, so that it does not always coincide with the position of the physical body. This happens in RHI experiments, where the illusion is typically associated with a mislocalization of the real hand toward the fake hand. Inherent to the RHI paradigm is the delivery of visuotactile stimulation, which has to be synchronous in order to evoke the illusion. However, it has been shown that the illusion is also experienced when visuotactile stimulation is substituted by other modalities of multisensory and/or sensorimotor stimulation, e.g., with sensorimotor contingencies in active or passive movements (Tsakiris et al., 2006; Kalckert and Ehrsson, 2012). This shows that the onset of the illusion is triggered more generally from a stream of congruent multimodal bodily signals (multisensory or sensorimotor) and does not necessarily require visuotactile integration. Finally, visual appearance has been found to play a critical role in the illusion: the fake hand does not need to be necessarily realistic for the illusion to take place, as shown by the numerous reports of ownership experienced over plastic-looking hands or elongated limbs (Schaefer et al., 2007; Kilteni et al., 2012; Preston and Newport, 2012); however, higher levels of realism of the artificial hand, in terms of texture and shape, have been found to enhance the strength of the illusion (Haans et al., 2008). The overall emerging scenario is that the sense of ownership over an external object requires the convergence of two main sources of information: (1) the on-line driving contribution from bottom-up processing of congruent multimodal perceptual cues and (2) the modulating top-down machinery based on a flexible but still robust prior internal body representation that requires that some key anatomical constraints in terms of body shape and visual perspective are preserved (see Graziano and Botvinik, 2002; Makin et al., 2008; Tsakiris, 2010).

Analogous perceptual components have been identified for the illusions of owning a whole artificial body. However, the relative importance of each of these components and their mutual interaction are still a subject of debate. This is partly due to the fact that different experimental procedures have been introduced to extend the RHI for dealing with whole bodies. Two main set-ups have been used and, interestingly, the illusions evoked in the two cases were not the same. Both set-ups use a head-mounted-display (HMD) to occlude the real body from vision and to display the artificial body in stereo. In one case participants saw their own body or that of a mannequin as filmed from 2 m behind. When exposed to synchronous stroking seen on the back of the visualized body and felt on their own back, participants reported experiencing the sensation of “seeing their own perceived body from a distance” and of perceiving touch as originating from the distant body (Lenggenhager et al., 2007, 2009; Aspell et al., 2009; Ionta et al., 2011).

Alternatively, when the stroking was felt on the chest and seen from a first person perspective (i.e., the stick seen as stroking the spatial location corresponding to that of the real chest), the resulting illusion was characterized as a feeling of having one’s own center of awareness moved behind the seen body, to the first person perspective position from where the scene was being observed. The true body seen in front was perceived as something like an “empty shell” or a “disowned body” (Ehrsson, 2007; Lenggenhager et al., 2009; Guterstam and Ehrsson, 2012). Although the illusions experienced in these two cases are notably different, they are both referred to as experimentally induced OBEs. In a different experimental set-up, a mannequin (Petkova and Ehrsson, 2008; Petkova et al., 2011) or a virtual body (Slater et al., 2010) was displayed from a first person perspective (1PP), where the artificial body visually substituted the obscured real body. Synchronous stroking of the real and virtual bodies typically induces the illusion of owning the artificial body, which is then perceived as the origin of sensory signals like touch and vision. We refer to this as full body

ownership illusion.

Two principal open issues emerge from the work so far on full body illusions. These are the role of visual perspective and the role of visuotactile stimulation. The role of visual perspective is a key subject on which two major classes of results are diverging. Reports about the feeling of self-identification that occurs during experimentally induced OBEs suggest that the sense of ownership can be experienced over an artificial body seen from a third person perspective (3PP) (Lenggenhager et al., 2007, 2009; Aspell et al., 2009; Ionta et al., 2011). However, studies focusing on the full body ownership illusion report that a 3PP over the artificial body does not result in the illusion even when synchronous visuotactile stimulation is delivered (Petkova and Ehrsson, 2008; Slater et al., 2010; Petkova et al., 2011). The difference between these findings could be ascribed to differences in the experimental designs adopted or alternatively to the fact that different kinds of perceptual illusions are involved. The full body ownership illusion experienced in 1PP is described as the feeling of owning an artificial body, which substitutes the real body as the origin of perceptual sensations. (e.g., Petkova and Ehrsson, 2008; Slater et al., 2010). Experimentally induced OBEs have been characterized in different ways according to the specific experimental protocol adopted. Depending on the stroking mode, participants have one of two different experiences: (1) the visual 1PP and tactile sensations coincide in the same body—since there is the sensation of being embodied behind the location of the real body that is seen in front (chest stroking); (2) the visual 1PP and the origin of tactile sensations are divorced, since the visual 1PP is at the real body location, but tactile sensations are attributed to the fake body that is seen in front (back stroking). For a comparative study see Lenggenhager et al. (2009). The latter illusion has been shown to correlate with a recoding of self-location in space as measured by walking responses (Lenggenhager et al., 2007) and mental imagery (Lenggenhager et al., 2009), as well as with a remapping of the spatial representation of visuotactile stimuli as measured by the crossmodal congruency effect (CCE; Aspell et al., 2009). It has been further found to correspond with the specific activation of a number of brain areas such as the temporo-parietal junction (TPJ), the bilateral premotor cortex (PMC) and the medial sensorimotor cortex (Ionta et al., 2011; Lenggenhager et al., 2011). Despite this, the possibility that the sense of ownership and touch could be experienced over a body located in the far extrapersonal space is still under discussion. It has been proposed that self-identification during OBEs is not an actual perceptual illusion, but rather a form of self-recognition similar to the self-recognition of oneself in a mirror (Petkova et al., 2011; Ehrsson, 2012). Whether the controversy concerning the role played by visual perspective is grounded in the very nature of the illusion or in uncertainties associated with the experimental set-ups adopted remains to be clearly established.

The second main issue under debate concerns the role of multisensory stimulation as a trigger to elicit the illusion. A conclusion drawn in most studies is that synchronous visuotactile stimulation is necessary to elicit the illusion. This is the case for all the OBE's studies mentioned above. Petkova and Ehrsson (2008) also reported that, together with a 1PP over a humanoid artificial body, synchronous visuotactile stimulation is necessary to trigger the full body ownership illusion (see also, Petkova et al., 2011). Using an immersive virtual reality (IVR) set-up, Slater et al. (2010) came instead to a different conclusion. In their experiment participants wore a tracked HMD, receiving visual sensorimotor contingencies, meaning that the displayed field of view is continuously updated according to head position and orientation. Additionally, a virtual mirror provided synchronous visual feedback of

head movements (visuomotor correlations). Participants received visuotactile stimulation either synchronously or asynchronously, and in both cases they experienced a strong full body ownership illusion. The fact that participants in this experiment could experience the illusion even when receiving asynchronous visuotactile stimulation seems to contradict the results of Petkova and Ehrsson (2008). However, there are two main differences between the two experimental set-ups. First, visual sensorimotor contingencies were provided in the IVR experiment, while in Petkova et al.'s experiment participants were exposed to a static field of view and were asked not to move their head, which was fixed looking down toward their body. Second, the virtual body in the IVR experiment had a realistic human body appearance, in term of skin texture and clothes, while in the other case the artificial body was a plastic mannequin. Whether these differences could explain the different conclusions drawn from the two experiments regarding the necessity or otherwise of visuotactile stimulation, is still not clear.

In this paper we report a set of experiments that systematically varies factors thought to contribute to the full body ownership illusion. Specifically, we consider the effect of visuotactile correlations and visual (head-based) sensorimotor contingencies, visual perspective and visual appearance. Our main aim was to fit previous results into a common framework and to propose a model that would allow assessment of the relative contributions and reciprocal interactions of such bodily signals to the full body ownership illusion.

2. MATERIALS AND METHODS

2.1. OVERALL DESIGN

Our study consisted of three experiments designed with the aim of exploring and disentangling the relative role of those factors that have been reported to be the building blocks of the full-body illusion: visual perspective, human-like bodily appearance, and visuotactile stimulation. Additionally, we consider the effects visual sensorimotor contingencies provided by head tracking, where the visual field displayed in the HMD is updated according to the tracked movements of the participant's head, in the same way as it would be in physical reality.

In experiment 1 we examined the effects of visuotactile and visual sensorimotor stimulation and their possible interaction. For this experiment we used a between-groups 2×2 design with two binary factors: visuotactile stimuli could be synchronous (VT) or asynchronous ($\perp$ VT); head tracking could be enabled (HT) providing visual sensorimotor contingencies, or disabled ($\neg$ HT), which is with no head movements and with a fixed field of view, as in the set-up of Petkova and Ehrsson (2008). The design of this first experiment was mainly driven by the attempt to account for the difference in the results reported in Petkova and Ehrsson (2008) and Slater et al. (2010), since one important difference between the two studies concerns visual sensorimotor contingencies that are provided in the latter, but not in the former.

Experiment 2 was designed to explicitly test the hypothesis that visual perspective is a critical factor for the full body ownership illusion. For this we adopted a single-factor design, perspective, which had two levels (1PP vs. 3PP). Head tracking was set to HT and visuotactile to VT. This was

to examine the effect of perspective in the otherwise most favorable condition for the illusion, i.e., with synchronous visuotactile stimulation and visual sensorimotor contingencies. If 3PP prevents the illusion in this case, we can safely extrapolate that the same will happen for other configurations where at least one of the two stimulations is in an incongruent mode (e.g., $\perp$ VT), or is not provided (e.g., $\neg$ HT).

In experiment 3 we examine the impact of the level of realism for the appearance of the artificial body, comparing the effect of seeing a realistic human avatar (HA) vs. a plastic mannequin avatar (MA). The hypothesis was that the level of realism of the visualized body (in terms of skin texture and clothing) can modulate the intensity of the full body ownership illusion. As in the case of experiment 1, the design of this experiment has been motivated by the second critical difference among the experimental set-ups of Petkova and Ehrsson (2008) and Slater et al. (2010): the visual appearance of the fake bodies. We employed a single-factor design where the bodily appearance varied on two levels (HA vs. MA) with the other factors in the [1PP, $\perp$ VT, $\neg$ HT] configuration. This choice enabled us to disentangle the hypothesized modulation of the illusion intensity by the visual appearance of the artificial body from the effects of multisensory and sensorimotor contingencies.

Table 1 | Combinations of experimental factors adopted for the three experiments.

Factors	Experiment 1	Experiment 2	Experiment 3
Visuotactile	VT vs. $\perp$ VT	VT	$\perp$ VT
Head tracking	HT vs. $\neg$ HT	HT	$\neg$ HT
Visual perspective	1PP	1PP vs. 3PP	1PP
Body appearance	HA	HA	HA vs. MA

Table 1 Combinations of experimental factors adopted for the three experiments.

All experimental factors vary on two levels: “visuotactile” could be synchronous or asynchronous (VT vs. $\perp$ VT); “headtracking” could be enabled or disabled, providing or not visual sensorimotor contingencies (HT vs. $\neg$ HT); “visual perspective” could be first person or third person perspective (1PP vs. 3PP); and “body appearance” could be either human or mannequin appearance (HA vs. MA). The variables in orange show the levels of the experimental factors, while the ones in black show the fixed configuration adopted for each experiment. There were nine participants in each of the four factorial cells of experiment 1, another nine participants in the 3PP condition of experiment 2, and another nine in the MA condition of experiment 3, resulting in a total of 54 participants.

2.2. IMPLEMENTATION

The factors that were manipulated in the three experiments are summarized in Table 1: visual perspective (1PP vs. 3PP), bodily appearance (HA vs. MA), visuotactile stimulation (VT vs. $\neg$ VT), and visual sensorimotor stimulation from head tracking (HT vs. $\neg$ HT). Although all the four factors vary on two levels, the three experiments planned for this study involve in total six conditions, as some factor combinations could be used for more than one experiment.

When head tracking was enabled, participants could explore the virtual environment and, looking down, they could see the virtual body when in the 1PP condition. In the $\neg$ HT conditions the virtual scene was instead static and participants were instructed not to move their head and gaze direction, which was fixed looking down toward the virtual body.

Figures 1A, B (1D, E) show the perspective levels for a female (male) participant. For the case of 3PP, the point of view was shifted horizontally 40 cm away to the right; head tracking was enabled, so that participants could see the virtual body to their left, in their near peripersonal space (i.e., within reach). Participants in this condition also saw the avatar's head moving as their own while exploring the environment, which provided them with additional visuomotor correlations. Note that since the avatar's head followed the movements of the participant's head, participants never got to see the avatar's face (see Figures 1B, E). The avatars used to test the role of the body visual appearance are shown in Figures 1A, C (1D, F) for the case of a female (male) participant.

The apparatus used to implement the visuotactile stimulation is shown in Figure 2.2. Touch was delivered via mechanical vibrators attached to a haptic vest, while the seen touch was provided in the form of a ball bouncing on the virtual body along a pre-recorded path. The location of the vibrators on the haptic vest was adjusted for each participant, so as to match the contact points of the ball's pre-recorded trajectory with the chest of the avatar. In the VT condition each vibrator was activated for a short time interval (20 ms) when the simulator detected a collision of the ball with the avatar mesh in the corresponding point (Spanlang et al., 2010; Pomes et al., 2012). The time delay of the vibrator activation with respect to the virtual collision corresponds to the communication time between the machine running the IVR software and the haptic vest and was negligible (<10 ms). The asynchronous condition was implemented by randomly activating the vibrators when the virtual tapping was visualized, so that the touch and the visual collisions were not correlated.

2.3. PARTICIPANTS

A total of 54 naïve subjects were recruited for the study, 9 for each of the six conditions over the three experiments (Table 1). Participants were recruited from the University campus or from a database of persons who had previously agreed to being contacted for participation in VR experiments. All subjects participated in only one experiment — i.e., it was a between-groups design. Experiment 1 tested 36 subjects (18 female, mean age 23.3, SD 5.1). Experiments 2 and 3 each involved 18 subjects (experiment 2: 7 female, mean age 29.4, SD 7.6; experiment 3: 8 female, mean age 25.4, SD 4.6). Note that the [VT, HT] group in experiment 1 has the same experimental

configuration as the 1PP experimental group in experiment 2. For this reason we could use the same experimental group independently for the two experiments. The same applies for the [$\neg$ VT, $\neg$ HT] group in experiment 1 and the HA group in experiment 3.

Figure 1. Perspective levels and body appearances levels used for the different conditions of the experiments. Gender-matched avatars were assigned to each participant. [A,B (D,E)] Show the two levels of the factor “perspective” for a female (male) participant: in the 1PP conditions (A,D,C,F) when looking down participants could see a virtual body co-located with their own physical body, while in the 3PP conditions (B,E) participants saw a virtual body in their near extrapersonal space when looking to the left. The two levels of the factor “bodily appearance” are shown in [A,C (D,F)] for a female (male) participant: in the HA conditions participants had a co-located virtual body with a realistic human appearance (A,D), while in the MA condition a co-located virtual body resembling a plastic mannequin (C,F).

The study was performed according to institutional ethics and national standards for the protection of human participants, and it was approved by the Comité Ético de Investigación of the University of Barcelona. All participants signed an informed consent form and filled in a pre-questionnaire to

collect demographic information before taking part in the experiment. They were then assigned arbitrarily to one of the six conditions and were paid €10 after the experiment was concluded. In the pre-questionnaire all participants were asked “Have you ever experience ‘virtual reality’ before?”, with possible responses on a scale from 1 (no experience) to 7 (extensive experience). The response was on average low (median value 1), with only 6 participants out of 54 scoring 4 or higher values.

Figure 2. *The vibrotactile device used in the experiments. The left panel shows the haptic vest used to deliver touch sensations: vibrators were located on the vest, mapping the location of the contact points of the ball's pre-recorded path with the avatar's chest. The right panel shows the paths followed by the virtual ball (blue lines) and its contact points with the avatar chest (yellow dots). In synchronous conditions the vibrators array was synchronized with the pre-recorded path, so that each vibrator was activated when the ball reached the corresponding path-chest contact point.*

2.4. EXPERIMENTAL PROCEDURE

Participants were instructed to sit comfortably on a chair with their legs resting on a footstool. They entered the virtual environment using a wide field-of-view head-tracked, HMD. We used a NVIS nVisor SX111 HMD with dual SXGA displays of $76^{\circ}\text{H} \times 64^{\circ}\text{V}$ degrees field of view per eye, corresponding to a global field-of-view of 111° horizontal and 60° vertical, with a resolution of 1280×1024 per eye displayed at 60 Hz. Head tracking was performed by a 6-DOF Intersense IS-900 device. Depending on the gender and the condition assigned, each participant was exposed to one of the scenes displayed in stereo within the HMD, shown in Figure 1.1. Participants in every condition were instructed to not move their body from the neck down for the whole duration of the experiment. Participants in HT conditions were explicitly asked to turn their head and look around the environment, while those in $\neg\text{HT}$ conditions were asked not to move the head and not to gaze around.

After an adaptation period of about 30 s, a yellow ball appeared in the scene and moved toward the virtual body. When it struck the body it activated the vibrators on the haptic vest (in synchronous or asynchronous mode according to the condition). Then it bounced off the body moving away again. This tapping phase lasted for an interval of 2 min. In this phase participants were instructed to pay attention to the virtual body and to the tapping ball. At the end of the tapping phase the ball disappeared and the vibrators stopped. Participants were then asked to focus their attention on the virtual body, and after about 30 s they were exposed to a disturbing event: the lower legs slowly moved away from the rest of the body for 10 s, covering a distance of about 1 m in the virtual room, and after that they returned to the original position to recompose the whole body (see Figure 3). The choice of this particular kind of disturbing event instead of a more classic threat to the virtual body is based on two main motivations: first, we wanted to avoid any kind of threat (even if virtual) directed to the spatial location of the real body; second, we looked for an event that explicitly breaks the integrity of the whole body.

Figure 3. Snapshots of the legs separation event are shown for the mannequin and human appearance modes in the case of a female participants. The legs separation event lasted 10 s during which the legs moved away from the body reaching a maximum distance of 1m. The legs returned to their original position immediately after the 10s, recomposing a whole body.

2.5. RESPONSE VARIABLES

2.5.1. QUESTIONNAIRE

For all the three experiments we used a 7-item questionnaire designed to assess the level and quality of the illusion experienced by the participants. Each question was scored by participants on a given scale from 0 (not at all) to 7 (very much). The choice of an even number of points on the Likert scale

was meant to force scoring either on the agreement or on the disagreement side. Having four points on each side further allowed for various degrees of agreement/disagreement, so as to detect differences in the intensity of the experienced sensations (Cohen et al., 2011).

The questionnaire is shown in Table 2. The items were formulated by adapting questions from previous experiments on full body illusions (Lenggenhager et al., 2007; Petkova and Ehrsson, 2008; Slater et al., 2010). The main critical item is the one tagged as *mybody*, which relates directly to the feeling of owning the virtual body. The clothing item was also meant to test the feeling of ownership following Slater et al. (2010) where it was found that the body ownership illusion was highly correlated with the illusion of wearing the same clothes as the virtual character. The items *stress* and *discomfort* were formulated to detect the subjective response to the disturbing event. These two apparently similar statements were meant to distinguish the feeling of weirdness (something weird is happening to my body, but it is not stressful) from the feeling of stress that is a state of anxiety. The *catch* item tested the desire of participants to move and act in the virtual environment. The *touch* item was meant to test the appropriate implementation of the visuotactile stimulation: the proper functioning the vibrotactile vest and its integration in the virtual environment had to be demonstrated by having low/high scores to the *touch* item in the asynchronous/synchronous modalities. Finally, the *twobodies* item was a control question.

Table 2. Questionnaire

Variable name	Item	Statement category
<i>Mybody</i>	I felt that the body I saw was my body	Ownership
<i>Clothing</i>	I felt that I was wearing different clothing to my real clothing	Ownership
<i>Stress</i>	I was stressed when I saw the legs coming apart	Psychophysical reaction
<i>Discomfort</i>	I felt physical discomfort when the legs were coming apart	Psychophysical reaction
<i>Catch</i>	I wanted to try to catch the yellow ball	Interaction in VR
<i>Touch</i>	It seemed as though the touch I felt was caused by the yellow ball touching my body	Implementation
<i>Twobodies</i>	I felt that I had two bodies	Control

2.5.2. HEART RATE DECELERATION

We monitored the physiological behavior of the participants by recording their electrocardiogram (ECG) throughout the whole duration of the experiment. This was used to obtain a measure for the heart rate deceleration (HRD) in various stages of the experiment. HRD has been previously shown to be a response variable that significantly correlates with states of stress and anxiety induced by sudden unpleasant stimuli (Bradley et al., 2001; Cacioppo et al., 2007), and has been successfully used in previous studies as a physiological correlate of the full body ownership illusion (Slater et al., 2010) and other perceptual illusions (e.g., Tajadura-Jiménez et al., 2012). In our study, instead of using a sudden threat, we have adopted a threat to the integrity of the body that is extended in time, i.e., the legs separating from the rest of the virtual body, in slow motion, over a period of 10 s. For this reason it is not possible to identify the precise moment at which participants noticed this event. To account for this, we introduced a new procedural definition for the HRD.

The ECG signal was sampled at 256 Hz using the g.tec portable bio-signal acquisition device g.MOBllab¹. ECG signals were processed to extract the heart rate (HR) by first applying the automatic search for QSR complex implemented in the gtec biosignal analysis software g.BSanalyze², and then by visually inspecting the search results to correct for possible missing or false identifications. The HRD response to the legs separation, HRD_{legs}, was calculated within the period of 6 s immediately after the legs started to move away from the rest of the virtual body, by looking for the first sustained deceleration event occurring in this time window (i.e., the earliest time interval in which the HR signal was monotonically decreasing). In order to have a reliable detection of sustained deceleration associated to the unpleasant event, we imposed two constraints: (1) the extent of the time interval of monotonic deceleration had to be larger than 1.5 s, so as to ensure that this was a sustained deceleration; (2) the starting point of the sustained deceleration should be at most 2 s away from the starting edge of the 6 s period. The latter constraint was meant to account for the possibility that the participants did not immediately detect the onset of the unpleasant event. Once we identified the deceleration event in the HR signal, we calculated the HRD as: $\Delta HR / \Delta t$, with $\Delta HR = HR(t_{max}) - HR(t_{min})$ and $\Delta t = t_{min} - t_{max}$. Here t_{min} and t_{max} denote the location in time of the minimum and maximum, respectively. For those cases in which the HR signal was monotonically increasing within the whole 6 s window, we have used an analogous procedure to obtain negative HRD values, describing in fact a heart rate acceleration.

As the HRD measurements are expected to be subject-dependent, we have further estimated a measure for the HRD baseline of each participant. In order to obtain a representative baseline value, we have applied the same procedure described above for measuring HRD from single sustained deceleration event, in 10 different time windows (each of 6 s) within the 20 s rest period preceding the legs separation. The baseline value, HRD_{base} was defined as the mean of these 10 HRD measures.

3. RESULTS

3.1. STATISTICAL METHODS

Since the responses to the questionnaires are ordinal and not interval scaled, we used non-parametric tests for the questionnaire analysis. Data from experiment 1 were analyzed with the Friedman test for non-parametric analysis of 2×2 designs for testing the effect of each factor, while taking into account the other as a blocking factor. Note that the Friedman test does not allow detection of interaction effects. When comparing two samples, as in experiments 2 and 3 and in some post analysis of experiment 1, we used the Mann–Whitney U test.

The HRD data were inspected in order to look for changes induced by the legs separation event, one that obviously affected the integrity of the body, with respect to the baseline. We performed analysis of variance (ANOVA) comparing the change in HRD induced by the threat and measured as $\Delta HRD = HRD_{legs} - HRD_{base}$, between the experimental conditions of each experiment. Finally, we bring various results together in one simple path analysis model that helps understand the results of the experiments.

1 <http://www.gtec.at/Products/Hardware-and-Accessories/g.MOBllab-Specs-Features>

2 <http://www.gtec.at/Products/Software/g.BSanalyze-Specs-Features>

All analysis was carried out using the Stata 12 statistical package³

3.2. EXPERIMENT 1: MULTIMODAL CONTINGENCIES

3.2.1. QUESTIONNAIRE

Experiment 1 was a 2×2 design with factors visuotactile (VT vs. $\perp$ VT) and head tracking (HT vs. $\neg$ HT). Figure 4 shows the boxplots comparing the distributions of scores in the four conditions for relevant items. It is evident that there is no significant difference between the four conditions with respect to the sensation of body ownership (item *mybody*). The Friedman test applied to the *mybody* item confirmed that there is no significant difference with respect to both the visuotactile and head tracking factors. Median scores were at least 4 in all the four groups, suggesting that participants experienced some illusion of body ownership over the virtual body whatever the visuotactile and head tracking modes. Responses to the *clothing* item also received high scores in all the four conditions (all medians at least 4).

The *stress* and *discomfort* items had median values below 4 and no significant difference was found between the four conditions. Nevertheless, verbal reports revealed that most participants experienced a strange sensation while seeing the virtual legs separating, a fact often corroborated by spontaneous exclamations and verbalizations during and after the legs separation.

Scores to the *touch* item were significantly higher for the VT conditions than for the $\perp$ VT, for both the HT ($p = 0.009$, Mann–Whitney; average ranks: 6.28 for $\perp$ VT, 12.72 for VT) and $\neg$ HT ($p = 0.001$, Mann–Whitney; average ranks: 49 for $\perp$ VT, 122 for VT) groups, showing that our implementation of the visuotactile stimulation via automatic mechanical vibrators was effective. On the other hand participants had significantly greater scores in the HT compared to the $\neg$ HT mode, in the $\perp$ VT mode ($p = 0.048$, Mann–Whitney; average ranks: 7.06 for $\neg$ HT, 11.94 for HT), while no significant difference between the HT levels is present in the VT mode group. The Friedman test applied to the *touch* item detected significant differences with respect to both the VT factor ($p < 0.0005$) and HT factor ($p = 0.042$). It is noticeable that the asynchronous visuotactile stimulation was clearly perceived as wrong (median score is 1) only in the [$\perp$ VT, $\neg$ HT] condition, while in the [$\perp$ VT, HT] condition the same asynchronous stimulation still had a median score of 4. Hence some participants still perceived this as a touch sensation congruent with the collision of the virtual ball with the body—as indicated from their reports and scores that reached as high as 6.

³ <http://www.stata.com/stata12/>

Figure 4. Questionnaire data from experiment 1, in which we investigate the role of visuotactile and visual sensorimotor contingencies. No difference was found in the *mybody* item showing that the illusion was not affected by either of the two multisensory modalities (when a 1PP is provided over a realistic virtual body). Significant differences were found for the *touch* item with respect to the visuotactile mode, for both levels of the head tracking factor. This showed that the vibrotactile device used to deliver touch sensations was effective. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ from Mann–Whitney test.

Scores to the *catch* item were significantly greater in the HT condition than in the ¬HT for the ¬VT group ($p = 0.014$, Mann–Whitney; average ranks: 6.5 for ¬HT, 12.5 for HT). No significant difference was found for the VT group. Analogously, a significant difference with respect to the visuotactile factor was found for the ¬HT group ($p = 0.015$, Mann–Whitney; average ranks: 6.5 for ¬VT, 12.5 for VT) but not for the HT one. The Friedman test detected significant differences between the scores to the *catch* item with respect to the head tracking factor (0.005), but not for the visuotactile one. It is interesting to note that the median score was much smaller only in the [¬VT, ¬HT] condition. For the other three groups, when congruent multisensory and/or visual sensorimotor correlations were provided (VT or HT or both), the scores tended to be quite high with medians at least 4. This showed that the desire to move and act in the virtual environment was mainly driven by multisensory/sensorimotor correlations and did not depend on the sense of ownership over the virtual body alone.

Since the level of ownership turned out to be independent of two experimental factors, we can further examine whether there are some undetected differences in the scoring to the *mybody* item by combining samples. We first compared the two visuotactile levels irrespectively of the head tracking mode and vice versa (18 subjects per group). In both cases the Mann–Whitney test found no significant difference. The same procedure was applied to the other questionnaire items for which no dependence on either VT and HT was found (all but *touch* and *catch*). This confirmed previous

findings, i.e., that the feeling of ownership over the virtual body did not depend on either the visuotactile and the head tracking modes signals.

3.2.1. HEART RATE DECELERATION

Two-Way ANOVA of ΔHRD showed that neither of the two factors, nor their interaction, was significant in modulating the HRD response when threatening the integrity of the body [VT: $F_{(1,32)} = 0.40, p = 0.53$; HT: $F_{(1,32)} = 1.32, p = 0.26$; interaction: $F_{(1,32)} = 1.80, p = 0.19$]. We have further checked specifically for the effect of the visuotactile factor, collapsing together the two headtracking levels. The same was done for testing further the effect of the headtracking factor, grouping together the visuotactile levels. In both cases no significant differences were found [VT: $F_{(1,34)} = 0.39, p = 0.54$; HT: $F_{(1,34)} = 1.31, p = 0.26$].

3.3. EXPERIMENT 2: PERSPECTIVE

3.3.1. QUESTIONNAIRE

Figure 5 shows the boxplot comparing scores to the *mybody* items from 1PP and the 3PP groups. From the figure one can see a noticeable effect of visual perspective. Comparing the two groups, [1PP,VT,HT] vs. [3PP,VT,HT] with 9 participants each, a Mann–Whitney test returned a significant difference ($p = 0.004$; average ranks: 5.89 for 3PP, 13.11 for 1PP). For all the other items no significant differences were found.

Given the results from experiment 1, i.e., visuotactile and head tracking modes have no effect on the ownership illusion, we combined the groups across these levels in order to increase the power of the test. The Mann–Whitney test comparing the 3PP group (9 subjects) with that of 1PP with both visuotactile and head tracking levels merged (36 subjects), resulted in significant differences in the perspective levels for both the item *mybody*, now with greater significance ($p = 0.0007$; average ranks: 10 for 3PP, 26.25 for 1PP), and *clothing* ($p = 0.024$; average ranks: 14.28 for 3PP, 25.18 for 1PP).

3.3.2 HEART RATE DECELERATION

One-Way ANOVA of ΔHRD resulted in no significant effect of the perspective factor on the HRD response when threatening the integrity of the body [$F_{(1,16)} = 1.21, p = 0.26$]. No difference was found when further comparing the 3PP group with the 1PP₃₆ group [$F_{(1,16)} = 0.10, p = 0.75$]

Figure 5. Questionnaire data from experiment 2, in which we compare groups with different perspective levels. 3PP (9 subjects), 1PP₉ (9 subjects) and 1PP₃₆ (36 subjects, where all 1PP conditions were grouped together irrespectively of the visuotactile and head tracking modes). The significant difference in the *mybody* item showed that 1PP is an essential condition for the full body ownership illusion.

** $p < 0.01$, *** $p < 0.001$ from Mann–Whitney test.

3.4. EXPERIMENT 3: BODILY APPEARANCE

3.4.1. QUESTIONNAIRE

Figure 6 shows the boxplots comparing the scores to the item *mybody* for the HA and MA groups. No significant differences were found between the two groups in the [1PP, $\perp$ -VT, $\neg$ HT] configuration (9 subjects per group; HA₉ vs. MA). However, since there was no dependence of the ownership illusion on the visuotactile and head tracking factors (results from experiment 1), we could group the levels of these two factors. Doing so we obtained a larger sample of 36 subjects for the HA (HA₃₆) condition to be compared with the MA group (9 subjects). In this case we found significant difference for both the items *mybody* ($p = 0.003$; average ranks: 11.44 for HA, 25.89 for MA) and *clothing* ($p = 0.011$; average ranks: 13.17 for HA, 25.46 for MA). This suggests that a realistic body appearance significantly enhances the ownership illusion. It is important here to note that despite the differences found in the two visual appearance groups and despite the asynchronous visuotactile stimulation, the sense of ownership was present to some extent even when the virtual body had a mannequin appearance, as shown from the fact that participants in the MA group had a median score of 3 on the *mybody* item.

Figure 6. Questionnaire data from experiment 3, in which we compared two groups that had different virtual bodies. Mannequin appearance: MA (9 subjects); human appearance: HA₉ (9 subjects) and HA₃₆ (36 subjects, where all the human appearance conditions in the 1PP were grouped together irrespectively of the visuotactile and head tracking mode). Significant differences were found when comparing the MA group with the HA₃₆ group. This showed that a realistic body appearance significantly enhances the illusion experience. ** $p < 0.01$ from Mann–Whitney test.

3.4.2. HEART RATE DECELERATION

One-Way ANOVA showed no significant difference in ΔHRD between the two body appearance groups [$F_{(1,16)} = 1.24, p = .28$]. No difference was found when further comparing the MA group with the HA₃₆ group [$F_{(1,16)} = 0.60, p = 0.44$].

3.5. PATH ANALYSIS

It is not too surprising that we found no apparent effect on the HRD of the legs separation threat to the body, since there was no differential effect on body ownership of most of the factor levels. We would expect that only in conditions of a high body ownership illusion would the threat to the integrity of the body cause the type of abhorrent response that might be reflected in HRD_{legs} . We found a strong impact on ownership only for the manipulation that involved perspective (experiment 2). Hence in this case we would expect an impact on HRD_{legs} . However, the situation is not straightforward since the HRD during the event would be likely to be associated with the baseline HRD but also and separately be associated with the level of ownership, which itself is impacted by the manipulation in perspective (1PP or 3PP). For this reason we used path analysis to

further explore the possibility that HRD_{legs} is indirectly affected by perspective through the feeling of ownership, a possibility that is not testable using simple analysis of variance. We propose the path model in Figure 7, in which perspective directly affects ownership, ownership affects HRD_{legs} , and HRD_{legs} further depends on HRD_{base} . The latter path takes into account intrinsic HRD differences between individuals. We used the scores from the questionnaire item *mybody* as a quantitative estimate of ownership. Note that here we treat *mybody* as an interval scaled variable; even if this is not formally justified, it is an approximation usually adopted as it provides useful exploratory tool.

Figure 7. Path analysis model that fits data from experiment 2. The boxes represent the variables: perspective can be 0 or 1 for 3PP and 1PP, respectively; ownership is the response to the questionnaire item *mybody*; HRD_{base} is the heart rate deceleration baseline, and HRD_{legs} is the heart rate deceleration measured right after the legs start separating. The circles represent random error terms.

We used the structural equation modeling software of Stata 12 to estimate the coefficients and the corresponding significant levels, using the asymptotic distribution free option, since we had no reason to suppose that the variables involved follow a multivariate normal distribution.

The model proposed provides a very good fit to the data. A test of the goodness of fit of the model against the saturated model showed a good fit, with $\chi^2(2) = 2.04$, $p > 0.36$. All estimates are summarized in Table 3. This result shows how the feeling of ownership is strongly affected by perspective as already discussed. Additionally it shows that, even though there is not a direct significant impact of perspective on HRD, the response to the threat in terms of HRD increases with ownership. Also, as expected, the HRD response to the threat is highly correlated with HRD_{base} , reflecting the intersubject HRD variability.

The factor perspective then has an effect on HRD mediated through the subjective level of ownership as measured by the questionnaire variable *mybody*.

Table 3. Coefficients, standard errors, and *p*-values estimates from path analysis applied to the model in Figure 6, using data from experiment 2.

Variable	Coefficients	Standard errors	<i>P</i>
OWNERSHIP			
Perspective	2.89	0.60	<0.001
Intercept	2.79	0.51	<0.001
HRD_{legs}			
Ownership	0.21	0.70	0.003
HRD _{base}	0.82	0.60	<0.001
Intercept	-1.03	0.27	<0.001

4. DISCUSSION

Our study contributes several key findings regarding the full body ownership illusion. Three experiments were specifically designed to pinpoint the main perceptual cues that contribute to the full body ownership illusion, to determine their specific role and assess their interaction. Motivated by previous results in the literature, we focused on the following main perceptual cues: visuotactile and visual (head-based) sensorimotor stimulation, visual perspective, and body appearance. The main findings are compatible with the following statements:

- First person perspective is a necessary condition for the full body ownership illusion.
- The full body ownership illusion can result from the sole effect of seeing a realistic virtual body in the same location and posture as the physical body, a configuration that contributes toward the experience of correct visuoproprioceptive cues, with no need for the additional contribution of congruent multisensory and/or head-based sensorimotor cues.
- The appearance of the virtual body and more specifically its level of realism in terms of skin texture and clothes, can influence the strength of the full body ownership illusion.
- Multisensory and/or sensorimotor contingencies can influence the level of the full body ownership illusion, having a reinforcing effect when congruent and a damping effect when incongruent.
- The full body ownership illusion can modulate the way touch is perceived, in that asynchronous visuotactile cues can be consciously perceived as correct, especially when there is first person perspective and a realistic virtual body.

Note that we did not directly explore the effect of visuomotor correlations, as participants could only move the head and were not allow to move the rest of the body. We speculate that congruent visuomotor correlations provide powerful multimodal cues that have a similar —though stronger— effect on the ownership illusion as the multisensory and head-based visual sensorymotor

contingencies explored in our experiments. This speculation needs to be further tested in a future study.

In the following we discuss the above findings in the context of the relevant literature, highlighting the new findings with respect to previous studies.

4.1 THE ROLE OF PERSPECTIVE

In experiment 2 we found clear evidence for 1PP being a critical factor for eliciting the full body ownership illusion. The questionnaire results showed a strong significant difference between participants with 1PP and 3PP, in that only the first group experienced the illusion of ownership with respect to the virtual body. HRD data further support this finding (see section 3.5). Moreover, our experimental set-up showed that 3PP inhibited the illusion even when various form of congruent multisensory and sensorimotor cues were provided. Therefore, as a general result, it could be said that first person perspective over the fake body is a necessary condition for the onset of the full body ownership illusion. Our results bring also further insights on the issue raised in Petkova et al. (2011) as to whether 3PP prevents the illusion because it violates the 1PP as such, or less restrictively, because (as in their experiment) the body to be owned is seen in the far extrapersonal space. In our experimental set-up, the virtual body is seen from 3PP and it is located within the peripersonal space. The finding that the illusion is suppressed in this set-up demonstrates that violation of 1PP over the fake body is sufficient to prevent the full body ownership illusion, even if the body is seen in the peripersonal space.

Our results are consistent with previous findings from studies on both the RHI and the full body ownership illusion. In the RHI paradigm, experiments by different groups have investigated the effect of displacing the position of the artificial hand with respect to the real physical one in order to determine the role of spatial congruency between visual and proprioceptive information. For the sake of the present discussion, the majority of these manipulations could be interestingly reinterpreted in terms of perspective over the body-part to be integrated, having 3PP for those cases in which the fake limb position violates constraints from 1PP, i.e., when the limb is outside the peripersonal space (Armell and Ramachandran, 2003; Lloyd, 2007) or in anatomically impossible configurations, e.g., at 180° (Ehrsson et al., 2004) and when handendness does not match (Tsakiris and Haggard, 2005). By doing this, the result is that all those cases in which the fake hand position violates constraints from 1PP have been found to work against the illusion, supporting the general conclusion that first person perspective is indeed a critical factor for eliciting the illusion of ownership over an external object. Analogously, studies focused on the full body ownership illusion showed that the illusion could not be induced in various configurations of 3PP, e.g., seeing the body laying in extrapersonal space (Petkova et al., 2011) or seeing the body located to the side in peripersonal space (as in our experiment 2). In both configurations, participants did not experience the illusion despite synchronous visuotactile stimulation and/or visual sensorimotor contingencies being provided.

A second group of studies reported, however, different conclusions on the role of visual perspective

in ownership illusions. Preston and Newport (2012) presented an experimental setting in which participants experienced an illusion over their own arm filmed from a distance of 2 m and displayed on a screen (the arm image in the video was also manipulated so to show it elongated). Similarly, a number of studies concern experimentally induced OBEs, in which participants experience self-identification with a virtual full-body seen from a 3PP (Lenggenhager et al., 2007, 2009; Aspell et al., 2009; Ionta et al., 2011). The resulting sense of ownership and touch experienced over a body located in far extrapersonal space is in contradiction with the results reviewed above.

How can these two classes of results be compatible with each other? A possible explanation that has been recently proposed (Petkova et al., 2011; Ehrsson, 2012) is that the self-identification experienced during OBEs is in fact a form of visual self-recognition rather than a somatic ownership illusion, similar to the experience of recognizing oneself in a mirror. An element in favor of this interpretation can be found in the seminal experiment from Lenggenhager et al. (2007), where the same stroking protocol was applied while visualizing either the filmed participant's body or that of a plastic mannequin. Although in both cases a significant difference was found among the synchronous and asynchronous stroking modes, the actual scores of the questionnaire item related to self-identification were lower in the mannequin condition (Lenggenhager et al., 2007—supporting online material). This seems to suggest that the self-identification actually occurred only for participant seeing their own filmed body, supporting the “self-recognition” hypothesis. On the other hand, there are several objective measurements that provide evidence for the back-stroking induced OBE to be an authentic somatic illusion. Participants experiencing this illusion seem to undergo a remapping of the visuotactile receptive field (RF) (Aspell et al., 2009) and of the self-location in an allocentric spatial reference frame (Lenggenhager et al., 2007, 2009). A selective activation of the TPJ analogous to that occurring in neurological OBEs (Ionta et al., 2011), and of bilateral PMC and medial sensorimotor cortex (Lenggenhager et al., 2011) have also been found. We suggest here that the full body ownership and the back-stroking OBE are in fact two different kinds of body illusions, which involve the activation of different neural patterns (see section 4.4). A rigorous comparison of the two illusions requires, however, a dedicated experimental set-up and is beyond the scope of this paper.

A recent study of patients with the somatoparaphrenic delusion of disowning their own left arm (Fotopoulou et al., 2011) provided further insights on the role of visual perspective. It showed that the disownership of the arm in these patients can be suddenly extinguished when the arm is seen from 3PP (in a mirror). Disownership was reinstated, however, a few seconds after switching again to a 1PP over the arm. These results seem to suggest that the sense of ownership requires the activation of a perceptual mechanism specific to 1PP that is impaired in somatoparaphrenic patients. When the perspective is switched to 3PP with the use of mirrors, the visual processing of the own body undergoes a spatial transformation, and it may no longer require the impaired mechanisms responsible for the perceived ownership/disownership. Given the prompt switching between the sense of ownership and disownership, when changing from 1PP to 3PP and vice versa, this mechanism is likely to be purely perceptual and bottom-up. We propose that a plausible candidate for this is provided by consistent visuoproprioceptive cues and by the resulting pattern of neural activation. We discuss this possibility in the following section as well as in section 4.4.

4.2. THE ROLE OF MULTIMODAL CONTINGENCIES

Results from experiment 1 showed that subjects in an immersive virtual environment may experience a sense of ownership over a highly realistic virtual body seen from a first person perspective, independently of the visuotactile and head-based visual sensorimotor cues received. This is supported from both questionnaire and HRD responses to the event disrupting the integrity of the whole virtual body; no significant differences between the four groups were found in either measurement. This suggests that, when the body is not moving, the effect of congruent visuoproprioceptive cues alone, as provided by having a high degree of spatial overlap between the physical body and the realistic virtual body, is a sufficient condition for inducing a full body ownership illusion. Since the ownership illusion occurs when there is congruent visuoproprioceptive feedback, for a static body, then it should be all the more powerful when there is additionally congruent visuomotor feedback—so that the virtual body moves synchronously with, and spatially matches, real body movements. Note that the requirement for a high degree of overlap between the physical and virtual bodies is a stronger constraint than 1PP by itself, so that it is possible to have 1PP and no congruent visuoproprioceptive cues at the same time. For example, one could have 1PP over a virtual body with a plausible body posture that is nevertheless different from the posture of the obscured physical body, or 1PP over a human-like body that have different size and/or body proportions with respect to the real body. While 1PP seems to be a necessary condition for experiencing an ownership illusion, other work seems to suggest that the exact position and posture of the real and virtual bodies (body parts) do not need to coincide in space (e.g., de la Peña et al., 2010; Petkova et al., 2011). Somatic illusions can be experienced in such configurations if additional congruent multisensory and/or sensorimotor cues are provided, and in these cases proprioception can be altered and shifted toward the virtual body, as shown by measurements of the proprioceptive drift in the RHI (e.g., Botvinick and Cohen, 1998) and OBEs (e.g., Lenggenhager et al., 2007), as well as reports of changes in the perceived body posture (de la Peña et al., 2010). With our experiment we have shown that when there is a high degree of overlap between the real and virtual body, the illusion can be experienced with no need for additional congruent multisensory and/or sensorimotor cues.

Our results further show that the illusion arising from having a high degree of spatial overlap between the virtual and physical bodies can be sustained, even when asynchronous visuotactile stimulation is delivered to the participants and in the absence of any other form of congruent multimodal stimulation. As a further interesting outcome, we found that having or not visual sensorimotor contingencies from head tracking affected the way participants perceived touch; in the group that received visual sensorimotor contingencies from head tracking throughout the experiment, the asynchronous visuotactile stimulation was not perceived as completely wrong, while when head movements were not allowed and the field of view was static the same visuotactile stimulation was clearly reported to be wrong. This is an important finding that clearly indicates that there is an interaction effect in the way these multimodal stimulations are processed, and that the way touch is consciously perceived can be modulated by the processing of other perceptual cues, possibly via the onset of the illusion.

Altogether, our results present various novel insights with respect to previous studies. In fact, it

has been extensively reported that the processing of congruent visuotactile and/or sensorimotor stimulation is a necessary condition for the experimental elicitation of bodily illusion in healthy subjects. This is the case for most of the reported experiences of extracorporeal object assimilation (Botvinick and Cohen, 1998; Schaefer et al., 2009; Guterstam et al., 2011) and of body deformation illusions (Lackner, 1988; Ehrsson et al., 2005; Schaefer et al., 2007; Newport and Preston, 2010; Normand et al., 2011; Kilteni et al., 2012; Preston and Newport, 2012), as well as of full body ownership and out-of-body illusions (Lenggenhager et al., 2007, 2009; Petkova and Ehrsson, 2008; Aspell et al., 2009; Ionta et al., 2011). In some cases, it has been noticed that incongruent multisensory information can be assimilated without destroying the illusion. For example, Slater et al. (2010) found that asynchronous visuotactile stimulation did not prevent a full body ownership illusion in an IVR setting where participants had 1PP over the virtual body and received visual sensorimotor congruent stimulation from head-tracking.

The first question that arises when comparing our results with those from previous studies concerns the reason why previous studies have repeatedly found that synchronous visuotactile (or head-based sensorimotor) stimulation was a necessary condition for eliciting a body ownership illusion, while we have found that this is not the case. There are two main points that may answer this question. First, the hypothesis that “the sole effect of congruent visuoproprioceptive cues, provided by a high degree of spatial overlap between the physical and virtual bodies, is a sufficient condition for inducing a full body ownership” has never been tested explicitly. The RHI paradigm intrinsically involved the use of visuotactile stimulation, with the control condition being the asynchronous mode rather than a “no touch” condition. This paradigm has been extended automatically to the case of full body illusions. In spite of this, it has been shown that the RHI can persist during period in which visuotactile stimulation was not delivered (Hohwy and Paton, 2010). The experimental design included nevertheless an initial phase of synchronous visuotactile stimulation that may have induced the illusion, which then persisted. Importantly, this experiment used stereo goggles that allowed a high degree of spatial matching between the real and virtual hands. In the same study, it was shown that after a period of synchronous visuotactile stimulation participants kept perceiving touch sensations when real touch was no longer delivered on the real hand, but appeared to be applied on the virtual hand. These findings are in perfect agreement with our results. Second, the reason for which other studies did not come to a similar conclusion can also be due to the fact that in most RHI experiments, apart from those using immersive stereo displays, the spatial locations of the real and artificial hand cannot perfectly coincide and consequently the visuoproprioceptive information provided is not fully congruent. It is interesting to note that all those experiments in which the ownership illusion was not disrupted by incongruent visuotactile stimulation (Hohwy and Paton, 2010; Slater et al., 2010; our experiment 1), used stereo vision, thus achieving a high degree of spatial overlap between the real and the virtual body (or body part) and, additionally, found that the asynchronous visuotactile information was not consciously perceived as wrong.

In order to have a unitary scenario that would allow the unification of the findings of different studies, we further need to address the following question: why other studies in which the physical and virtual bodies were highly spatially coincident (Petkova and Ehrsson, 2008; Petkova et al., 2011) found synchronous visuotactile stimulation to be necessary for the full body ownership illusion? To answer this question we move to the next section, where we discuss the role of the visual

appearance of the virtual body.

4.3. THE ROLE OF BODY APPEARANCE

We have explicitly explored the role played by bodily appearance in experiment 3. Previous studies have already shown that non-humanoid shaped objects fail to be integrated and assimilated as pertaining to one's own body. The RHI does not work when a wooden no-hand-shaped object is stroked synchronously with the real hand (Tsakiris and Haggard, 2005). Tsakiris et al. (2010) further extended this finding, pointing out the need for an object to preserve precise, informative corporeal structural features in order to be integrable as one's own body part. Analogously, full body ownership illusions, as well as experimentally induced OBEs do not work when substituting the virtual body with a wooden block having the same dimensions of the fake body (Lenggenhager et al., 2007; Petkova and Ehrsson, 2008). Our experiment went beyond this by testing whether the level of realism of a humanoid body could modulate the intensity of the ownership illusion, and whether it interacts with other factors, such as the provided visuotactile stimulation.

The results from our experiment showed that participants experienced on average significantly higher levels of illusion when seeing a virtual body with common human features in term of skin texture and clothes, compared to the condition in which they were seeing a plastic mannequin. Nevertheless, the view of human-shaped mannequin does not completely dampen the illusion, consistent with previous reports (Petkova and Ehrsson, 2008; Petkova et al., 2011). When compared with findings from previous studies, our results further suggest that there may be an interaction of the body appearance with the visuotactile component. When seeing a mannequin body, synchronous visuotactile stimulation is found to be necessary to induce a vivid full body ownership illusion (Petkova and Ehrsson, 2008; Petkova et al., 2011). At the same time we found that, when the realism of the body is enhanced, a vivid illusion can occur without the need for additional synchronous visuotactile stimulation. Moreover, the illusion was preserved also when incongruent visuotactile information was processed. This result supports the possibility of a top-down cognitive mechanism that modulates the way in which multisensory information is processed from the bottom-up perceptual stream. Our findings are in fact analogous to what has been established for the RHI: first the hand-object needs to pass a fitness test in terms of anatomical, volumetric and postural constraints (see Tsakiris et al., 2010 and reference therein). Once the fitness test is passed, other features enhancing the realism of the object to incorporate, e.g., the skin texture, can modulate the intensity of the illusion (Haans et al., 2008).

4.4. A BASIC MODEL FOR THE FULL BODY OWNERSHIP ILLUSION

In this section we sketch a speculative basic model for the neural underpinning of the full body ownership illusion on the basis of key findings from neurophysiological studies in the monkey. We first review the main relevant neurophysiological results that provide a rationale for the proposed model. Graziano et al. (2000) reported finding visuoproprioceptive bimodal neurons in the area 5

of the primate parietal cortex, whose properties are extremely relevant for the present discussion. These bimodal neurons respond to both the seen and the perceived (by proprioception) positions of a limb, even when the seen limb is fake. The first important property of such neurons is that they are sensitive to the visual content of the stimuli, so that their response is modulated by the position of an object in their visual RF only if the object contains the proper anatomical features of the limb that the same neurons encode by proprioception. Interestingly, the fake arm used in that study is extremely realistic, having been prepared by a taxidermist from a monkey of the same species. Visual and proprioceptive signals can be additive or may be combined in more complex fashion, according to the specific neuron. However, the overall averaged activity of this bimodal neuronal population shows a modulation associated with the relative positions of the fake and real arms, the activity being the highest when the locations of the two limbs are the closest. The third important property of such neurons is that their response is modulated by the relative position of the fake and real arms only when the fake arm location has a plausible position with respect to the rest of the body, meaning that no modulation was observed when the realistic fake arm was in a non-matching handedness position or in a backward orientation (with the hand being near the shoulder and the cut end extended outward). A further fundamental finding of the same study is the identification of a second population of trimodal neurons (responding to visual, tactile, and proprioceptive signals) in the same area 5. Neurons in this population encode the position of the real arm by proprioception, but not that of a just-seen fake arm; they become sensitive to the view of the fake arm only when the latter is stroked synchronously (but not asynchronously) with the real arm. Area 5 have been also found to host neurons with large RF, which can be bilateral and can involve multiple body parts (Iwamura et al., 1994; Iwamura, 1998), making them plausible candidates for encoding information about the whole body. Other higher-ordered somatosensory areas have been shown to host bimodal and multimodal neuronal populations with large and bilateral RF. These include the ventral intraparietal (VIP) area and a polysensory zone in the precentral gyrus, hosting bimodal visuotactile neurons, as well as trimodal neurons that additionally responds to auditory or vestibular stimuli (Duhamel et al., 1998; Bremmer et al., 2002; Graziano and Cooke, 2006). A more comprehensive review of the neurophysiological studies of body representation in the monkey brain, which are relevant for the study of human body perception is beyond the scope of this paper and can be found in Blanke (2012).

In the following we propose a speculative basic model for the full body ownership illusion, influenced by the numerous analogies between the findings from neurophysiological recording in the monkey discussed above and the results from the work done on experimentally induced bodily illusions, including the main results of the present study. The same model would apply for the RHI. We propose that distinct bimodal and multimodal neuronal populations are responsible for the ownership illusion. A driving population of bimodal visuoproprioceptive neurons, with properties analogous to those of area 5 neurons in the monkey, would yield the minimal contribution necessary for the illusion to occur. Other bimodal and multimodal populations would have instead a secondary modulating effect. The visuoproprioceptive population activates when the seen body looks similar to and is located close to the real hidden body (i.e., when highly congruent static visuoproprioceptive correlations are provided). As for area 5 neurons in the monkey, this population activates only when the virtual body satisfies the main basic anatomical constraints in terms of shape and visual perspective. The higher the spatial coincidence between the virtual and the real

body, the more intense would be the driven activity in this population and the resulting sense of ownership. Visuotactile, visual sensorimotor and other multimodal stimulations would trigger other bimodal and/or multimodal populations that have the effect of enhancing or dampening the sense of ownership, depending on whether they are delivered with proper correlations or not.

In this scenario we can isolate various steps for the “building-up” of an ownership illusion, encompassing most of the results that have been found in experimental studies on bodily illusions. If anatomical constraints are not satisfied in terms of body shape and visual perspective, no illusion occurs, because the driving visuoproprioceptive population is shut down, no matter whether other proper multimodal contingencies are provided. When anatomical constraints are satisfied, a high degree of spatial overlap between the virtual body and the real body could enhance the strength of the illusion. The additional contribution of the top-down effect from a high visual realism of the fake body could bring the illusion to saturation. In this condition, the reinforcing modulation of congruent multimodal correlations cannot be appreciated easily, because the illusion is already strong; moreover, the illusion can be sustained despite the dampening effect of incongruent multimodal stimulation (as in experiment 1), although severe and sustained incongruency could break the illusion completely. If anatomical constraints are met but the realism and colocation are not at a high degree, the driving visuoproprioceptive population will be activated, but with a moderate/low intensity that does not necessarily correspond to a perceptual illusion. In this condition, the modulating effects of additional multimodal stimulations can be critical for eliciting a vivid ownership illusion, when congruent, and more effective in breaking the illusion (if present), when incongruent [as in experiment 3, Petkova and Ehrsson (2008), and most of the RHI experiments].

In a recent review, Blanke (2012) has proposed that the changes in self-identification occurring during an OBE could correspond to changes in the size and position of the visual RFs of visuotactile trunk-centered neurons in VIP. Under the effect of synchronous back-stroking, these RFs would extend far enough to encode the fake body that comes to be part of the participant’s peripersonal space (Maravita and Iriki, 2004). An additional subpopulation of trimodal neurons integrating visuotactile and vestibular signals would instead be responsible for changes in self-location and visual perspective. Taken together, the basic model we propose here for the full body ownership illusion and the model proposed for OBEs in Blanke (2012), would provide an evidence for the two types of full body illusions to be different perceptual illusions with different underlying patterns of neural activation.

5. Conclusions

The aim of our study was to identify the main perceptual cues underlying the full body ownership illusion and to determine their role and mutual interaction in the elicitation of the illusion. We have selectively manipulated visuotactile and visual sensorimotor stimulation, visual perspective, and the appearance of the virtual body.

We have found that having a first person perspective is an essential condition for experiencing the sense of ownership over the virtual body. When 1PP is provided over a realistic virtual body with a

high degree of spatial overlap with the real body, the sole effect of congruent visuoproprioceptive cues can provide a sufficient condition for the illusion. In this condition, the additional contribution of congruent visuotactile and/or sensorimotor stimulation is indeed not necessary. Nonetheless, when the degree of spatial overlap (between the real and virtual body) and/or of the visual realism (of the fake body) is not high, congruent multisensory and/or sensorimotor cues are needed to trigger the illusion. In this case, such multimodal cues can be effective in both boosting the illusion, when congruent, and in suppressing it, when incongruent. We furthermore found that, when a high level of illusion is achieved by the synergic merging of various components, incongruent cues can be processed without breaking the illusion and can be perceived as not incorrect.

We discussed these findings showing that they are consistent with most of the previous results on part- and full-body ownership illusions. Motivated by a number of findings from neurophysiological recordings in the macaque monkey, we further propose a speculative basic model for the full body ownership illusion that accounts for most of the published results.

The present work advances our understanding of the critical mechanisms involved in the full body ownership illusion and provides useful implications for research in body-perception, self-consciousness, and numerous virtual reality applications.

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CHAPTER 3

THE SENSE OF BODY OWNERSHIP RELAXES TEMPORAL CONSTRAINTS FOR MULTISENSORY INTEGRATION

Related publication:

The sense of body ownership relaxes temporal constraints for multisensory integration.
Maselli, A., Kiltner, K., López-Moliner, J., and Slater, M.
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ABSTRACT

Experimental work on body ownership illusions showed how simple multisensory manipulation can generate the illusory experience of an artificial limb as being part of the own-body. This work highlighted how own-body perception relies on a plastic brain representation emerging from multisensory integration. The flexibility of this representation is reflected in the short-term modulations of physiological states and perceptual processing observed during these illusions. Here, we explore the impact of ownership illusions on the temporal dimension of multisensory integration. We show that, during the illusion, the temporal window for integrating touch on the physical body with touch seen on a virtual body representation, increases with respect to integration with visual events seen close but separated from the virtual body. We show that this effect is mediated by the ownership illusion. Crucially, the temporal window for visuotactile integration was positively correlated with participants' scores rating the illusory experience of owning the virtual body and touching the object seen in contact with it. Our results corroborate the recently proposed causal inference mechanism for illusory body ownership. As a novelty, they show that the ensuing illusory causal binding between stimuli from the real and fake body relaxes constraints for the integration of bodily signals.

1. INTRODUCTION

During body ownership illusions (BOIs) healthy adults experience artificial limbs or bodies as part of their own body representation. BOIs are thought to rely on the integration of synchronous but independent perceptual stimuli, for example visual stimuli seen on the dummy hand and tactile ones felt on the real hand in the case of the Rubber Hand Illusion (RHI) (Botvinik and Cohen, 1998). Similar multisensory manipulations have been shown effective to induce the illusion of ownership over supernumerary limbs (Folegatti et al., 2012; Newport et al., 2010; Guterstam et al., 2011) and artificial bodies (Petkova and Ehrsson, 2008; Maselli and Slater, 2013), demonstrating how our own-body perception relies on a plastic brain representation emerging from multisensory integration (Graziano and Botvinik, 2002; Takiris et al., 2010; Makin et al., 2008; Kilteni et al., 2015).

Evidence for the flexibility of this brain representation comes not only from vivid subjective reports about illusory ownership experienced over artificial limbs and full bodies, whose appearance can importantly deviate from the one of the real counterpart, e.g. in size (Kilteni et al., 2012; Pavani et al., 2007; van der Hoort et al. 2011), skin color (Farmer et al. 2012; Peck et al., 2013), age (Banakou et al., 2013) and realism (Bertamini and O'Sullivan 2014; Martini et al., 2015). This flexibility is also robustly supported by a number of short-term modulations of behavior and physiological states. As representative examples, it has been reported that during a RHI the temperature of the “substituted” hand drops (Moseley et al., 2011) together with its tactile sensitivity (Moseley et al., 2011; Zopf et al., 2011; Zeller et al., 2014), and that histamine reactivity to noxious stimuli increases (Barnsley et al., 2011). On the behavioral side, it was shown, for example, how experiencing ownership over a dark-skin body can reduce implicit racial-bias (Peck et al. 2013; Maister et al., 2013), or how ownership over a child body can affect size perception and induce implicit attitude changes (Banakou et al., 2013). These are just some examples of the profound impact on self-perception and behavior that can occur during body ownership illusions, over time scales of few tens of seconds.

Multisensory integration has been at the core of research into body ownership illusions since their first reports (Botvinik and Cohen, 1998; Graziano and Botvinik, 2002), and is indeed regarded as the basic causal mechanism for their emergence (Makin et al., 2008; Tsakiris 2010; Ehrsson 2011). However, the converse has not been previously studied, which is concerned with how BOIs modulate the processing and merging of cross-modal stimuli. On the other hand, extensive research in multisensory perception shed light over the intrinsic flexibility of multisensory integration processing, which allows adapting efficiently to the continuously changing environment. In this study we face this gap and explore potential effects of ownership illusions on multisensory processing.

Integrating the different multimodal signals streaming from an object or an event is essential for having a coherent and meaningful perceptual experience, but this is not a straightforward task for the central nervous system (CNS). In fact, due to differences in transduction and transmission characteristic times, the temporal lag for a signal to trigger a response in the corresponding primary sensory cortex can significantly vary across modalities. For example, due to the long transduction time of photoreceptors (Kuffler et al., 1953) , which is longer with respect to that of tactile receptors,

a truly synchronous visuotactile event typically triggers activity in SI in advance with respect to activity triggered in V1. Furthermore, the relative delay can change importantly according to the lighting conditions and the ambient temperatures that affects transduction (Barnett-Cowan and Harris, 2009), and also depending on the body part that is touched, which affects transmission time of tactile stimuli (Harrar and Harris, 2005). Therefore, in order to assure a coherent perception of the environment, the CNS has to flexibly compensate for such differences by modulating the temporal window on which multisensory integration is effective (Kopinska and Harris, 2004; Harris et al., 2010; Keetels and Vroomen, 2012). One of the factors that efficiently modulates the temporal window for multisensory integration is “causal binding”, also referred to as “unity assumption”. Having implicit knowledge of the existence of a common origin for two sensory signals was indeed shown to facilitate integration. In the case of audiovisual speech perception, larger temporal lags are indeed tolerated (perceived as synchronous) under the assumption of a common cause for the visual and auditory signals (Vatakis and Spence, 2007).

In the light of the results discussed, we argue that body ownership illusions could act as a “causal binding” factor for stimuli seen on the fake body and independent somatosensory signals, and therefore that BOIs could modulate multisensory processing. As a further support to this proposal, a number of studies showed that, during BOIs, visual threats to the artificial body trigger enhanced neurophysiological correlates of anxiety (Armel and Ramachandran, 2002; Ehrsson et al., 2004) thus revealing how visual stimuli on the fake body are processed as if seen on the own physical body. In the present work, we focus on the temporal constraints for visuotactile integration. We specifically hypothesized that, during the illusion, there is an expansion of the temporal window within which visual (on the fake body) and tactile (on the physical body) stimuli are perceived as simultaneous.

To test this hypothesis we performed two experiments. In Experiment 1, we assessed whether the assumption of a common origin – for a tactile stimulus and a correspondent visual cue on the fake body – could expand the temporal window of integration in the visuotactile domain, similarly to what has been found for the audiovisual domain (Vatakis and Spence, 2007; Vatakis et al., 2008). In Experiment 2, we tested whether this “causal binding” effect emerges as a consequence of the body ownership illusion itself.

We relied on a temporal order judgment (TOJ) task as an established procedure to estimate the temporal window of integration. In TOJ tasks, pairs of target stimuli with varying temporal separations (typically referred to as Stimulus Onset Asynchrony – SOA) are presented to participants that have to judge which stimulus came first. The analysis of how responses vary across the tested range of SOAs, allows estimating two main quantities of interest: the Point of Subjective Simultaneity (PSS) – a measure of the average time one stimulus has to precede the other in order for the two to be perceived as simultaneous (Shore et al., 2001; Kennett et al., 2001) – and the Just Noticeable Difference (JND) – a measure of the temporal window in which the two stimuli are perceived as simultaneous (Yamamoto and Kitazawa, 2001; Shore et al., 2005; Gallace and Spence, 2005). In particular, for a multimodal TOJ task, the JND can be regarded as a proxy for the temporal window of multisensory integration (Vatakis and Spence, 2007; Mégevand et al., 2013; Vroomen and Keetels, 2010), and as such it is the quantity of interest for the current

study.

Figure 1: Experimental setup. (A) Participants performed a visuotactile Temporal Order Judgment (TOJ) task, while wearing head-mounted display. (B) Piezoelectric motor used to deliver vibrotactile stimuli. The visual stimulus was a 50 ms rotation of a virtual geared-wheel: the geared-wheel was seen (C) in contact with the virtual finger (Exp. 1: Touch condition; Exp. 2: Body condition), (D) separated from the virtual finger (Exp. 1: No-Touch condition) or (E) touching a wooden stick (Exp. 2: Stick condition). The 3D graphics elements were designed with Autodesk® 3ds Max® and controlled through the Unity® software platform.

We implemented a visuotactile TOJ task that participants had to perform while wearing a head-tracked head-mounted display (HMD) streaming a digital 3D replica of the experimental room. When looking down towards their real occluded body, participants could see either a virtual body or two wooden sticks, depending on the experimental condition. Participants performed the TOJ task while resting their arms on a Table (Fig. 1A). The tactile stimulus was a 50 ms vibration delivered to the right index fingertip. The visual stimulus was a rotation (50 ms duration) of a virtual geared-wheel

(Supplementary Video S1¹). For further details on the TOJ task implementation and on methods for estimating the JNDs, we refer the reader to Materials and Methods.

In Experiment 1, we explicitly manipulated the causal relationship between the visual and tactile stimuli. Participants had a first person perspective over a gender-matched virtual body that was spatially coincident with their real body. This configuration is known to be sufficient for inducing an ownership illusion through congruent visuo-proprioceptive cues (Maselli and Slater, 2013, 2014). Participants performed the TOJ task in two conditions: the geared-wheel was seen either in contact with the index finger of the virtual body (*Touch*) (Fig. 1C) or separated from it by 6 mm (*No-Touch*) (Fig. 1D, Supplementary Video S1¹).

In Experiment 2, we tested whether this illusory “causal binding” is mediated by the ownership illusion. Participants performed the TOJ task in two conditions with different manipulations of illusory body ownership. One condition (*Body*) was the same as the *Touch* one in Experiment 1 (Fig. 1C). In the other (*Sticks*), the sense of ownership was inhibited by displaying two wooden sticks placed on the Table and spatially coincident with the arms of the participants during the TOJ task, with the tip of the right stick being in touch with the geared-wheel (Fig. 1E, Supplementary Video S1¹). This manipulation of the shape of the virtual body was used since successful induction of a BOI requires that the fake body or body part should have a humanoid shape (Petkova and Ehrsson, 2008; Tsakiris et al., 2010).

Tag	Questionnaire Item
<i>Ownership</i>	During the temporal order judgment task I felt as if the <i>virtual hand</i> (stick) I was looking at was my own hand
<i>Touch</i>	During the temporal order judgment task I felt as if my right index finger was touching the virtual wheel
<i>Cause</i>	During the temporal order judgment task I felt as if the rotation of the virtual wheel produced the tactile stimuli on my finger
<i>Move</i>	I felt as if the <i>virtual arms</i> (sticks) were following the movements of my own arms
<i>Ctrl</i>	I felt as if I had two right hands

Table 1: Questionnaire items. The Table lists the six items presented to participants at the end of each experimental session. The items were presented in a randomized order across participants and experimental conditions. Participants had to indicate their level of agreement with each of the statement, on a Likert scale from - 3 to 3. The text in parentheses was used to replace the italic text in the Stick condition in Experiment 2.

¹ Supplementary videos can be found at: <https://www.nature.com/articles/srep30628#supplementary-information>

A six-item questionnaire, presented at the end of each experimental session, was administered to assess the subjective illusory experience (Table 1). Each item was scored on a -3 to +3 Likert scale, according to the level of agreement with the statement.

2. RESULTS

In Experiment 1 we expected to find higher JND in the *Touch* condition, because seeing the virtual finger touching the moving geared-wheel during an ownership illusion should provide hints for a common origin of the two target stimuli. This was indeed the case for 10 out of 14 subjects, with an average JND difference across conditions of 46 ms (Fig. 2A, B). Data from all 14 participants were analyzed using a Generalized Linear Mixed Model (GLMM). The GLMM analysis revealed a significant difference across conditions in the slopes of the fitted psychometric curves ($p < 0.0001$). Corresponding bootstrap estimates of the JNDs were 155 ms (95% CI = 142 to 168 ms) and 127 ms (95% CI = 117 to 136 ms) in the *Touch* and *No-Touch* conditions respectively (Fig. 2C).

Results from the subjective scores to the six-item questionnaire are summarized in Table 2. Participants reported a strong illusion of virtual body ownership (median scores of 2) in both conditions ($p > 0.48$). The feeling that the wheel was directly touching their finger was positively reported only in the *Touch* condition ($p = 0.002$; median scores of 1.5 for *Touch* and -3 for *No-Touch*). Consistently, the feeling of the virtual wheel being the origin of the vibrotactile TOJ cues was higher in the *Touch* condition (median scores of 1 for *Touch* and -0.5 for *No-Touch*), although the difference between conditions did not reach the significance level ($p = 0.06$). These results support our hypothesis that the illusory experience of touching the virtual wheel acts as a “causal binding” factor, expanding the temporal window for visuotactile integration.

Table 2: Questionnaire Results

Experiment 1					
Item	Touch	No-Touch	Touch - No-Touch	p-value	PS _{dep}
Ownership	2 (1)	2 (1.5)	0 (0.75)	0.48	0.53
Touch	1.5 (4.5)	-3 (1)	2.5 (3.75)	0.002	0.96
Cause	1 (2)	-0.5 (4.5)	1 (3)	0.06	0.75
Move	3 (1)	3 (1)	0 (0.75)	0.78	0.46
	-3 (1.75)	-3 (0)	0 (0.75)	0.10	0.64
Experiment 2					
Item	Body	Stick	Body - Stick	p-value	PS _{dep}
Ownership	2 (1)	-2 (3)	3 (4)	0.005	0.84
Touch	1.5 (3)	-2 (3.75)	1.5 (3)	0.01	0.79
Cause	1 (1.75)	1 (3.5)	0 (1.75)	0.12	0.61
Move	3 (1)	-3 (1.75)	5 (2)	0.001	0.06
Ctrl	-3 (0)	-3 (0)	0 (0)	0.58	0.50

Figure 2: Results from Experiment 1. (A) Boxplot showing the distribution of JND estimates from individual fits in the two experimental conditions; JND estimates from single subjects are overplotted as scatter points. (B) Boxplot showing the distribution of JND differences in the two conditions ($\Delta JND = JND_{Touch} - JND_{No-Touch}$), estimated from individual fits; ΔJND for single subjects are overplotted as scatter points. For 10 out of 14 participants the JND was higher in the Touch condition. The mean value of individual ΔJND was 46.6 ms. (C) JNDs estimates ($n = 14$) from Generalized Linear Mixed Model (Bootstrap method) were equal to 127 ms and 155 ms in the No-Touch and Touch conditions respectively. Vertical bars represent the 95% CI estimated with the bootstrap method. GLMM analysis revealed a significant difference in across conditions ($p < 0.0001$).

Figure 3: Results from Experiment 2. (A) Boxplot showing the distribution of JND difference in the two conditions ($\Delta JND = JND_{Body} - JND_{Sticks}$), estimated from individual fits; ΔJND for single subjects are overplotted as scatter points. For 11 out of 14 participants the JND was higher in the Body condition. The mean value of individual ΔJND was 16.3 ms. (B) JNDs estimates ($n=14$) were equal to 127 ms and 155 ms in the Stick and Body conditions respectively. Vertical bars represent the 95% CI estimated with the bootstrap method⁶⁷. GLMM analysis revealed a significant difference across conditions ($p=0.011$). (C) JND estimates from individual fits are plotted as a function of subjective scores given to the “Ownership” (left panel), “Touch” (central panel), and “Cause” (right panel) questionnaire items (full statements listed in Table 1), together with the robust linear fits and associated 95% CIs. Spearman correlation analysis revealed significant positive correlations for the three cases.

In Experiment 2 we explicitly manipulated illusory body ownership to test the hypothesis that the illusion itself mediates the “causal binding” effect observed in Experiment 1. Results from the subjective scores to the questionnaire items are summarized in Table 2. Participants experienced a strong sense of ownership only in the Body condition (median scores of 2 for Body and -2 for Stick; $p=0.005$). Analogously, the reported sensation of touching the geared-wheel (touch item) was high

only for the *Body* condition (median scores of 1.5 for *Body* and -2 for *Stick*; $p=0.01$). Contrary to our expectation, this was not reflected in a significant difference for the reported sensation that the geared-wheel was the cause of the vibrotactile stimuli during the TOJ (cause item: $p=0.12$).

Importantly, for 11 of the 14 participants the JND was larger in the *Body* condition, with an average JND difference across conditions of 16 ms (Fig. 3A). Analysis of the 14 subjects performance using GLMM showed a significant difference across conditions for the fitted slope of the psychometric curves ($p=0.011$), with bootstrap estimates of the JNDs being 117 ms (95% CI=95–131 ms) and 105 (95% CI=83–118 ms) in the *Body* and *Sticks* conditions respectively (Fig. 3B). Crucially, the JND was positively correlated with subjective scores rating the sense of ownership ($r_s=0.41$, $p=0.033$), the illusory sensation of touching the geared-wheel ($r_s=0.46$, $p=0.014$), and of the geared-wheel being the cause of the vibrotactile target cues ($r_s=0.46$, $p=0.014$) (Fig. 3C). This latter result may seem at odd with the unexpected lack of significant difference across conditions in the cause item scores. In fact, according to the rationale of our hypothesis, the illusion of ownership (triggered by the view of the spatially overlapping virtual body and reinforced by synchronous visuomotor stimuli) would generate the illusion of touching the virtual geared-wheel. This illusory touch would then trigger the illusory experience of the geared-wheel being the origin of the vibrotactile stimuli and in turns would relax temporal constraints for visuotactile integration (measured in terms of JNDs).

Results from Experiment 2 thus support our hypothesis, indicating that the effect of “causal binding” on the temporal window of visuotactile integration revealed in Experiment 1 is selectively mediated by the sense of ownership experienced toward the virtual body.

Taken together results from Experiment 1 and 2 highlight the reciprocal connection between multisensory integration and body ownership: multisensory integration builds the body ownership illusion, while the illusion, once induced, modulates subsequent multisensory processing.

3. DISCUSSION

Spatiotemporal correlations of concurrent stimuli from different sensory channels and the motor system provide an essential contribution to self-perception and self-recognition (Gibson, 1986; van den Bos and Jeannerod, 2002; Rochat, 1998). Experimental protocols for ownership illusions rely on this principle: the spatiotemporal congruence of cross-modal bodily signals triggers the integration of truly independent stimuli, giving rise to the illusory experience that an external object is part of the own-body (Maselli and Slater, 2013; Makin et al., 2008; Ehrsson 2010; Botvinik 2004).

Here we provide novel experimental evidence that illusory ownership modulates multisensory integration. The results of the two experiments combined show that during the illusion the temporal window for visuotactile integration of body related cues expands. In the first experiment, we induced an ownership illusion over a virtual body so to be able to dissociate visual and tactile bodily signals: participants could see a rotating geared-wheel in touch or not with the virtual finger while

receiving tactile stimuli on the real fingertip. When the finger was seen in touch with the moving object, the estimated temporal window for visuotactile integration was wider. This showed that when pairs of visuotactile bodily stimuli are attributed to the same cause, the temporal constraints for their integration get relaxed.

An alternative interpretation would be that visuotactile integration is inhibited in the *No-Touch* condition because of the spatial offset between visual and the tactile stimuli. While in the *Touch* condition the visual and tactile stimuli were aligned in space, in the *No-Touch* condition a small offset (6 mm) was introduced between the two, as the virtual finger was slightly displaced (with respect to the real one) so to be seen separated from the virtual wheel. Previous studies have shown that the perceived distance between target-stimuli can significantly affect TOJ performances, with better performances found for more distant stimuli (Shore et al., 2005; Shore and Spence, 2005). Notwithstanding, in our case the change in distance between the visual and tactile stimuli across conditions was extremely small, and of the same order of magnitude of the intrinsic precision of the hand position sense (van Beers et al., 1998). Therefore the introduced offset should not significantly affect the perceived location of the tactile stimuli, remapped in external space towards the location of the slightly displaced virtual finger. It is worth noticing that previous studies reported changes in JND, as estimated from TOJ performances, of the order of 10 ms for an actual change in the target-stimuli distance of about 1 m (Shore et al., 2005), while here we found a change in JND almost three times larger for an actual change in distance of just 6 mm. We can therefore conclude that the change in JND we found is not an effect of different displacements between target stimuli, but is instead due to the illusory causal binding elicited in the *Touch* condition and absent in the *No-Touch* condition.

In the second experiment, we manipulated illusory body ownership to show that the effect of causal binding observed in Experiment 1 is selectively modulated by the sense of ownership. We found that, if the sense of ownership is inhibited (by showing a wooden stick instead of the virtual hand touching the geared-wheel) the temporal window for visuotactile integration is indeed smaller with respect to the case in which the body ownership illusion was strong.

All together, results from our two experiments suggest that the relaxation of temporal constraints for multisensory integration observed in body ownership illusions is driven by a causal mechanism that binds together visual stimuli on the fake body and tactile stimuli on the physical body.

Interestingly, our results could explain why participants undergoing an intense ownership illusion fail to notice asynchronies in visuotactile stimulation that are otherwise (in the absence of the illusion) detected (Maselli and Slater, 2013). Furthermore, the present results provide robust experimental support to previous proposals suggesting that the illusion can be sustained despite exposure to asynchronous visuotactile stimulation (Maselli and Slater, 2013; Kiltner et al., 2015).

Our results fit well within the framework provided by Bayesian causal inference models for illusory ownership (Kiltner et al., 2015; Samad et al., 2015). According to such models, the illusion arises when the brain associates a higher than chance probability to the existence of a single cause (the own-body) for all the incoming sensory input: the visual from the fake body and the somatosensory/motor from the physical body. Importantly, the causal inference approach predicts that, under the assumption of a common cause, the integration of cross-modal sensory stimuli is facilitated

(Körding et al., 2007; Shams and Beierholm, 2010; Parise et al., 2012). This prediction is indeed corroborated in the present study that showed facilitation in terms of an expanded temporal window for visuotactile integration.

The influence of causal binding on temporal aspects of multisensory perception has been previously reported. In the audiovisual domain, similar expansions of the temporal window of integration have been found, but only for functionally relevant stimuli such as speech (Vatakis and Spence, 2007; Vatakis et al., 2008). Similarly, intentional binding – a form of causal binding manipulated through voluntary motor actions – has been shown to anticipate the conscious perception of auditory stimuli (Haggard et al., 2012) and to suppress color-motion asynchronies (Corveleyn et al., 2012), otherwise observed in the perception of truly simultaneous changes in the color and position of an object (Moutoussis and Zeki, 1997). These results highlight the predictive nature of causal binding effects: predictions are indeed an intrinsic component of both voluntary motor control (Wolpert et al., 1995; Blakemore et al., 1999) and speech perception (Peelle, J. E. & Sommers, 2015). In line with these findings, our results suggest that the sense of body ownership involves predictive cause-effect mechanisms that shape the processing of bodily signals during body-environment interactions. Notably, we show that such predictive mechanisms, which have the functional role of preserving and guiding the physical body through the environment (Graziano and Cooke, 2006), are operating likewise during body ownership illusions.

The modulation of visuotactile processing reported in this study relies probably on the same mechanisms for simultaneity constancy, which allows correct perception of truly synchronous cross-modal stimuli despite intrinsic differences in their processing latencies (Harrar and Harris, 2005; Kopinska and Harris, 2004). Mechanisms suggested for such temporal compensation, including sliding temporal binding windows (Sugita and Suzuki, 2003) or temporal ventriloquisms (Morein-Zamir et al., 2003), provide phenomenological descriptions but hardly insights into their neurophysiological basis. Although indirectly, our results provide support for a top-down modulation of multimodal neurons processing bodily signals (Graziano and Botvinick, 2002; Huang et al., 2012), and strongly indicate that such modulation can happen on the short time-scale of few tens of seconds.

In conclusion, our results provide experimental evidence that body ownership illusions affect multisensory integration. We have shown that, by establishing a causal link between the fake and physical bodies, the sense of body ownership enhances the temporal flexibility of visuotactile integration. This adds an important contribution to previous results on the sense of body ownership and ownership illusions. It was known that short periods of conflictive multisensory stimulations can induce dramatic illusory changes in our own-body representation, with important consequences at physiological (Moseley et al., 2008; Barnsley et al., 2011), psychological (Osimo et al., 2015) and behavioral (Peck et al., 2013; Banakou et al., 2013) levels. Here we show that changes occur also at the level of basic processing of multisensory information, which is relevant for the interaction of the body with the environment. Furthermore, these results demonstrate how the sense of body ownership guarantees a flexibility in visuotactile integration that goes beyond what is required in our normal daily experience where visual and tactile stimuli from the body are locked in space and time.

4. MATERIALS AND METHODS

4.1. PARTICIPANTS

Fourteen healthy subjects (8 female; mean age $\pm$ SD: 20.7 ± 2 years) took part in Experiment 1 and another fourteen in Experiment 2 (8 female; mean age $\pm$ SD: 21.6 ± 4.6). No participant had a history of neurological disease and all had normal or corrected-to-normal vision. They signed an informed consent form and received 10 euros as compensation. The experimental protocol was approved by the “Ethical Committee for research” of the University of Barcelona, in line with the institutional ethics and national standards for the protection of human participants.

4.2. EXPERIMENTAL SETUP

Participants sat in front of table where a coin-vibrator was placed along the participant’s sagittal plane (Fig. 1A). A wide field-of-view, stereo head-tracked, head-mounted display (HMD) was used to stream in 3D a virtual reproduction of the experimental room. By moving their head, participants could explore the environment. According to the experimental condition, when looking down towards their own body participants saw either a gender-matched virtual body from a first-person-perspective and spatially coincident with their physical body, or two virtual sticks placed on the table. Participants’ head and arms movements were tracked via a combination of infrared cameras and inertial devices. Vibrotactile stimulations were delivered via the coin-vibrator (Fig. 1B) controlled through an Arduino board.

4.2.1 MATERIAL AND EXPERIMENTAL SETUP

The virtual scenario was programmed with the Unity® software platform, using 3D graphics elements designed with Autodesk® 3ds Max®. The head mounted display has a $102^\circ\text{H} \times 64^\circ\text{V}$ total field-of-view, 1280×1024 resolution per eye and 60 Hz frame rate. The coin-vibrator used to deliver vibrotactile stimuli has the following specifics: 0.78 cm^2 , 3V, 100mA, 50Ω , 1200 ± 300 r.p.m. The table was high enough (94 cm) to avoid participants having to bend their neck down during the temporal order judgment (TOJ) task (Figure 1A). The coin-vibrator was placed along the participant’s sagittal plane at 24 cm from the table edge.

4.2.2 SYSTEM CALIBRATION

An oscilloscope (HAMEG Instruments) was used to measure the relative latencies of the visual and tactile target cues in the TOJ task, and to verify their effective duration (50 ms). When triggered at the same timeframe from the Unity® software script, the presentation of the visual cue on the HMD had a 30 ms time lag with respect to the onset of the vibration. This delay was compensated ad hoc in the Unity® script, so that the coded stimulus onset asynchrony (SOA) was precisely controlled.

4.3. TEMPORAL ORDER JUDGMENT (TOJ) TASK

The TOJ task consisted in a forced choice discrimination of the temporal order of two target cues.

The tactile one was a 50 ms long vibrotactile stimulus (single burst) delivered on the fingertip of the right index by a piezo-electric motor (0.78 cm^2 , $1200 \pm 300\text{ r.p.m.}$). The visual cue consisted in a 50 ms long rotation of a virtual geared-wheel object about its axis (Supplementary Video S1²). A complete session included 200 trials spanning a SOA range of $[-600, 600]$, sampled at $\{\pm 600, \pm 300, \pm 200, \pm 80\}$ ms. Each trial was presented 1200 ms after receiving the participant's response to the previous trial. The visual and tactile stimuli were spatially aligned in external space in all conditions but the *No-Touch* one in Experiment 1. In the latter case, the rotating wheel was seen slightly displaced from the virtual finger (6 mm), so that a small offset was introduced between the visual and tactile TOJ target-cues. This was implemented by slightly displacing the right virtual arm, during the TOJ, so that the tip of the virtual index was 6 mm away from the tip of the real index in the direction of the interphalangeal joint. During the task participants were instructed to keep their arms and head still, and fix their gaze on a blue dot displayed on the geared-wheel (Fig. 1C–E; Supplementary Video S1²). They used two pedals to provide responses.

4.3.1 SOA SAMPLING

The TOJ task consisted of 200 trials spanning a SOA range of $[-600, 600]$ ms and sampled at $\{\pm 600, \pm 300, \pm 200, \pm 80\}$ ms, with associated sampling frequency of $\{10, 20, 30, 40\}$. The SOA order was arranged in 10 cycles of 20 trials each; each cycle included all the sampled SOA values, one to four times according to their corresponding sampling frequency. Trials within each cycle were presented in a random order, independently for each subject and condition.

4.4. PROCEDURE

Participants wore the HMD and headphones streaming white noise. First, they familiarized with the environment and performed a TOJ training session (25 trials). Next, they underwent two experimental sessions, counterbalanced across participants. The 200 TOJ trials were presented in blocks of 25 trials, alternated with breaks in which participants were asked to mark with their hands the position of a cross appearing on the table at different positions (Video S2²). In all conditions, but *Stick* in Experiment 2, the virtual body moved along with the participants tracked-movements. These breaks were included to make participants move their head and arms, so to relax tension and to keep high the sense of body ownership through congruent visuomotor correlations (Kokkinara and Slater, 2014). Each session had an average duration of 18 minutes. After its completion, participants filled a 5-item questionnaire customized to assess different aspects of the subjective illusory experience (Table 1).

4.5. ANALYSIS

Questionnaire scores across conditions were compared with the Matched-pairs Wilcoxon tests, and the associated effect size was quantified in terms of “probability of superiority” of dependent measures, PS_{dep} , (Grissom and Kim, 2012).

2 Supplementary videos can be found at: <https://www.nature.com/articles/srep30628#-information>

TOJ responses, from each subject and condition, were converted into probabilities of “touch-first” response, $P(Y_j)$, at each SOA point tested. These values were next fitted with a psychometric curve of the form:

$$P(Y_j) = \phi(\beta_0 + \beta_1 \times SOA)$$

where $\phi(\cdot)$ denotes the probit function. The temporal window of integration was then estimated in terms of the Just Noticeable Difference (JND), by definition proportional to the inverse of the slope, β_1 , and corresponding to the 75% threshold in the probability distribution (Moscatelli et al., 2012).

These fits provided the individual JND estimates adopted in the correlation analysis and used to generate the boxplots in Figs 2A,B and 3A. Correlations among questionnaire scores and individual JND estimates were assessed in terms of Spearman rank coefficients.

At the group level, TOJ data were analyzed with a Generalized Linear Mixed Model (GLMM) that extends model (1) to include fixed effects associated to the experimental manipulation, and random effects associated to the variability within and between subjects (Agresti, 2002). The advantage of GLMMs with respect to group analysis based on parameters extraction from single subject fits, is that they take into account both inter and intra subject variability and have a higher statistical power (Agresti, 2002). Estimates of the JNDs and the associated 95% CIs were computed with the bootstrap method (Agresti, 2002). Statistical analysis was performed in R. The GLMM analysis was performed using the glmer function from the lme4 R package (Bates et al., 2015).

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CHAPTER 4

THE BODY FADES AWAY: INVESTIGATING THE EFFECTS OF TRANSPARENCY OF AN EMBODIED VIRTUAL BODY ON PAIN THRESHOLD AND BODY OWNERSHIP

Related publication:

The body fades away : investigating the effects of transparency of an embodied virtual body on pain threshold and body ownership.

Martini, M., Kiltner, K., Maselli, A., and Sanchez-vives, M.V.
Sci. Rep. 5, 13948, 2015

ABSTRACT

The feeling of “ownership” over an external dummy/virtual body (or body part) has been proven to have both physiological and behavioural consequences. For instance, the vision of an “embodied” dummy or virtual body can modulate pain perception. However, the impact of partial or total invisibility of the body on physiology and behaviour has been hardly explored since it presents obvious difficulties in the real world. In this study we explored how body transparency affects both body ownership and pain threshold. By means of virtual reality, we presented healthy participants with a virtual co-located body with four different levels of transparency, while participants were tested for pain threshold by increasing ramps of heat stimulation. We found that the strength of the body ownership illusion decreases when the body gets more transparent. Nevertheless, in the conditions where the body was semi-transparent, higher levels of ownership over a see-through body resulted in an increased pain sensitivity. Virtual body ownership can be used for the development of pain management interventions. However, we demonstrate that providing invisibility of the body does not increase pain threshold. Therefore, body transparency is not a good strategy to decrease pain in clinical contexts, yet this remains to be tested.

1. INTRODUCTION

Visual feedback has been shown to effectively modulate pain sensations in experimental studies with both healthy participants and chronic pain patients (Martini et al., 2013; McCabe, 2002; Ramachandran and Altschuler, 2009; Hoffman et al., 2011). In particular, there is increasing evidence from pain studies showing how vision of the body may lead to effective pain relief (Longo et al. 2009; Mancini et al. 2011; Hegedüs et al., 2014; Martini et al., 2014; Romano and Maravita, 2014; Siedlecka et al., 2014). For instance, in a seminal study by Longo and co-workers, it was shown that the vision of one's hand produces analgesic effects compared to when the gaze is oriented toward an object or another's hand (Longo et al. 2009). In the same study the authors demonstrated that the attenuated behavioural response was paralleled by a significant decrease in the brain response elicited by the nociceptive stimuli. Further experimental research has confirmed that there is an effective interaction between the vision of the body and the sensation of pain. For example Mancini and co-workers demonstrated that the visual size of someone's own hand manipulated through mirrors leads to modulation of the pain threshold. In particular these authors reported that the vision of a smaller hand seen through a concave mirror leads to a higher pain threshold, while the vision of a bigger hand through a convex mirror decreases pain perception (Mancini et al., 2011). The rubber hand illusion provided researcher with a paradigm to experimentally induce illusory ownership of external body parts, so that the fake limb is felt as belonging to one's body (Botvinick and Cohen, 1998). However, there are contradictory findings regarding whether looking at an owned rubber hand is analgesic or not. Recently, it has been reported that the analgesic effect of looking at one's own hand is not present when looking at an owned rubber hand (Mohan et al., 2012). However, a subsequent study using a similar paradigm found the opposite results, with an effect comparable to that obtained by the vision of the real limb (Hegedüs et al., 2014). Moreover, further experimental evidence has shown how the analgesic effect of looking at one's own body is present also when the painfully-stimulated volunteer is looking at an avatar's limb, provided that this is felt as her/his own (Martini et al. 2014). Furthermore, the vision of dynamic colour changes applied to the skin of the owned avatar's limb modulates pain threshold with heat stimuli such that a reddish skin colour leads to lower threshold compared to the vision of a bluish one (Martini et al., 2013). Hansel and co-workers reported that during an out-of-body experience, an increase in the self-identification with an avatar's body seen in front of the participant is associated with an increase in pressure pain threshold (Hänsel et al., 2011). Lately, following a similar paradigm, Romano and colleagues reported a reduced skin conductance response to painful stimuli when participants saw and identified themselves with the avatar body displayed in front of them (Romano et al., 2014). All of these studies provide interesting insights on how the vision of the body can play a major role in the modulation of pain perception.

Body-related visual feedback is known to produce analgesic or pain relief effects in clinical populations as well. The experience of a phantom limb, typically reported by amputees, is often accompanied by painful sensations that are elicited or exacerbated by different physical and psychological factors (Flor, 2002). Phantom limb pain has been treated by means of mirror therapy, where the patient can see an intact limb at the location where the phantom limb is felt to be, thus providing an illusory visual feedback that the lost limb is still there (Ramachandran and Altschuler, 2009). Also, it has been

shown that viewing one's painful limb as becoming smaller decreases the pain related to that limb (Moseley et al., 2008). The same manipulation though has been shown to lead to the opposite effect in healthy participants (Mancini et al., 2011), probably due to the different clinical conditions.

While the effects related to the vision of the body are classically related to dichotomous body versus no-body paradigms, namely to seeing or not seeing the body part, it remains unknown whether and how different levels of visibility of the body could affect pain perception. One could hypothesize that the vision of a body that fades away could increase analgesia by perceiving one's own body as less likely to be harmed by the painful stimulus because it is fading away, or, conversely decrease analgesia due to the analgesic effect of the vision of the body (Longo et al., 2008; Hegedüs et al., 2014; Martini et al., 2014). Therefore an investigation on the effects of body transparency is needed. However, from a technical point of view, rendering a visible object "transparent" or "semi-transparent" is not trivial. For instance, paradigms relying on visual masking (Breitmeyer and Ogmen, 2000) or on binocular rivalry (Arnold et al., 2007) provide only transient illusions and do not really offer valid solutions to make solid, non-transparent matter invisible. Also, these techniques usually use simple visual cues rather than complex physical entities such as human bodies. Immersive Virtual Reality (IVR) technology represents an effective tool as it allows the creation of sensory environments that can be replicated almost identically and that are under the full control of the experimenter (Sanchez-Vives and Slater, 2005). Furthermore, not only does IVR allow one to feel immersed and present in a computer-generated environment, but it also makes possible the induction of the illusion of owning a virtual body (Sanchez-Vives and Slater, 2005; Kiltner et al., 2012), a body that can be rendered with the morphological characteristics that the experimenter determines (Banakou et al., 2013). This illusion has been shown to affect the perceptual responses of participants (Llobera et al., 2013). So, thanks to its unique advantage to manipulate visual information in a controlled and systematic manner, IVR represents an excellent tool for investigating body-related human perception, including pain perception, under both healthy and clinical conditions.

Here we aimed at investigating whether and how much the illusion of body ownership over a virtual body and pain threshold change as the body becomes increasingly more transparent. We presented healthy participants with a co-located virtual body with four different levels of transparency, while participants were tested for pain threshold by increasing ramps of heat stimulation.

2. RESULTS

The experiment comprised different visual conditions where participants could see the avatar's body from a first person perspective with different degrees of transparency (see Fig. 1). In particular, this within group design entailed a single factor, "transparency", with 4 different levels (0%, 25%, 50%, 75% of transparency). The order of the conditions was counterbalanced between participants. Three heat ramps were provided for each condition, where participants were instructed to stop the stimulation as soon as they felt the heat to be painful. After each heat stimulation participants were also asked to rate the level of the illusion of ownership over the virtual limb (for further details see

Methods section).

Figure 1: *The experimental set-up (i.e. real body, RB) and the experimental conditions. From top to bottom, the avatar's body is rendered fully opaque (0% transparency), or with 25%, 50% and 75% of transparency. The exemplifying picture was taken by MM and the person depicted is KB (both authors of the present manuscript). The virtual environment was programmed using the XVR system (VRMedia S.r.l., Pontedera, Italy; Tecchia et al., 2010,) and the virtual body using the HALCA library (Gillies, M. and Spanlang, 2010)*

DEPENDENCY OF OWNERSHIP ON OPACITY/TRANSPARENCY OF THE VIRTUAL ARM

The reported levels of ownership showed a clear dependence on the transparency levels, being ownership lower with higher transparency (Fig. 2). Indeed we found a significant negative correlation (Spearman correlation: $r_s = -0.32$, $p = 0.0017$) between the two. Thus, in these conditions, the higher the level of transparency the lower the sense of ownership. An ordered logistic regression revealed that the factor “transparency” (treated as a numeric variable) was a significant predictor of “ownership” (treated as an ordered categorical variable), which was fit with a negative coefficient ($c = -0.52$) at a confidence level $p = 0.0016$. A Friedman One-Way Anova was then run to check whether there were different body ownership levels among the four conditions. This test showed that indeed the body ownership levels were significantly different under the diverse transparency conditions ($\chi^2 = 15.87$; $p = 0.001$). Single comparisons were run with matched pairs Wilcoxon tests. Together with the p-value we report the effect size in terms of the probability of superiority of dependent measures (PS_{dep}): in the most transparent condition (75%) ownership was significantly lower than in the 50% ($z = -2.57$, $p = 0.01$, $PS_{dep} = 0.79$), 25% ($z = -2.97$, $p = 0.003$, $PS_{dep} = 0.79$) and 0% ($z = -3.1$, $p = 0.002$, $PS_{dep} = 0.82$) transparency conditions (see method sections for more details on how different levels of transparency were implemented); in the 50% condition ownership was significantly lower than in the 0% condition ($z = -1.97$, $p = 0.048$, $PS_{dep} = 0.68$); the rest of comparisons resulted in no significant difference ($p = 0.13$ for 25% vs 0% and $p = 0.16$ for 50% vs 25%), showing nevertheless a trend for lower ownership scores in the higher transparency condition.

Figure 2: The box-and-whisker plot shows levels of ownership of the avatar's body according to the different levels of body transparency (from 0% = fully opaque to 75% of transparency).

DEPENDENCY OF PAIN THRESHOLD ON OPACITY/TRANSPARENCY OF THE VIRTUAL ARM

The data from our experiment show no direct dependence of the pain threshold (PT) on the transparency of the virtual body. In fact, a repeated measure one-way ANOVA with factor “transparency” gave no significant results ($F_{(3,23)} = 0.87, p = 0.46$). Analogous results were found when including the temporal order of conditions as a covariate (ANCOVA), which would account for habituation effects (transparency: $F_{(3,23)} = 1.59, p = 0.2$; block: $F_{(3,23)} = 57.9, p < 0.0001$). The latter were nevertheless taken into account in the experimental design via the perfect balance in the order presentation of the four experimental conditions.

Figure 3: Scatterplots of ownership levels and pain threshold per participant and condition. Trend-lines show a trend or significant negative correlations only for the semi-transparent bodies (25%, 50% and 75%).

Interestingly, the data showed a negative correlation of PT with the level of ownership (Spearman correlation: $r_s = -0.27, p = 0.007$); note that higher PT values indicate a higher tolerance to painful stimuli, so this result suggests that the higher the sense of ownership the less the tolerance to

painful stimuli. However, including all conditions together such correlation could be plagued by the autocorrelation bias. So, we ran the correlation separately for each level of transparency, and we found: [$r_s = -0.30$, $p = 0.152$] for 75% transparency; [$r_s = -0.39$, $p = 0.064$] for 50% transparency; [$r_s = -0.42$, $p = 0.04$] for 25% transparency; [$r_s = -0.1$, $p = 0.46$] for 0% transparency. Therefore, we found that the negative correlation between PT and ownership holds (i.e. is significant or in trend) only for the conditions with a transparent body (75%, 50%, 25%). No negative correlation is found for the case of a normal, fully opaque, virtual body (Fig. 3). Putting together data from the three conditions with a transparent body we found a significant negative correlation with PT [$r_s = -0.33$, $p = 0.005$], meaning that the higher the ownership of the transparent virtual arm, the lower the PT.

Not taking into account the level of ownership, PT shows no relationship with transparency (Spearman correlation: $r_s = -0.03$, $p = 0.74$).

3. DISCUSSION

Motivated by gathering new insights into the effects of visual exposure to the body and pain perception, and in an attempt to find a novel visual mechanism capable of modulating pain, in the present experiment we changed the virtual body visibility by making the avatar's body progressively transparent. To our knowledge, this is the first study that addresses the influence of body visibility on both the sense of ownership and its impact on pain perception.

The results obtained from our set-up suggest that while the illusion of ownership is significantly reduced by increasing the transparency of the virtual body, pain threshold does not seem to be directly modulated by it. On the other hand, significant negative correlations were found between pain threshold and the subjective level of ownership of the transparent body. More specifically, this relation was found to hold for all the conditions in which participants were in view of a transparent body, but not when staring at a fully opaque virtual body. In other words, experiencing a greater sense of ownership over a transparent body results in a diminished pain threshold, and so in a higher sensitivity to painful stimuli. Importantly, our results are compatible with previous studies showing that the vision of one's own body part (either real, dummy, or virtual) leads to analgesic effects (Longo et al., 2008; Hegedüs et al, 2014; Martini et al., 20014 respectively). Indeed there is no negative relationship between body ownership and pain threshold when the displayed body is normally displayed (0% transparency).

There are various possible interpretations for the negative relationship between pain and body transparency. First, it can be argued that a transparent body can imply some sort of weakness or vulnerability and therefore it can be perceived as more sensitive and susceptible to be hurt. In agreement with this argument, a recent study demonstrated that the illusion of owning a marble hand, induced by replacing the auditory impact of a hit on the participants' hand with the sound of a hammer against a piece of marble, people perceived their hand to be harder and less sensitive (Senna et al., 2014). Further, Osumi and coworkers recently reported that when participants are painfully stimulated while they experience the illusion of owning a rubber hand that is injured (i.e.

presenting a bloody scar along the rubber limb), their pain threshold decreases (Osumi et al., 2014a).

In addition, owning a transparent body may lead to general negative feelings toward the body and consequently, this attitude may influence the pain perception negatively. In agreement with this explanation, a recent study showed how unpleasant emotions toward a modified (specifically: magnified) image of one's hand are related to lower pain thresholds (Osumi et al., 2014b). Interestingly, in this study, no association with a lower pain threshold was found when the limb was not visually modified, which is in accordance with our findings. With an alternative interpretation we speculate that transparency may result in blurring the body limits, thus decreasing the predictability for potential injuries; hence, being uncertain about the body boundaries, the brain proceeds in a general lowering of the pain threshold as an alert system, strengthening the protective mechanisms.

Our results could also be complementary to those showing that seeing one's own body produces analgesia and that this effect vanishes when the visual cue is something else, namely another's body or an object (Longo et al., 2008; Martini et al., 2014). The neural underpinnings of this effect are associated to reduced activations of key areas of the putative 'pain matrix' during the vision of the body (Longo et al., 2012). Indeed, studies with chronic pain patients and healthy participants point at the intracortical excitability in the primary somatosensory cortex as the mechanism underlying pain modulation (Longo et al., 2012). The vision of the body would not only increase the intracortical inhibition within somatosensory cortex but it would also facilitate a reorganization of its somatosensory maps sharpening the receptive fields of the neurones (Haggard et al., 2013). These two mechanisms have been proposed to underlie the analgesia that follows the vision of the body, an effect that vanishes in the absence of such visual cue. In line with these proposed mechanisms, we found that there is a relationship between owning a virtual body that gets transparent and the loss of the analgesic effect derived from seeing one's own body (Longo et al., 2008).

In addition, our results reveal that the ownership of a virtual arm by means of co-location decays with the transparency of the arm; in other words, ownership of an opaque arm is significantly higher than that of a semi-transparent arm. This result is in agreement with several findings in the literature on body ownership illusions that emphasize the role of top-down influences in modulating the level of illusion, in terms for example of body volume (IJsselstein et al., 2006), body length (Kilteni et al., 2012), or body connectivity (Perez-Marcos et al., 2011). Our results of reduced body ownership scores toward a semi-transparent arm may apparently disagree with the results by Guterstam and coworkers who recently demonstrated that people can experience strong sensations of body ownership toward an empty area of the space when congruent visuotactile correlations are provided to the participant's limb and the empty area (Guterstam et al., 2013). However, any comparison between the two studies should be done with caution due to significant methodological differences; for example, in Guterstam's study, there was no body part displayed, while in our experiment a body was always shown under different transparency levels. In addition, these authors provided visuotactile stimulation in order to induce the "ownership" of the empty area, while in our study the first person perspective of a collocated avatar's body was sufficient to achieve the virtual body illusion (Maselli and Slater, 2013; Tieri et al., 2015). We did not provide additional visuotactile stimulation in order to avoid ceiling effects on the level of the ownership illusion, which might have hindered the detection of modulations effects associated to different levels of transparency.

4. CONCLUSION

A number of studies have been conducted to explore how bodily illusions may affect our perception. However, how body visibility affects body ownership and pain processing is new since it is an effect hard to achieve in the real world. Such approach not only expands our knowledge about how we perceive our body and interact with it and the environment, but it can also be a critical tool for the development of pain management interventions relevant for clinical therapy (Ramakonar et al., 2011). In the present study we found that the vision of a transparent body may lead to lower levels of ownership over that body. Participants reporting stronger ownership over the transparent body showed lower levels of pain threshold. Therefore, although visual transformations of the owned virtual body can lead to useful applications in therapeutical settings, making the body transparent does not seem to be useful to increase the pain threshold. From these observations we could predict that if a patient reports pain in a limb, making this limb (virtually) transparent would not decrease his/her pain. However, such hypothesis remains to be confirmed by future studies. Here we studied pain threshold on healthy subjects, however chronic pain has additional emotional and psychological components, and therefore the transparency of the painful limb could have a different impact in this clinical population.

5. METHODS

5.1 PARTICIPANTS

24 right-handed female healthy participants (age: 21.1 ± 1.8) were recruited for the experiment. We intentionally chose participants of the same gender given that men and women adapt differently (sensory habituation) to pain stimuli. All participants had normal or corrected-to-normal vision and no history of neurological or psychological disorders. Also, any condition potentially interfering with pain sensitivity (e.g. drug intake) was considered as a further exclusion criterion. Upon arrival at the laboratory they were asked to read and sign a consent form and the experiment was carried out in accordance with the regulations of the local ethics committee (Comité Ético de Investigación Clínica de la Corporación Sanitaria Hospital Clínic de Barcelona) and with the declaration of Helsinki. The study was approved by the ethics committee of the Hospital Clínic of Barcelona. All participants received a monetary compensation for their participation (10 €).

5.2 VIRTUAL REALITY SYSTEM

The stereoscopic head-mounted display (HMD) was a NVIS SX111 with a resolution of 1280×1024 per eye and a total field of view of $102^\circ \times 64^\circ$, displayed at 60Hz. The head-tracking was realized with a 6-DOF Intersense IS-900 device (InterSense, Billerica, USA). The virtual environment was implemented using the XVR system (Tecchia et al., 2010. VRMedia S.r.l., Pontedera, Italy) and the virtual body was displayed using the HALCA library (Gillies and Spanlang, 2010). Transparency of the virtual body was achieved by adjusting the value of alpha channel of the texture of the virtual body to levels of either 100% (maximum opacity), 75%, 50% or 25% (very transparent) (see Fig. 1).

Noise isolation was ensured by the administration of pink noise through a surround audio system (Creative technology Ltd., Singapore), with a constant volume set at 65 dB.

5.3 PAIN THRESHOLD MEASUREMENT

Thermal heat stimuli were delivered by means of a Samedic-Thermotest machine (Somedic, Stockholm, Sweden) with a 2.5 cm × 5.0 cm thermode tied with a Velcro strap on the front of the participant's right forearm, close to the distal extreme of the radius (see Fig. 1). Pain thresholds were assessed with the method of limits (Yarnitsky et al., 1995). The probe temperature was increased from normal skin temperature (constant baseline temperature = 31 °C) at 2 °C/s. The temperature stimulation was provided in a continuous fashion, gradually and constantly increasing from the baseline temperature till the subjective pain threshold level. Participants were instructed to press a button with their left hand as soon as they perceived the stimulation on their right hand as being painful. Immediately after pushing the kill-switch button, the probe temperature rapidly decreased to the baseline temperature. For safety reasons, maximal temperature was set at 48 °C.

5.4 PROCEDURE

Participants sat comfortably on a chair with both arms resting on a table covered with a black cloth as shown in Fig. 1. Before starting the main part of the experiment, participants were given 2-3 heat stimuli to familiarize them with the heat ramps. Afterwards, the participant put on the HMD, the room's lights were turned off and the pink noise played. The posture of the participant was calibrated in order to ensure a close co-location of the real body with the virtual one. The HMD allowed participants to experience an immersive virtual environment around them and to see a virtual body from a first-person perspective so that, when they looked down towards their own body, they could see the virtual body in place of their own. Participants were asked to keep still throughout the experiment. Importantly, no other sensory correlations were provided (visuo-tactile or visuo-motor correspondences) since a first person perspective over a realistic fake humanoid body has been shown to be sufficient in eliciting a strong body ownership illusion (Maselli and Slater, 2013). Four brown stripes of tape were stuck on the real table and displayed in the virtual table to facilitate the perception of a transparency of the avatar's arm and to boost the visuo-tactile correspondence between the real and the virtual hand (both the real and the virtual hand touching the first stripe with the finger and the second stripe with the thumb).

Before each condition, participants were given approximately one minute to familiarize with the virtual room in which they were in and with the virtual body. The experiment consisted of four different conditions, presented in blocks, with the avatar's body transparency set at 0%, 25%, 50% or 75%. All participants completed the four conditions, with the order of the blocks balanced across participants. Each condition started with the participant looking at and describing the entire body and then focussing on the avatar's right wrist (i.e. where the painful stimuli came from). The inter-stimulus interval was set at around 40 seconds and three heat ramps were provided for each condition.

Within each trial, about 2 seconds after the thermal stimulation had been stopped, a "beep" sound prompted the participants to judge the level of ownership over the virtual limb. They were instructed to verbally report a number on a scale from 1 to 7 ("1" = not at all, "7" completely) to reply to the

question: “Did you feel as if the virtual right arm was your own right arm?”. Participant’s ratings were promptly annotated by the experimenter.

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CHAPTER 5

OVER MY FAKE BODY: BODY OWNERSHIP ILLUSIONS FOR STUDYING THE MULTISENSORY BASIS OF OWN-BODY PERCEPTION

Related publication:

Over my fake body: body ownership illusions for studying the multisensory basis of own-body perception.
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ABSTRACT

Which is my body and how do I distinguish it from the bodies of others, or from objects in the surrounding environment? The perception of our own body and more particularly our sense of body ownership is taken for granted. Nevertheless, experimental findings from body ownership illusions (BOIs), show that under specific multisensory conditions, we can experience artificial body parts or fake bodies as our own body parts or body, respectively. The aim of the present paper is to discuss how and why BOIs are induced. We review several experimental findings concerning the spatial, temporal, and semantic principles of crossmodal stimuli that have been applied to induce BOIs. On the basis of these principles, we discuss theoretical approaches concerning the underlying mechanism of BOIs. We propose a conceptualization based on Bayesian causal inference for addressing how our nervous system could infer whether an object belongs to our own body, using multisensory, sensorimotor, and semantic information, and we discuss how this can account for several experimental findings. Finally, we point to neural network models as an implementational framework within which the computational problem behind BOIs could be addressed in the future.

1. INTRODUCTION

“I swear to God, cross my heart, I haven’t (been kidding). A man should know his own body, what’s his and what’s not—but this leg, this thing.... doesn’t feel right, doesn’t feel real—and it doesn’t look part of me” (Sacks, 1985).

There would be nothing wrong or weird with the above statement, if we thought that the person speaking had been referring to a fake leg, which for an unknown reason was placed close to his body. However, in fact the quote is from a brain-damaged patient talking with his doctor about his own paralyzed leg. The bizarre neurological syndrome of somatoparaphrenia reveals that our ability to recognize our own body parts can dramatically deteriorate in certain brain damage conditions (Vallar and Ronchi, 2009; Feinberg et al., 2010). Astonishing as it is, the case of somatoparaphrenia gives prominence to the multidisciplinary research topic (Gallagher, 2000; Jeannerod, 2003; Blanke and Metzinger, 2009; de Vignemont, 2011) that aims to address a seemingly trivial question: how does our brain distinguish between our own body and those of other people or objects?

A key difference between the perception of our own body and that of others’ bodies or objects in the environment lies in the type of sensory input available to the brain. In processing our own body, the brain has access to a set of sensory information—such as somatosensation, thermosensation, nociception, interoception, and vestibular signals—that is not available for the perception of other objects or bodies. Yet, evidence from somatoparaphrenic patients suggests that the intact sensory processing from separate modalities may not be in itself sufficient for the emergence of the feeling of body ownership. Indeed, it has been proposed that somatoparaphrenia may be due to an impairment in processing multisensory signals (Vallar and Ronchi, 2009). Therefore, the sense of body ownership should be regarded as the outcome of the brain’s processes that integrate different sensory cues into the unified perception of “my body.”

Another key difference concerns the fact that in own-body perception all the sensory and motor cues that converge into the “my body” percept are strictly bound by physical laws. For example, when striking a fist on a table, the view of the contact is always accompanied by the punching tactile sensation in our hand. This is not the case for the perception of external objects or others’ bodies that, although multisensory in nature, is not subject to such strict constraints. Just consider this example: you see a dog in a park and you hear a barking sound at about the same moment and coming from the same direction. Even if it is probable that it was the seen dog that was barking, there is also the possibility that there is a second dog just behind the tree. Thus, while in the perception of external events we can contemplate the possibility of different sources, in the perception of “my body” this is not the case, since all multimodal cues involved originate from the same source: the physical body.

Due to the fact that the body-related multimodal cues are tightly bound together and not independent, it is difficult to experimentally investigate body ownership with the methods adopted in multisensory research. In contrast, when studying the multisensory perception of external objects, including others’ bodies, experiments typically involve the concurrent presentation of sensory

signals that are independent. This permits the introduction of delays between the occurrences of the stimuli, to present them from different positions, or even to manipulate their information content so that these may refer to the same context or not. Therefore, it is possible to investigate how multisensory perception is influenced by the spatial, temporal, and semantic relationships between the manipulated stimuli (Doehrmann and Naumer, 2008; Alais et al., 2010). The same methods cannot be directly applied to study body ownership. For example, it is not possible to introduce a temporal delay between seeing our fist striking the table and feeling the punching sensation in the hand, unless through the use of devices such as cameras and displays.

Given the limitations inherent in the study of the physical body, experimental research has been extensively conducted through exploiting the illusions of body ownership. In these illusions, healthy adults experience non-bodily objects (e.g., artificial limbs) as belonging to their own body, when presented with crossmodal stimuli applied to the hidden real body part and its fake counterpart. Due to the fact that the stimuli have two independent sources (i.e., the real and the fake body part), experimenters have been able to flexibly manipulate their spatial, temporal, and semantic relationships. In this way, body ownership illusions (BOIs) therefore offer a powerful experimental tool to examine how the sense of body ownership emerges from multisensory processing operated by the brain.

Our understanding of how the brain builds the sense of body ownership can benefit from identifying the basic principles that govern the induction of body ownership illusions and formulating the latter within a computational framework. Consequently, the aim of this paper is two-fold. First, to review the experimental literature, investigating how the spatial, temporal, and semantic congruencies of the tested crossmodal stimuli contribute to eliciting body ownership illusions. Second, to discuss and propose different theoretical accounts that could possibly cast the experimental findings into a unifying computational context. We start by introducing body ownership illusions and distinguishing these from other classes of body illusions that, together with the former, have provided essential insights on how the own-body percept is built through multisensory and sensorimotor information. Following this, we present the main results of experimental work on body ownership illusions, classifying them on the basis of the crossmodal triggers and semantic information that these have manipulated. This classification is functional to the discussion of different theoretical accounts of body ownership.

2. BODY ILLUSIONS TO STUDY OWN-BODY PERCEPTION

Body illusions refer to those psychological phenomena in which the perception of one's own body importantly deviates from the configuration of the physical one, e.g., in terms of size, location, or ownership. Since their induction is achieved through multisensory and/or sensorimotor stimulation, body illusions provide essential insights on how the own-body percept is built in real-time, on the basis of the stimuli that are currently available to the brain.

A representative example of body illusions are the body distortions illusions, in which people can

perceive that the size or the posture of their body part(s) have changed dramatically without necessarily satisfying the anatomical constraints of the human body. A method to induce illusory body distortions relies on kinaesthetic illusions, in which blindfolded subjects experience the illusory movement of a static body part and therefore non-veridical proprioceptive states, when the tendon muscle of a physically constrained joint is mechanically vibrated (Goodwin et al., 1972). Importantly, the illusory motion of the stationary body part can capture other non-movable body parts it is in contact with, yielding the impression that these change in size (Lackner, 1988; deVignemont et al., 2005; Ehrsson et al., 2005b). Similar distortion illusions have been shown to occur for numerous other body parts (Lackner, 1988), to correlate with activation of areas in the lateral parietal cortex (Ehrsson et al., 2005b) and to modulate the tactile processing on the body part perceived as distorted (de Vignemont et al., 2005). A well-known example is the Pinocchio illusion (Figure 1A). Alternatively, a distortion illusion similar in phenomenology can be induced through temporal correlations between undistorted proprioceptive information and tactile input, as for example the phantom nose illusion (Ramachandran and Hirstein, 1998) (Figure 1B). Independently of the employed methodology, the body distortion illusions demonstrate that the brain computes the perceived body posture and shape dynamically and in a flexible fashion, without the need to satisfy the anatomical constraints of the human body.

Another remarkable class of body illusions are the experimentally induced out of body experiences, in which people perceive their self to be dislocated from the spatial origin of their visual perspective (Lenggenhager et al., 2007), and/or of looking at their body from a distance (Ehrsson, 2007). One of the first reports of these illusions was attained through the use of a mirror device and goes back to the end of the nineteenth century (Stratton, 1896). In the recent experimental settings participants wear a head mounted display (HMD), which is fed by a camera that records the back of the participants from distance. Thus, participants see their body from the back, i.e., from a third person visual perspective (3 PP), in contrast with the first person visual perspective (1 PP) that we normally have on our body when looking downward. Through applying tactile stimulation on the participants' back while they see the instrument touching their back in the online video, participants experience illusory drifts in their self-location toward the body seen in the video (e.g., Lenggenhager et al., 2007) (Figure 1C). Illusory changes in self-location were also reported when subjects were tapped on their chest with a stick while another stick was synchronously waived underneath the cameras (e.g., Ehrsson, 2007). Analogous illusory experiences were reported by subjects standing between two mirrors that face each other, while stroking their cheek and watching the several reflections of their bodies (Altschuler and Ramachandran, 2007). Systematic experimental findings from the out of body illusions demonstrate that the perceived location of the self can be detached from that of the physical body, similar to reports from patients undergoing out-of-body experiences of neurological origin (Blanke and Mohr, 2005). This class of illusions provides therefore an important benchmark for studying the role of multisensory integration in the sense of self-location and self-consciousness (Blanke and Metzinger, 2009; Blanke, 2012).

Figure 1. Examples of body illusions. (A) The Pinocchio illusion. A blindfolded participant receives vibration on his biceps while touching the tip of his nose with his fingers. The illusory extension of the arm (Goodwin et al., 1972) generates the illusion that his nose, his fingers or both are elongating (Lackner, 1988). (B) The phantom nose illusion. The experimenter moves the finger of a blindfolded participant to tap the nose of another subject, while simultaneously tapping the nose of the participant. As the participant's movements and his finger contact with the other subject's nose are synchronous with the touch he receives on his nose, the participant experiences the illusion of tapping his very long nose (Ramachandran and Hirstein, 1998). (C) An out of body illusion. The participant sees a video of his back as if he were located behind it. The experimenter touches the back of the participant with a stick while the participant sees it online in the video. As the seen and the felt stimulation is synchronous, the participant perceives illusory drifts in his self-location toward the seen body (Lenggenhager et al., 2007). (D) The rubber hand illusion. The participant sees a rubber hand placed in front of him, while his real hand is concealed from view. The experimenter strokes both hands at the same time, and after some time the participant perceives the fake hand as if it were his own hand (Botvinick and Cohen, 1998).

2.1. BODY OWNERSHIP ILLUSIONS

In distinction to body distortion and out of body illusions, Body ownership illusions refer to the illusory perception of non-bodily objects (e.g., artificial limbs) as being parts of one's own body and as being the source of the associated bodily sensations, such as touch. For example, one can get to experience a mannequin's hand as his/her own hand, and have strong physiological responses when seeing it being attacked with a knife (Ehrsson et al., 2007).

One of the earliest versions of this class of illusion was reported by Tastevin (1937), who described how people could perceive an artificial finger protruding from a cloth as their own finger, when the latter was hidden from view. Sixty years later, Botvinick and Cohen (1998) provided the first report of the rubber hand illusion (RHI), in which healthy adults experience a rubber hand as if it were their own hand. In this experimental setup, subjects have their hand concealed from view, while they see a rubber hand of the same laterality, placed in a similar posture. The experimenter strokes both rubber and real hands simultaneously, and after some time the majority of participants report perceiving the touch as if coming from the rubber hand, and the latter as being part of their own body (Figure 1D). In addition, when asked to point blindly to the position of their left hand, participants typically give proprioceptive estimations that are shifted toward the rubber hand compared to their estimations before the stimulation (e.g., Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005).

Apart from proprioceptive drifts, the RHI has been shown to decrease the temperature and slow down the processing of tactile input from the real hand (Moseley et al., 2008; Hohwy and Paton, 2010) and to trigger the participants' autonomic responses when seeing the rubber hand under threat (e.g., Armel and Ramachandran, 2003). Interestingly, it has been shown that brain areas associated with anxiety and interoceptive awareness selectively activate when, during the RHI, the fake limb is under threat and at a similar level as when the real hand is threatened (Ehrsson et al., 2007). Moreover, the subjective reports about the intensity of the illusion, typically addressed through questionnaires, have been shown to correlate positively with many of the objective measures mentioned above—e.g., proprioceptive drifts (Longo et al., 2008b), brain activity (Ehrsson et al., 2004; Limanowski et al., 2013), and decrease in temperature of the real counterpart (Moseley et al., 2008).

Beside correlated visuotactile cues, the RHI has been demonstrated also under different multimodal stimuli. For example, the illusion has been induced with correlated visual and motor information, that is when participants are performing movements with their unseen body part while seeing the fake counterpart moving similarly (e.g., Dummer et al., 2009; Kalckert and Ehrsson, 2012, 2014a,b). In addition, just seeing the rubber hand at the same position of the occluded real hand, that is in the mere presence of coincident visual and proprioceptive information, can elicit the illusion of body ownership (Giummarra et al., 2010).

The illusions of body ownership have been also induced toward full humanoid bodies, by using HMDs that permit seeing the fake body in the same spatial location as the real body (Petkova and Ehrsson, 2008; Slater et al., 2010; Petkova et al., 2011b; Maselli and Slater, 2013). These full body illusions were induced through visuotactile (e.g., Petkova and Ehrsson, 2008), visuomotor (e.g., Peck et al., 2013), and visuoproprioceptive information (Maselli and Slater, 2014). Moreover, they were shown to have physiological and proprioceptive correlates analogous to those of the RHI (Petkova and Ehrsson, 2008; Llobera et al., 2013; Maselli and Slater, 2013, 2014).

The induction of these illusions was shown even in the absence of any visual input. In the so-called “somatic RHI,” blindfolded participants have their left index finger passively moved by the experimenter to touch a rubber hand, whereas the experimenter synchronously touches their right hand. After some seconds of correlated tactile and proprioceptive information, the participants typically report the illusion of touching their own hand, instead of the rubber one (Ehrsson et al., 2005a). Although

using a different methodology, the somatic RHI was found to correlate selectively with enhanced activity in the premotor cortex, as in the classic RHI and the full body ownership illusion (Ehrsson et al., 2004, 2005a; Petkova et al., 2011a). This remarkable convergence of results supports the view that body ownership is not determined by the type of sensory triggers employed, but emerges from the synergetic processing of the multimodal information available at a specific time.

Extending the findings from other bodily illusions, body ownership illusions reveal that our brain dynamically computes which are our own body parts on the basis of the available multisensory and sensorimotor information. Nevertheless, although the numerous studies bring along a wealth of insights about the multisensory mechanisms that underlie own-body perception, little emphasis has been devoted to casting this information into a coherent and comprehensive picture. In the following, we review the literature on body ownership illusions with the aim of identifying the multimodal triggers and constraints that govern them. Given the different response variables used by different experimenters, our criterion about the impact of the manipulation of the experimental variable in eliciting the illusion is primarily based on the most common measure, the subjective scores collected through questionnaires. However, we also refer to other objective measures especially in the cases where no questionnaires were administered. Moreover, given the extensive literature, we limit our scope to the body ownership illusions where visual information was available.

3. MULTIMODAL TRIGGERS AND SEMANTIC CONSTRAINTS IN BODY OWNERSHIP ILLUSIONS

The elicitation of body ownership illusions (BOIs) has been shown under different experimental setups that provide different crossmodal stimuli (Figure 2). In this section, we present several experimental studies on BOIs by classifying them in terms of the main crossmodal stimuli provided (i.e., visual and tactile, visual and proprioceptive, and visual and motor), or of the semantic feature of the fake body that these have manipulated. With the specific aim to highlight the principles that permit the induction of BOIs, we investigate the importance of spatial and temporal correspondence for each pair of crossmodal stimuli, as well as the role of semantic information that the view of the non-bodily objects brings along. To provide a link between the illusions of body ownership and our normal sense of body ownership, for each of considered the components we present a brief overview of its known role in our own-body perception.

Figure 2. Different induction methods of Body Ownership Illusions (BOIs). (A,D) Visuotactile triggers: the participant is watching the fake hand/body placed in a plausible posture and being touched, while receiving synchronous tactile stimulation in the real counterpart that remains out of view. (B,E) Visuomotor triggers: the participant is performing movements with his real hand/body that remains out of view, while watching the fake counterpart moving synchronously. (C,F) Visuoproprioceptive triggers: the participant is watching the fake hand/body placed in an overlapping position with the real counterpart that remains out of view.

3.1.VISUOTACTILE TRIGGERS FOR BODY OWNERSHIP ILLUSIONS

3.1.1.VISUOTACTILE INTEGRATION IN OWN-BODY PERCEPTION

The experience of our own body is importantly shaped by visual and somatosensory signals. One of the main contributions of visuotactile integration concerns the information about contact events between our body and the surrounding environment. For example, when a fly lies on our hand, both

vision and touch inform the brain about the time and the location of the contact. But even before the physical contact occurs, vision can provide anticipatory information about where and when the fly is probably going to land, which allows us to take actions accordingly.

Beside its established role in determining the shape and texture of objects we explore with our hands (Ernst and Banks, 2002; Lacey et al., 2010; van Beers et al., 2011; Helbig et al., 2012), visuotactile integration is considered to be critical in perceiving our body and the space nearby. This was first suggested by the discovery of visuotactile neurons in the brain of monkeys: the visual receptive fields of these cells extends outwards from the mapped body part into the external space and shifts along with body movement (Rizzolatti et al., 1981; Graziano and Gross, 1993; Duhamel et al., 1998). Because of these properties, these bimodal neurons were proposed to build an enlarged and flexible representation of the space surrounding the body—the peripersonal space—that mainly serves to guide our movements (Graziano and Gross, 1994; Fogassi et al., 1996; Graziano and Cooke, 2006).

Homologous visuotactile populations have been identified in the human brain with analogous properties and functionality (Lloyd et al., 2003; Makin et al., 2007; Gentile et al., 2011; Sereno and Huang, 2014). In addition, the importance of visuotactile integration in the spatial representation of the body, has been largely supported by behavioral studies (Spence et al., 2004).

Altogether, experimental evidence from monkey neurophysiology to human behavior indicates the fundamental role of visuotactile populations in flexibly defining the dynamics of our own body spatial boundaries.

3.1.2. METHODS AND APPARATUS FOR VISUOTACTILE STIMULATION IN BOIs

Turning to BOIs, the first report of the RHI was induced through applying tactile stimuli on the occluded real hand and the visible fake counterpart (Botvinick and Cohen, 1998). The procedure was quickly established as a standard protocol and extended to full BOIs as well (Figures 2A,D).

With respect to the employed methods, seen and felt touch have been typically delivered manually by the experimenter (e.g., Botvinick and Cohen, 1998; Armel and Ramachandran, 2003; Petkova and Ehrsson, 2008). Alternative setups used cameras, screens or virtual reality methods. By these technological means, some experimenters manually stimulated only the real body (or body part), whilst the participants watched a video stream of the real body part being touched (e.g., Tsakiris et al., 2006) or a virtual object touching an artificial body (or body part) seen in stereo mode (e.g., Slater et al., 2008). Alternatively, computer-controlled administration of touch was implemented by programming robot arms or stepper motors that touched both the real and the fake body (or body parts) (Tsakiris et al., 2008; Rohde et al., 2011), or by attaching mechanical vibrators on the real body and programming them to fire when the participants watched the virtual body being touched through the HMD (Pabon et al., 2010; Evans and Blanke, 2013; Maselli and Slater, 2013).

3.1.3. SPATIAL AND TEMPORAL PRINCIPLES OF VISUOTACTILE INTEGRATION AS TRIGGER OF BOIs

Systematic experimental evidence has shown that the RHI is induced when the real hand and the fake counterpart are touched at the same time and at homologous regions in hand-centered

coordinates. For example, when spatiotemporal mismatches were introduced between the seen and felt touch, the RHI was significantly inhibited (Armell and Ramachandran, 2003; Ehrsson et al., 2004; Slater et al., 2008). Similar results were found for full BOIs toward plastic mannequins seen from a 1 PP; participants perceived the mannequin's body as their own body when the real and the fake abdomen part were touched synchronously, but not when asynchronously (Petkova and Ehrsson, 2008). Nevertheless, other studies have shown that when the fake body (or body part) is realistic and has overlaps in space with the real body counterpart, positive scores of ownership can be reported even in presence of asynchronous visuotactile stimulation (Longo et al., 2008a; Maselli and Slater, 2013).

A systematic study on the importance of temporal alignment revealed that, when delays smaller than 300 ms between the stimulations were introduced, participants perceived the touch on their hand as if caused by the stimulation applied to the rubber hand, while for larger delays these illusory feelings were significantly attenuated (Shimada et al., 2009, 2014). In addition to the temporal coupling, spatial congruence was also found to be essential for the induction of the illusion. Stroking the rubber and the real hands in temporal synchrony but at different locations (e.g., index vs. little fingers, palm vs. forearm, or index vs. middle finger) abolished the illusion (Kammers et al., 2009; Limanowski et al., 2013; Riemer et al., 2014), demonstrating that temporal matching alone is not sufficient for the RHI. Similar were the findings on proprioceptive drifts when a spatial mismatch was introduced between the seen and the felt synchronous strokes (Costantini and Haggard, 2007).

3.1.4. SUMMARY

Overall, the experimental results suggest that the induction of BOIs depends critically on the spatiotemporal congruence between the seen and the felt stimulation, which is a sufficient condition to induce the illusions. However, the fact that BOIs could occur in presence of visuotactile asynchronies when the fake body is seen superimposed onto its real counterpart, indicates that visuotactile correlations are not a necessary prerequisite for the illusion under such configuration.

3.2. VISUOMOTOR TRIGGERS FOR BODY OWNERSHIP ILLUSIONS

3.2.1. VISUOMOTOR INTEGRATION IN OWN-BODY PERCEPTION

Our own-body perception is highly determined by our movements since these provide information that facilitates self-other distinction. For example, when a pianist plays the piano in a duet, she uses—amongst others—her motor information together with visual, tactile and proprioceptive feedback to recognize which of the two right hands she sees is her own.

The experience of moving and acting in space involves an extremely rich content of body related information that goes far beyond the multisensory integration of two or more sensory modalities. This can be better understood considering the distinction between active vs. passive movements. In a passive movement there is no motor intention: an externally generated force displaces our body (body part) and consequently, a number of sensory information, including vision and proprioception, are updated (Burke et al., 1988). In contrast, when we perform an active movement, our brain

generates and implements a motor plan that relies on internal simulations of our motor system (Wolpert et al., 1995): the motor plan is executed, monitored and corrected by comparing the efference copy with the generated sensory feedback (Miall and Wolpert, 1996; Todorov and Jordan, 2002). The implication of internal body simulations renders the processing of visuomotor cues during active movement much richer in body-related information content. Indeed, this is supported by experimental evidence. For example, it was shown that participants are better at discriminating synchronous vs. asynchronous visuomotor cues when performing active movements compared to passive (Shimada et al., 2010).

It is also relevant that visual monitoring and recognition of one's own actions has been proposed to contribute critically to the sense of body ownership (Jeannerod, 2003), and to play a major role in self-other discrimination (Jeannerod, 2004). Developmental studies have shown that, at 4- to 5-months of age, infants are already able to distinguish their limbs from those of other babies on the basis of synchronous visuomotor correlations: they can distinguish an online video stream of their own moving limbs from similar videos of other babies, from delayed videos of their own moving limbs, (Bahrick and Watson, 1985; Schmuckler, 1996), as well as from online videos in which their body spatial configuration is seen modified (Rochat and Morgan, 1995; Schmuckler, 1996).

A set of experimental studies has shown how healthy adults rely on visuomotor stimuli to discriminate whether a seen moving hand is their own. For example, in the experiment of Daprati and colleagues, participants were asked to perform a movement while looking at a screen in which their filmed hand or the experimenter's was displayed in the same position of their occluded hand. When asked to indicate whether the seen hand was their own hand, participants' performance showed a high rate of erroneous self-attribution when seeing the experimenter's hand doing the same movement (Daprati et al., 1997). In a similar setup, participants saw a virtual hand moving as their own occluded hand, under different spatial orientations and temporal delays. When asked to decide whether the displayed movement corresponded to their own movement, subjects made significantly more self-recognition errors for temporal delays smaller than 150 ms and for angular deviations smaller than 15° (Franck et al., 2001). A variation of the same setup was used to investigate how action and visual cues about the body spatial configuration are used in body-recognition processes (van den Bos and Jeannerod, 2002). Participants were presented with an online video of their own hand and the hand of the experimenter performing either the same, different or no movement at all, while displayed simultaneously in different orientations. The results showed that when the hands performed different movements, participants were almost always able to recognize their own hand. In contrast, when the visuomotor information was ambiguous (same movements) participants were less accurate and their responses were affected by the seen spatial configuration of the hands.

Overall, it becomes apparent that humans exploit the tight coupling of visual and motor signals not only for optimizing their movement performance, but also for attributing their body parts and body movements to themselves.

3.2.2. METHODS AND APPARATUS FOR VISUOMOTOR STIMULATION IN BOIs

The induction of BOIs has been demonstrated in presence of visuomotor stimulation instead of

visuotactile. In those experimental setups, the participants perform either active or passive movements while seeing the artificial body (or body part) moving (Figures 2B,E).

The animation of the fake body has been typically achieved through mechanical devices that permitted linking the real and the fake body parts, such as wooden rods (Kalckert and Ehrsson, 2012, 2014a), pulleys and strings (Azañón and Soto-Faraco, 2007), couplings (Walsh et al., 2011), pneumatically driven plungers (Riemer et al., 2013, 2014), and braces (Dummer et al., 2009). Alternative experimental setups used cameras to record the participants' moving hand and project it to a surface or a screen (Tsakiris et al., 2006, 2010b). The intrinsic delays of the apparatus are typically of the order of 70–100 ms (Tsakiris et al., 2006; Riemer et al., 2013, 2014), and thus below the threshold of 150 ms for detecting visuomotor delays (Franck et al., 2001; Shimada et al., 2010). Other experimenters, using virtual reality techniques, captured the participants' movements—through inertial systems and/or infrared cameras—and animated the virtual limbs or bodies accordingly (Sanchez-Vives et al., 2010; Yuan and Steed, 2010; Normand et al., 2011; Kiltner et al., 2012, 2013).

3.2.3. SPATIAL AND TEMPORAL PRINCIPLES OF VISUOMOTOR INTEGRATION AS TRIGGER IN BOIs

Several studies have demonstrated that BOIs are induced when both real and fake bodies move homologous body parts at the same time. This has been shown, for example, with fingers (Tsakiris et al., 2006, 2010b; Sanchez-Vives et al., 2010; Walsh et al., 2011; Kalckert and Ehrsson, 2012, 2014a,b; Riemer et al., 2013), hands (Dummer et al., 2009), arms (Yuan and Steed, 2010; Normand et al., 2011; Kiltner et al., 2012; Llobera et al., 2013), upper body (Kiltner et al., 2013), legs (Kokkinara and Slater, 2014), or full bodies (Banakou et al., 2013; Peck et al., 2013). In contrast, when introducing temporal delays of the order of 500 ms or more (Kalckert and Ehrsson, 2012, 2014a; Riemer et al., 2013, 2014), or when manipulating the seen movements independently from the real movement (Dummer et al., 2009; Sanchez-Vives et al., 2010; Walsh et al., 2011; Banakou et al., 2013), the corresponding illusions were inhibited. In addition to the temporal coupling, moving homologous real and fake body parts was also found to be essential for the induction of the illusion; for example, moving the index finger while seeing the artificial middle finger moving synchronously did not elicit the ownership illusion (Riemer et al., 2014).

3.2.4. SUMMARY

Similarly to visuotactile stimuli, the experimental results suggest that the induction of BOIs depends critically on the spatiotemporal congruence between the seen and the felt movements.

3.3. VISUOPROPRIOCEPTIVE MODULATIONS AND TRIGGERS FOR BODY OWNERSHIP ILLUSIONS

3.3.1. VISUOPROPRIOCEPTIVE INTEGRATION IN OWN-BODY PERCEPTION

Our own-body perception is greatly influenced by visual and proprioceptive information. The main contribution of visuoproprioceptive integration relies on defining where our body is in space. Both modalities inform the brain about where a specific body part is located at a given point in time. For example, we can estimate where our hand is with our eyes closed, and our judgement can further

be confirmed by looking at our own hand.

Experimental evidence has shown that when vision and proprioception provide conflicting information, the perceived position of our body parts can significantly deviate from the veridical one. For example, when the hand is seen in a non-veridical location through mirrors or prisms, subjects perceive their hand to be in one single location, somewhere between the seen and the felt position (Hay et al., 1965; Pick et al., 1969; Warren, 1980) and closer to the visual one (van Beers et al., 1999). This visual capture of proprioception has been shown to influence the performance of reaching movements (Rossetti et al., 1995; Sober and Sabes, 2003; Holmes et al., 2004) and to play a crucial role in monitoring online movement execution (Lajoie et al., 1992; Sober and Sabes, 2003, 2005; Bagesteiro et al., 2006; Boulinguez and Rouhana, 2008). Interestingly, a recent study with 5–7 years old children has shown that the visual capture effects increase with age, suggesting a progressive maturation of visuoproprioceptive integration (Bremner et al., 2013).

Analogously to the visual capture of proprioception, it has been shown that in absence of direct vision of the body, proprioception can distort the perception of visual cues associated to the body spatial configuration. For example, participants sitting in a dark room while holding a luminous target with their static hand, report seeing the (static) luminous target moving in space when experiencing the kinaesthetic illusion of moving their (static) arm (Lackner and Levine, 1978). Similarly, moving the hand while seeing its afterimage (Gregory et al., 1959) was shown to distort the hand image or even to fade it out, despite that this should be perceptually static on the sole basis of visual input (Davies, 1973).

Most studies on visuoproprioceptive populations have been carried out in the context of reaching actions and motor control in both monkeys (e.g., Battaglia-Mayer et al., 2000) and humans (e.g., Filimon et al., 2009). Nevertheless, neural populations have been found in the monkey brain, which integrate static visual and proprioceptive cues to encode the position of the arm (Graziano et al., 2000). To our knowledge, no analogous studies have been performed with humans.

Overall, experimental evidence suggests that visual and proprioceptive information significantly contribute to the perception of our own body and more particularly, in determining its perceived spatial configuration.

3.3.2. METHODS AND APPARATUS FOR VISUOPROPRIOCEPTIVE MANIPULATIONS IN BOIs

BOIs, including their full body versions, have been tested against differences between the seen spatial configuration of the fake body (or body part) and the one of the real body (or body part) that is experienced through proprioception.

In its original version (Botvinick and Cohen, 1998), the RHI was induced despite the spatial mismatch between the positions of the real and the rubber hand. The same spatial arrangement, with the rubber hand closer to the participants' body midline (Figure 2A), was quickly established as a standard protocol for subsequent studies (e.g., Armel and Ramachandran, 2003; Tsakiris and Haggard, 2005; Haans et al., 2008; Moseley et al., 2008; Schütz-Bosbach et al., 2009). In other studies, the rubber hand was instead placed above the occluded real one (e.g., Pavani et al., 2000;

Ehrsson et al., 2004; Azañón and Soto-Faraco, 2007; Haggard and Jundi, 2009).

The above-mentioned studies used a physical object (i.e., the rubber hand) and their setups therefore entail intrinsic limitations in the possible manipulations of visuoproprioceptive stimuli; it is in fact never possible to have the two hands overlapping in space without using devices. Different techniques including mirrors (e.g., Longo et al., 2008a; Zopf et al., 2010), cameras (e.g., Petkova and Ehrsson, 2008; Hohwy and Paton, 2010) and virtual reality techniques (e.g., Perez-Marcos et al., 2012), permitted experimenters to overcome this limitation by projecting the fake body (body part) in complete overlap with its real counterparts.

Manipulations of the position and orientation of the fake body (body parts) relatively to the real body, allowed experimenters to investigate the extent to which visuoproprioceptive discrepancies affect the induction and strength of BOIs. Furthermore, it was possible to test whether close correspondence in the seen and felt spatial configurations (i.e., apparent spatial coincidence) can trigger BOIs without further crossmodal stimulation (e.g., visuotactile) (Figures 2C,F).

3.3.3. VISUOPROPRIOCEPTIVE MODULATIONS OF BOIs

The case of visuotactile triggers

As long as the fake hand was placed close to the body midline and thus within the reaching space, the RHI was induced in presence of spatiotemporally congruent visuotactile stimulation, for several tested mismatches between the positions of the real and fake hands in either the horizontal or the vertical plane; e.g., of 10–20 cm (e.g., Zopf et al., 2010; Rohde et al., 2011; Kalckert and Ehrsson, 2014b), 20–40 cm (e.g., Ijsselstein et al., 2006; Haans et al., 2008; Kalckert and Ehrsson, 2014b), or above 40 cm (e.g., Ehrsson et al., 2004; Zopf et al., 2010).

With respect to the horizontal distance, no significant differences were found in the strength of the RHI under small (i.e., 15 cm) or large (i.e., 45 cm) distances between the hands (Zopf et al., 2010), suggesting that the between hands' distance is not a crucial factor. Different results have been found when the rubber hand was placed farer away from the participant's body midline than the real one. In this case, increasing the horizontal distance between the two hands can eventually prevent the RHI even when the rubber hand still lies within the reachable space (Preston, 2013). This different effect of visuoproprioceptive mismatch on the elicitation of the RHI can probably be explained by our higher expectation of seeing our hand closer to the midline than away from it. The between hands horizontal distance was instead found to significantly affect subjective scores for conditions of asynchronous visuotactile stroking (Zopf et al., 2010): ownership scores were significantly higher when the two hands were as close as 15 cm with respect to the case in which the distance was larger (45 cm). In her study Preston (2013) did not find differences in questionnaire scores, which were equally low, independently on the between hands distance. The different results may be due to the different delays adopted in the asynchronous condition (about 300 ms and 1 s, respectively): in fact the delay used by Zopf and colleagues was reported to mark the upper limit for temporal discrepancies, above which the RHI is significantly weakened (Shimada et al., 2009, 2014).

With respect to the vertical plane, no significant differences in ownership scores were detected

between placing the real and the fake hands at a vertical distance of 12 or 27.5 cm, though keeping both at the same horizontal position close to the participants' midline. However, increasing the vertical distance between the hands to 43 cm was found to significantly attenuate the RHI scores (Kalckert and Ehrsson, 2014b).

While in all the above-mentioned studies the real and fake hands differed in position but were mostly aligned in terms of orientation, other experiments have shown that BOIs can be induced in presence of an additional mismatch in orientation, provided that the fake body (body part) was seen in an anatomically plausible posture. For example, rotating the fake left hand by 44° clockwise did not prevent participants from experiencing the physical touch as if coming from the position of the rubber one, and further led to a recalibration of their perceived elbow joint angle (Butz et al., 2014). BOIs were experienced also when the seen fake hand, rotated away from the real one, crossed the body midline (Brozzoli et al., 2012; Perez-Marcos et al., 2012); but see (Costantini and Haggard, 2007; Cadieux et al., 2011) for effects in proprioceptive drifts. In addition, the RHI was induced toward a rubber hand placed palm-up when the fake palm was stroked synchronously with the palm of the real that was placed palm-down (Ionta et al., 2013). Moreover, by exploring different orientation mismatches, a recent study reported that tactile sensations were perceived to arise from the rubber mainly for those rotations that are easy to mimic with the real. Interestingly, the illusion onsets were found to be shorter when there were no orientation mismatches, without though any significant differences in the subjective reports (Ide, 2013). Instead, when discrepancies in both position and orientation were introduced by moving the rubber hand away from the participants' midline and rotating it, illusory tactile sensations were reported to gradually decrease in intensity with effects also in illusion onsets (Lloyd, 2007).

Consistent with these are the findings from full BOIs. These have been typically induced toward artificial bodies that appeared as if spatially coincident with the real ones, seen therefore from a 1 PP, and under spatiotemporally congruent visuotactile stimulation (Petkova and Ehrsson, 2008; Slater et al., 2010; Petkova et al., 2011b; Maselli and Slater, 2013). With respect to position, a recent study showed that a full BOI could be experienced toward a virtual body seen from a laterally shifted visual perspective (by about 25 cm), i.e., with the virtual body overlapping only partially with the real one, upon congruent visuotactile stimulation. When compared to a condition when the fake body was in complete overlap with the real one, no significant differences in ownership were detected (Maselli and Slater, 2014). Analogously for orientation, the illusion was induced when the mannequin's body was seen from a 1 PP but tilted upwards by 30° approximately (Petkova et al., 2011a).

The case of visuomotor triggers

Beside the information about the movement timings and the involved body parts, visuomotor stimuli provide information on how the relative position and orientation of the real and fake bodies change in time. Some of the studies that employed visuomotor stimulation of artificial body parts followed the RHI protocol and presented the artificial limb close to the midline and lateral to the real one, e.g., at a distance of 15–20 cm (e.g., Sanchez-Vives et al., 2010; Riemer et al., 2013, 2014) while others placed the fake limb above the real one at a vertical distance of about 12 cm (e.g., Walsh et al., 2011; Kalckert and Ehrsson, 2012, 2014a,b). With respect to the horizontal distance,

no significant differences were found in the subjective reports of body ownership when the fake and the real limb moved synchronously while keeping a distance of about 10 cm, compared to when these were spatially coincident (Yuan and Steed, 2010). Nevertheless, larger distances were not tested. With respect to the vertical distance, a recent study revealed that small distances (i.e., 12 cm) permitted the induction of a robust RHI through congruent visuomotor stimulation while larger distances (i.e., 27.5 or 43 cm) significantly attenuated the subjective scores (Kalckert and Ehrsson, 2014b).

3.3.4 .VISUOPROPRIOCEPTIVE INTEGRATION AS TRIGGER FOR BOIs

The fact that full BOIs were found to occur when having a static view of a highly realistic spatially coincident virtual body and under asynchronous visuotactile stimulation, suggests that congruent visuoproprioceptive cues alone could be sufficient to induce the illusion and further to sustain it under visuotactile discrepancies (Maselli and Slater, 2013). In partial agreement are findings from the RHI where participants seeing the rubber hand through a mirror, as if spatially coincident with their real one, did not disagree with statements of ownership when the visuotactile stimulation was asynchronous (Longo et al., 2008a).

In contrast to the large number of studies using visuotactile triggers, there have been fewer that explored whether spatial congruency of visuoproprioceptive cues can be by itself sufficient for the induction of BOIs. These studies, in which BOIs were assessed in “vision only” conditions, suggest that when there is neither visuotactile nor visuomotor stimulation the relative position and alignment of the real and fake body (body part) matters. When seeing through a mirror a rubber hand in the same position and orientation as the real one, participants gave positive scores for the illusion of ownership (Longo et al., 2008a; Giummarra et al., 2010). Nevertheless, upon direct comparison, additional synchronous visuotactile stroking elicited a significantly stronger illusion (Longo et al., 2008a). In contrast, when the fake and real hands were not spatially coincident, the mere vision of the rubber hand was not sufficient for inducing the illusion (as from participants’ self-reports) (Rohde et al., 2011). In line with this overall evidence, it was shown that the visual exposure to a realistic spatially coincident virtual body by itself, can induce a full BOI (as reported in post experiment debriefing) (Maselli and Slater, 2014).

3.3.5. SUMMARY

These findings reveal that spatial congruency of visuoproprioceptive cues (i.e., spatial coincidence) is not necessary for the illusion of body ownership to emerge, provided that the fake body (body part) is seen in an anatomical plausible configuration and in presence of congruent visuotactile or visuomotor stimulation. However, different degrees of visuoproprioceptive spatial mismatch significantly modulate both the intensity and the time onset of the illusion.

On the other hand, spatial coincidence may be a sufficient condition for eliciting BOIs. Although there is consensus in the literature that congruent visuotactile and visuomotor stimulation is necessary for inducing BOIs, this may specifically apply to conditions that include visuoproprioceptive mismatches.

3.4. SEMANTIC CONSTRAINTS IN BODY OWNERSHIP ILLUSIONS

3.4.1. SEMANTIC CONSTRAINTS IN OWN-BODY PERCEPTION

Beside the continuously updated sensory and motor information, our own-body perception largely relies upon higher-order, cognitive processes. Our semantic memories and knowledge contribute in shaping an abstract body model that contains information about the general and not self-specific visual, postural and structural properties of the human body. For example, we know how the human body is structured (e.g., the body has two hands), as well as how many degrees of freedom it has when it moves.

Given their non-self-specific nature, these cognitive processes depend, to an important extent, on neural mechanisms and brain areas that evolved for the visual perception of others' human bodies. Apart from brain areas specifically devoted to face perception (Haxby et al., 2000), several specialized regions for visual processing of bodies have been found in humans and non-human primates. This applies to hands, bodies (with and without heads), and to anatomically plausible body postures and motion (Peelen and Downing, 2007). Research in infants has shown that these selective areas are already functional at few days/months (Gliga and Dehaene-Lambertz, 2005; Hirai and Hiraki, 2005; Reid et al., 2006; Simion et al., 2008), suggesting that we are born equipped with structures for the visual encoding of body parts and human body kinematics.

Moving the focus away from own-body perception for a moment, semantic information has been proposed to be an important feature of multisensory integration. When considering two or more crossmodal stimuli, semantic congruence refers to their "close correspondence of content" (Doehrmann and Naumer, 2008). For example, a visual stimulus showing a dog is semantically congruent with a barking but not with a meowing sound (Alais et al., 2010). In this case, the semantic congruence of the audiovisual stimuli speaks in favor of a common underlying cause: a dog. Several studies have shown that the integration of crossmodal stimuli is enhanced when these are semantically congruent (Doehrmann and Naumer, 2008).

The relevance of semantic congruence in the context of own-body perception has been demonstrated in non-human primates with the seminal work of Graziano et al. (2000). The authors showed that the activity of visuoproprioceptive neurons in the monkey brain is importantly modulated by the semantic content of the visual stimulus. Single cell activity was recorded while manipulating the position of the occluded monkey's arm, and that of a seen object. The object was either a replica of the arm or another object, such as a white paper or an apple's slice. The activity of the neurons was significantly modulated by the position of the arm replica, if the latter was in an anatomically plausible configuration. In contrast, changing the position of the white paper, or of the apple slice, had no effect. Interestingly, if the arm replica was seen in non-anatomically plausible configurations, i.e., with opposite handedness or rotated by 180° so that the fake fingers were pointing to the chest, the observed activity was no longer affected by the fake arm's position (Graziano et al., 2000).

Altogether, experimental evidence suggests that our brain is equipped with highly specialized structures for the visual processing of body parts and, in order to be effectively integrated with

the somatosensory signals, visual cues should not only resemble body parts but further satisfy body semantic constraints in terms of anatomical plausibility of posture and structure.

3.4.2. SEMANTIC CONSTRAINTS IN BOIs

In the particular context of BOIs, the level of semantic congruence refers to which extent the non-corporeal object resembles a not self-specific human body (body part) in terms of shape, anatomy and structure. We first distinguish between objects with human body shape or not (Figures 3A,B). If the objects are body-shaped, their semantic information can be further characterized by their texture, the anatomical plausibility of their spatial configuration and the anatomical plausibility of their internal structure (Figures 3C–E).

Figure 3. Examples of objects with different semantic information. (A) Objects with non-human body shape. (B) Objects with human body shape. (C) Objects with non-human skin texture (D) Objects (blue) in anatomically implausible spatial configurations with respect to the participant's body (red). (E) Objects (blue) with anatomically implausible structure with respect to the human body.

3.4.3. THE ROLE OF SHAPE

Converging experimental evidence suggests that BOIs are shape-sensitive. For example, when a checkerboard (Zopf et al., 2010) was used instead of a rubber hand, the reports of the illusion were weaker if not entirely absent. Analogous inhibition in subjective reports was found for non-body shaped objects with hand-like skin texture (Haans et al., 2008) or size (Hohwy and Paton, 2010, experiment 3). Similar inhibitory effects were also detected for proprioceptive drifts when using a stick instead of a rubber hand (Tsakiris and Haggard, 2005). Analogously, full BOIs were suppressed when participants had a 1 PP view of a rectangular body-sized object instead of a 1 PP view of a mannequin (Petkova and Ehrsson, 2008). Furthermore, even smaller violations of shape were shown to have an effect; in the study of Tsakiris et al. (2010a) the RHI was reported only for the rubber hand and not for other objects, including a wooden block with sculpted wrist and fingers.

The results reported in the study of Armel and Ramachandran (2003) are somewhat in disagreement with these findings: stroking a table surface synchronously with the participants' hidden hand induced weak ownership sensations toward the table, though significantly higher in intensity compared to the control condition in which the real hand was visible. Despite this, subjective scores for the "table ownership" were significantly lower with respect to when a rubber hand was used—a condition that always preceded the table one. Motivated by this point, the study of Hohwy and Paton (2010) showed that while the mere synchronous visuotactile stimulation of a piece of hand-sized cardboard was not sufficient to induce the illusion (experiment 3), prior induction of the illusion (by using a rubber hand) could instead allow the illusion to be sustained and projected on the cardboard when the rubber hand was instantaneously replaced by it (experiment 2).

These results suggest that whereas BOIs are critically sensitive to shape, a prior exposure to the illusion can modulate this sensitivity by overriding the contribution of prior knowledge about the shape of human bodies to the illusion itself.

3.4.4. THE ROLE OF TEXTURE REALISM

Semantic information related to the realism of the fake body (body part) has been investigated through modifying its seen material texture. The realism of the seen texture is associated with the degree of the perceived biological plausibility of the seen object as a candidate for a human body part. Texture realism has been shown not to be crucial for BOIs; yet, modulations in the intensity of the illusion have been found when manipulating the texture. For example, the RHI has been elicited toward a fake hand wearing a latex glove, though at a significantly lesser intensity compared to when the realistically textured rubber hand was used (Haans et al., 2008). Similarly, a mechanical hand-shaped object made of wires, permitted the induction of the RHI through congruent visuotactile stimulation, albeit to a significantly lesser extent compared to when a realistic replica of a human hand was used (Bertamini and O'Sullivan, 2014). Turning to full BOIs, texture realism was proposed to have a modulatory effect when providing visuotactile stimulation (Maselli and Slater, 2013): whilst congruent visuotactile triggers were found to be necessary in eliciting the full BOI toward a spatially coincident plastic mannequin (Petkova and Ehrsson, 2008; Petkova et al., 2011b), using a realistically textured virtual body produced negligible differences between congruent and incongruent visuotactile stimulations (Maselli and Slater, 2013). Nevertheless, congruent visuomotor stimulation with a spatially coincident virtual body having an unnatural purple skin color induced

the illusion, without significant differences in strength compared to when a realistic skin texture was used (Peck et al., 2013). This last result suggests that visuomotor correlations may tend to saturate the illusion, so that modulations by texture become negligible.

3.4.5. THE ROLE OF ANATOMICAL PLAUSIBILITY OF SPATIAL CONFIGURATION AND OF VISUAL PERSPECTIVE

The anatomical plausibility of the spatial configuration of the fake body was shown to play a critical role in the induction of BOIs. For example, rotating the rubber hand by 180° (with the rubber fingers pointing toward the participant) prevented the RHI, despite congruent visuotactile (Ehrsson et al., 2004; Holle et al., 2011) or visuomotor (Kalckert and Ehrsson, 2012) stimulation. Analogously, a 90° rotation of a left rubber hand (with the rubber fingers pointing to the left) was shown to reduce the difference in proprioceptive drifts between synchronous and asynchronous visuotactile stimulation (Tsakiris and Haggard, 2005) and to delay the onset of the RHI (Aimola Davies et al., 2013). A systematic study in which different rotations were applied on the rubber hand, including both anatomically plausible and implausible configurations, has shown that illusory experiences were elicited mainly for anatomically plausible configurations (Ide, 2013).

Apart from violating constraints of human joints articulation, the plausibility of the body spatial configuration can be broken also by manipulating the visual perspective on the fake body or body part. For example, seeing directly one's own body from a distance is anatomically impossible. Similar to findings from the RHI, having a 3 PP over a distant virtual body or a mannequin was found to inhibit the illusion, despite congruent visuotactile stimulation between the real and the fake body. Upon direct comparison of 1 PP and 3 PP conditions, this inhibition was consistently found for different distances at which the fake body was seen: 100 cm (Slater et al., 2010), 80 cm (Maselli and Slater, 2013), 75 cm (Petkova et al., 2011b), and 40 cm (Maselli and Slater, 2014). In contrast, when the visual perspective was slightly shifted from the eyes of the virtual body, but still consistent with an anatomically plausible view of the own body, the full BOI was induced (Maselli and Slater, 2014). These results are consistent with evidence from RHI experiments that have shown an inhibition of the illusion for rubber hands placed beyond the reaching space. These, as well as other configurations, e.g., the fake hand rotated 180°, could be regarded as cases of having a 3 PP over the fake limb. Interestingly, Bertamini and colleagues induced a vivid RHI providing exclusively a 3 PP view of the rubber hand through a mirror (Bertamini et al., 2011). The apparent disagreement between this result and the findings mentioned above could be explained by the fact that the 3 PP view was provided through a mirror, and considering that we automatically attribute visual information from the mirror to the physical location of the reflected objects. Indeed, the critical role of the mirror in mediating the visual perspective was confirmed within the same study: the RHI was abolished when providing exactly the same visual information about the rubber hand and visuotactile stimulation, but without an intervening mirror.

3.4.6. THE ROLE OF ANATOMICAL PLAUSIBILITY OF STRUCTURE

The impact of anatomical plausibility of the structure of the seen object has been shown to vary importantly depending on the specific manipulation. For example, full BOIs have been shown toward artificial bodies of a significantly different scale from the real ones (van der Hoort et al., 2011; Banakou et al., 2013). With respect to the volume of the artificial body (body part), several studies

have successfully elicited BOIs toward two dimensional video projections of either the real or the rubber hand (Ijsselstein et al., 2006; Tsakiris et al., 2006; Shimada et al., 2009) or toward a normal-sized hand of non-biological texture and of reduced volume (Bertamini and O'Sullivan, 2014), although the illusion was found to be stronger when the fake body part was seen with normal volumetric characteristics (Ijsselstein et al., 2006). Concerning body connectivity, subjective scores of ownership toward a virtual hand were significantly stronger when this was seen to be connected to the virtual torso rather than disconnected (Perez-Marcos et al., 2012).

With respect to body proportions, several studies that manipulated the seen hands to be either smaller or larger than the average population size, revealed various effects, including weight and size perception (e.g., Haggard and Jundi, 2009; Bruno and Bertamini, 2010; Linkenauger et al., 2013), distance perception (e.g., Linkenauger et al., in press), and movement kinematics (e.g., Bernardi et al., 2013). When studying the particular effect of hand size on eliciting the RHI, high illusion scores without significant differences were reported when using either a small (e.g., hand size of a primary school child) or a large (e.g., hand size of a tall man) rubber hand (Heed et al., 2011). Similarly, no significant differences in the illusion scores were detected when using a two dimensional hand image that was either equal in size, magnified or shrunk by 3 cm with respect to the participants' real hand (Pavani and Zampini, 2007). Similarly, the RHI was elicited with a small and a large rubber hand, still within the range of anatomically plausible body structures (Bruno and Bertamini, 2010). In contrast, using artificial body parts that violated normal body proportions, as for example a fake arm 91 cm beyond the real one, was shown to elicit weaker feelings of ownership through congruent visuotactile stimulation, compared to when the fake arm was seen with a plausible length (Armell and Ramachandran, 2003). When providing both visuotactile and visuomotor stimulation, participants gave high scores of ownership over a virtual arm up to three times the length of the real one, but less strongly at four times the length (Kiltner et al., 2012).

A similar effect was found when manipulating the number of artificial body parts. For example, stroking a rubber hand synchronously with the participants' visible hand (Guterstam et al., 2011), or stroking two rubber hands placed side-by-side synchronously with the participants' occluded real hand (Ehrsson, 2009), was shown to induce the illusion of having multiple limbs or owning two hands of the same laterality at the same time, respectively. Nevertheless, in both cases the experienced ownership was stronger when employing the classic RHI setup. With respect to simultaneous ownership toward two rubber hands of the same laterality, it was shown that these need to be placed symmetrically with respect to the real limb (Folegatti et al., 2012). High illusion scores concerning having two limbs were further reported when participants were moving their hand while seeing two video replicas, projected symmetrically with respect to the real, moving accordingly (Newport et al., 2010).

The spatial arrangement of the artificial body part with respect to the participant's body was instead demonstrated to be critical. For example, seeing a right rubber foot being stroked synchronously with the participants' right hand did not induce ownership feelings (Guterstam et al., 2011). Analogously, no significant differences were found in proprioceptive drifts when comparing synchronous and asynchronous stimulation applied on a right rubber hand and the participants' left hand (Tsakiris and Haggard, 2005).

3.4.7. THE ROLE OF STIMULATION CONGRUENCE

Another aspect of semantic congruence concerns the compatibility of the seen and felt touch when inducing BOIs through visuotactile stimulation. In the majority of studies, the instrument seen to administer the touch on the artificial body was the same—e.g., paintbrushes (Botvinick and Cohen, 1998), sharp pins (Capelari et al., 2009), rods (Petkova and Ehrsson, 2008)—or a visually compatible one, with the one used to deliver the touch on the real body (Slater et al., 2008; Pabon et al., 2010; Normand et al., 2011; Maselli and Slater, 2013). Nevertheless, using different instruments could inhibit the occurrence of the BOI by violating the participants' tactile expectancies: the participant who sees the fake body being touched by a soft texture material, would expect sensations of analogous quality on his/her real body. This was investigated by using a piece of cotton to stimulate the rubber hand while using a piece of sponge to stimulate the real hand or vice versa. Results from both proprioceptive drifts and questionnaires were not significantly different from the case in which the same instrument was used (Schütz-Bosbach et al., 2009).

3.4.8. SUMMARY

Experimental evidence suggests that BOIs are greatly affected by the semantic information the visual cues of the fake body bring along, at least in terms of their shape, the anatomical plausibility of their spatial configuration and structure. Even if some forms of anatomical violations (e.g., larger or smaller bodies, longer or multiple limbs) can be tolerated and overcome by congruent multimodal stimulation, other forms of violation (e.g., spatial arrangement) may not. This suggests that, in order to be perceived as parts of the own body, fake objects need to satisfy to some extent semantic constraints from an abstract and not self-specific body model (Tsakiris et al., 2007; Longo et al., 2009; Tsakiris, 2010). Yet, the exact boundaries of tolerable violations are still to be determined.

4. THEORETICAL ACCOUNTS FOR INDUCTION OF BODY OWNERSHIP ILLUSIONS

The studies on BOIs that we have reviewed so far provide important insights on the contribution of multisensory signals and semantic knowledge on the emergence of our sense of body ownership. However, in order to gain a deeper understanding on how the brain infers which is our body and its limbs, it is necessary to understand why BOIs are induced at all. Although there is extensive consensus in the literature that multisensory processing of bodily signals underlies the induction of BOIs (Graziano and Botvinick, 2002; Makin et al., 2008; Tsakiris, 2010; Ehrsson, 2011; Maselli and Slater, 2013), very few researchers attempted to cast the experimental conclusions into a unitary framework.

The initial Botvinick and Cohen's proposal was that the RHI arises from the three-way interaction between vision, touch and proprioception (Botvinick and Cohen, 1998). This idea was reflected in the proposal of Makin et al. (2008). According to their model, visual and proprioceptive cues about the positions of the real and rubber hands are first combined into a single estimate of the hand's spatial configuration; following, visual and tactile information about the seen and felt touches are processed

in the common reference frame of the hand and, if integrated, elicit the illusion. This proposal was extended to account for experimental findings on the contribution of semantic information. According to the model proposed by Tsakiris (2010), the integration of multisensory cues is gated by semantic information in terms of the shape and anatomical plausibility of the seen object; only those objects that fit a pre-existing internal model of the human body can be therefore experienced as parts of the own body. In his account, Tsakiris proposed that this “test-for-fit” process takes place in the right temporo-parietal junction (Tsakiris et al., 2008). Alternatively, it was suggested that this selection process might be operated by visuoproprioceptive populations (Maselli and Slater, 2013).

Although these models offer a schematic description of the induction of BOIs, by referring also to candidate brain areas that operate the multisensory integration and the semantic gating, they do not explain what is the underlying computational problem, and how our brain solves it with the resulting illusory experience. In the following, we briefly review recent predictive coding accounts that propose a specific computational framework for the study of self-processing, including the sense of body ownership. Subsequently, we focus on two alternative computational accounts, namely the Bayesian causal inference models and the connectionist models. Both approaches have been developed to explain various multisensory perceptual phenomena and they could be adopted and extended in future works to address the problem of BOIs.

4.1. PREDICTIVE CODING APPROACHES

In a recent stream of work (Hohwy, 2007; Apps and Tsakiris, 2013; Clark, 2013; Limanowski and Blankenburg, 2013; Seth, 2013), the problem underpinning self-processing and self-recognition has been approached within the general framework of hierarchical generative models, such as predictive coding (Srinivasan et al., 1982; Rao and Ballard, 1999) and the free-energy principle (e.g., Friston, 2009). These models adopt the view, originally put forward by Von Helmholtz (Hatfield, 1990), that the brain needs to infer the hidden causes of the sensory signals; for example, the existence of a dog when hearing barking-like sound. It does so, by minimizing the error between the predictions it makes about the expected cues based on its internal causal model (e.g., what would be the auditory stimulus associated with a dog) and the available sensory information (e.g., the heard barking sound).

In this context it has been proposed that the RHI results from minimizing the prediction errors that arise from feeling the touch on the real hand and seeing the touch at a different location (i.e., on the rubber hand), as well as the errors concerning the rubber hand not looking exactly as the real hand. Error minimization would thus result in merging the spatial representation of the two hands and further in updating prior beliefs about one’s own hand appearance (Apps and Tsakiris, 2013; Seth, 2013). Interestingly, several findings from RHI studies can be explained as the effect of strategies for error minimization; this is the case of the attenuation of somatosensory processing in the real hand, like e.g., the slowing of tactile temporal processing (Moseley et al., 2008), the increase of tactile detection threshold (Zopf et al., 2011), and the reduction of primary somatosensory cortex responses to tactile stimuli (Zeller et al., 2014). Since the main source of errors arises from the spatial discrepancies between the visual position of the rubber hand and the

position of the real one provided by somatosensation, decreasing the precision of the latter could constitute an effective strategy to minimize the error (Zeller et al., 2014).

Despite the insights that these models provide about possible neurobiological mechanisms underlying BOIs, to date these proposals have been formulated mainly at a conceptual level, without tackling the underlying computational problem.

4.2. CAUSAL INFERENCE IN MULTIMODAL CUE INTEGRATION UNDER BOIs

In contrast to predictive coding accounts, Bayesian causal inference models offer a simpler and comprehensive computational account for multisensory phenomena, usually without addressing the neurobiological mechanisms. According to these models, when people are presented with two stimuli from different modalities, they initially infer whether these have the same origin (i.e., cause) or not, and then they combine their information according to these beliefs (Körding et al., 2007). For example, when we hear a barking sound and we see a dog close to the auditory source, we will be confident that the barking sound comes from the seen dog and we will therefore use both the visual and the auditory information to estimate the position of the dog. In contrast, when the sound is perceived to come from a very distinct position with respect to the position of the seen dog, we may consider the existence of two dogs as more likely. Causal inference models were shown to explain various phenomena in multisensory perception (Shams and Beierholm, 2010), including the spatial (Körding et al., 2007; Wozny et al., 2010) and temporal (Shams et al., 2005) ventriloquist effects, and visuomotor adaptation (Körding and Tenenbaum, 2006; Wei and Körding, 2009).

While these models have been typically used to describe the combination of two sensory cues, analogous ideas could be applied to explain the induction of BOIs. Indeed, Armel and Ramachandran (2003) proposed that the RHI is induced due to a Bayesian perceptual learning driven by the high likelihood of the visual and tactile stimuli to occur from one common event. In other words, it is more likely that the seen touch and the felt touch belong to the same event (i.e., my hand being stroked), than the existence of one artificial hand that is stroked synchronously with my hidden hand. Due to the fact that their proposal was exclusively based on the likelihood of sensory data, it was quickly put aside by other authors, as it was unable to explain the inhibition of the illusion under semantic violations (Tsakiris and Haggard, 2005; Tsakiris, 2010).

Nevertheless, a Bayesian model that includes semantic influences can be used to address the induction of RHI. For example, using the causal inference framework, the computational problem the brain needs to solve refers to inferring whether there is a common cause (i.e., my hand) or two different causes (i.e., my hand and the rubber one) generating the available visual, tactile, and proprioceptive signals (Figure 4). Mathematically formalizing the problem, the nervous system needs to calculate the probability of there being one hand ($C = 1$) vs. there being two hands ($C = 2$), given the available sensory information and prior knowledge. At time τ the sensory data consist of the static visual (x_v) and proprioceptive (x_p) spatial configuration of the real and rubber hands, the semantic information of the seen object mv , and the trains of tactile stimuli applied, up to the current moment τ , on the

rubber ($s_V^{\rightarrow\tau}$) and the real ($s_T^{\rightarrow\tau}$), respectively (Equation 1).

$$p(C = 1 \mid m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau}) = \frac{p(m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau} \mid C = 1)p(C = 1)}{p(m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau})} \quad (1)$$

Figure 4. A causal inference model for the classic version of the RHI. Left: one cause being responsible for all cues. In this case, the visually perceived configuration x_V , the proprioceptive perceived configuration x_P , the seen strokes $s_V^{\rightarrow\tau}$ and the felt strokes $s_T^{\rightarrow\tau}$ together with the seen morphological characteristics m_V , are mapped into a common cause ($C = 1$). Right: alternatively, two distinct causes may be inferred, decoupling the problem into two independent estimation problems. The brain infers whether the seen and felt spatial configurations, the tactile events and the seen morphology origin from the same causal structure, i.e., my hand ($C = 1$), or independent causal structures, i.e., the real and the rubber hands ($C = 2$), and then derives optimal predictions from this.

Under the simplifying assumption that the visual, tactile and proprioceptive information are conditionally independent, the problem can then be formulized as:

$$p(C = 1 \mid m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau}) = \frac{p(m_V \mid C = 1)p(x_V, x_P \mid C = 1)p(s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau} \mid C = 1)p(C = 1)}{p(m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau})} \quad (2)$$

The model described by Equations (1) and (2) states that the probability for a single hand existing, estimated at time τ given the sensory evidence, depends on the likelihood of the evidence given

only one hand — $p(m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau} | C = 1)$ — and on the prior expectation for only one hand being there — $p(C = 1)$. The likelihood of the data depends on (i) the distance between the two hands, i.e., $p(x_V, x_P | C = 1)$, (ii) the spatiotemporal discrepancies of the visuotactile stimulation, i.e., $p(s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau} | C = 1)$, and (iii) the level of semantic congruence between the seen hand and the real one, i.e., $p(m_V | C = 1)$. These visuoproprioceptive, visuotactile, and semantic factors contribute to the likelihood by increasing it in proportion to the congruency of the correspondent stimuli¹. The likelihood, in turn, is in continuous interplay with prior expectations (e.g., the position of the limbs close to the body midline, personality traits including suggestibility to illusory perceptions, previous experience of the illusion), to update the posterior probability of only one hand being responsible for the sensory inputs, $p(C = 1 | m_V, x_V, x_P, s_V^{\rightarrow\tau}, s_T^{\rightarrow\tau})$. The illusion is then experienced when this posterior probability exceeds a given threshold (Wozny et al., 2010).

This relatively simple model, at least qualitatively, can accommodate many of the experimental findings on the RHI. For example, when the rubber hand is placed close to the real hand and without violating anatomical constraints, spatiotemporally congruent visuotactile stimulation will accumulate evidence in favor of a common hand being the source of all sensations and would induce the illusion (e.g., Botvinick and Cohen, 1998). The progressive convergence of the model to a common hand scenario is also supported by experimental evidence that the RHI is not immediate but needs time to be elicited (Peled et al., 2000; Ehrsson et al., 2004; Perez-Marcos et al., 2012). On the other hand, when the visuotactile stimulation is asynchronous (e.g., Botvinick and Cohen, 1998; Armel and Ramachandran, 2003) or spatially incongruent (e.g., Kammers et al., 2009), the evidence will favor the existence of two hands, and the illusion will not be induced. In addition, semantic violations in terms of shape, anatomical plausibility and realism will render the contribution of the likelihood less important and therefore, the induction of the illusion more difficult, and its resulting strength weaker (Armel and Ramachandran, 2003; Haans et al., 2008; Ehrsson, 2009; Ide, 2013). Moreover, placing the rubber hand far from the real one and from the participant's midline corresponds to decreasing both the likelihood of visuoproprioceptive signals and the prior probability of the limb's position (Lloyd, 2007; Preston, 2013). Finally, when the two hands are overlapping or close in space, the high likelihood of visuoproprioceptive information can render the contribution of the visuotactile likelihood unnecessary (Giummarra et al., 2010) or less relevant (Zopf et al., 2010).

This formulation of the problem could be further extended to dynamically include the effects of having experienced the illusion at a given time, on the (prior) expectation for the illusion to occur at following times, as well as on the way the brain processes the incoming sensory signals (likelihood) later on. Computationally this could be done by adopting an iterative approach in which both the prior expectation and the probability densities representing the likelihoods at a given time step, evolve over time as a function of the posterior probability. Such an extension of the model could account for several aftereffects reported in the literature. In Hohwy and Paton (2010), for example, it was reported that if, after a period of congruent visuotactile stimulation in which the illusion is established, the stimulation switches to incongruent patterns (e.g., seeing elevated stroking on the rubber hand while receiving physical touch) then participants would keep experiencing the illusion together with unusual perceptual sensations (e.g., supernaturally caused tactile sensations). These results can indeed be explained by the fact that having experienced the illusion enhances the

1. The probability distribution functions in Equation (2) can be for example approximated as normal distributions in the correspondent metric.

expectation for the illusion to be there (increasing the prior probability) and, at the same time, this modulates the probability densities of the likelihoods involved ($p(s_v^{\rightarrow t}, s_r^{\rightarrow t} | C = 1)$ in this case), e.g., increasing the variance, so to “explain away” the ongoing illusion and suppress the sensory conflict. This formulation is conceptually analogous to minimizing prediction errors in predictive coding approaches and, as discussed in the previous section, can account for several after-effects of the illusion, e.g., the attenuation of the somatosensory processing on the real hand (see the previous section for references).

It is noteworthy that this type of model can be adapted to include the effects of patterns of visuotactile stimulations that go beyond spatiotemporal congruency, such as applied pressure, duration, trajectory, frequency, velocity or predictability. Recent studies have observed that some of these features, closely related to affective and emotional aspects of touch, (e.g., the velocity of the applied stimulation) can significantly modulate the RHI (Crucianelli et al., 2013; Lloyd et al., 2013; van Stralen et al., 2014). Particularly concerning the predictability of the visuotactile stimulation, the probability of two independent visuotactile patterns being spatiotemporally congruent is lower the higher their complexity. Therefore, being exposed to congruent patterns of increasing complexity should lead to stronger illusions, and/or to illusions established on shorter time scales. Although there is no study explicitly testing this, reports in the literature support that increasing the stimulation variability can avoid habituation effects and lead to a faster and stronger illusion (Niebauer et al., 2002; Armel and Ramachandran, 2003; Tsakiris et al., 2008; Petkova and Ehrsson, 2009; Guterstam et al., 2011). The same observations were reported for visuomotor stimulation (Tsakiris et al., 2006; Kalckert and Ehrsson, 2012). This evidence is consistent with the proposal that unpredictability increases the weight of multisensory likelihood in inferring a common body.

A similar causal inference model can be applied to address the induction of BOIs in presence of visuomotor stimuli. In this case, visual and proprioceptive inputs that change dynamically in time can provide accumulating evidence in favor of a single cause if congruent — $p(C = 1 | m_v, x_v^{\rightarrow}, x_p^{\rightarrow})$. Such a formulation can further bring forward the question of whether some crossmodal stimuli contribute more in inferring our own body than others. Congruent visuotactile or visuomotor stimuli between the real and rubber index finger was shown to elicit the RHI without significant differences (Riemer et al., 2013; Kalckert and Ehrsson, 2014a). Nevertheless, when testing the relative role of visuomotor and visuotactile correlations between the real and the virtual lower limbs under the same experimental condition, a stronger contribution of visuomotor stimuli was found in inducing the BOI, whilst incongruent stimulation of each of the two led equally to its break (Kokkinara and Slater, 2014). Given that visuomotor correlations contain a larger amount of information compared to visuotactile correlations (e.g., in terms of the internal model involved), the proposed model would predict a faster onset of BOIs. Moreover, this facilitation might also depend on which body parts are involved in the movements (e.g., moving the index finger vs. moving an entire upper or lower limb). However, these predictions need to be explicitly tested.

Finally, the same model could be reformulated and extended to account for the full BOIs taking into account the relevant pieces of multimodal and semantic information.

4.3. NETWORK MODELS

Connectionist models offer an alternative approach for addressing the problem of BOIs. Although they have not been previously envisioned in this context, these models have been successfully applied in the field of multisensory integration as an alternative approach to Bayesian models (e.g., Patton and Anastasio, 2003; Martin et al., 2009; Cuppini et al., 2011). Connectionist models implement artificial networks with architectures that are typically inspired from neurobiological structures and are suited to simulate learning mechanisms and collective neuronal behavior. They therefore offer an important advantage with respect to the Bayesian approaches, as they can provide deeper insights into the neural mechanisms involved in the processes under study, although at the expense of higher complexity (Fernandes and Kording, 2010)

Apart from reproducing some of the most relevant properties of multisensory processing at the level of neural activity (Patton and Anastasio, 2003; Rowland et al., 2007; Martin et al., 2009), recent implementations have been proposed to account for perceptual illusions. For example, relatively simple networks, consisting of two layers reciprocally interconnected, could reproduce common illusions such as the sound-induced flash illusion and fusion (Cuppini et al., 2014), as well as the ventriloquist effect and aftereffect (Magosso et al., 2012).

Particularly relevant for the present discussion is the implementation of neural networks whose dynamics reproduces several observed properties of visuotactile processing. For example, a network with two unimodal and one bimodal areas, could reproduce effects of visuotactile integration such as the facilitation of tactile detection, localization and acuity, by concurrent visual information (Magosso, 2010). Modifications of this implementation have been shown to reproduce other key aspects of visuotactile integration. For example, by including Hebbian learning mechanisms tuned by attentional effects (Ursino et al., 2007; Magosso et al., 2010b), it was possible to simulate the dynamical expansion of the peripersonal space observed after tool use (Maravita and Iriki, 2004). In addition, interhemispheric competition effects, similar to the ones observed in right-brain-damaged patients (di Pellegrino et al., 1997; Mattingley et al., 1997), have been further emulated with models in which two replications of the network described above (one for each hand) were interconnected by inhibitory interneuron modules (Magosso et al., 2010a,b).

All these remarkable results address the possibility to apply this class of model to develop new theoretical accounts for BOIs. A plausible scenario would be to initially combine these models with Bayesian modules. For example, while the visuotactile processing involved in the RHI could be simulated with neural networks, the test-for-fit gating associated with neural populations specialized in body parts recognition, could be more conveniently described with the Bayesian formalism. Alternatively, existing implementations of neural networks for the representation of semantic information (for a review see Ursino et al., 2014), provide a valid option for representing semantic factors in BOIs. Such envisioned hybrid models would be indeed ideal for gaining deeper insights into our current understanding of the BOIs and their implications for own-body perception.

5. CONCLUSIONS

One of the important questions in neuroscience, psychology, and philosophy concerns how we distinguish our body from the bodies of others as well as from objects in the surrounding environment (Gallagher, 2000; Jeannerod, 2003; Blanke and Metzinger, 2009; de Vignemont, 2011). Body ownership illusions (BOIs) are a powerful experimental tool to address this question, since they permit to investigate the conditions under which we can perceive artificial body parts or fake bodies as belonging to ourselves. In the present review, we focused on the role of multisensory integration and semantic knowledge in inducing BOIs. In particular, we reviewed the role of the temporal, spatial, and semantic relationship of crossmodal stimuli in the elicitation of the illusions as reflected in several experimental studies, and we further discussed and proposed theoretical accounts in order to cast all this information into one computational framework.

Given the vastness of the experimental literature around BOIs, the present review is not exhaustive. For example, we focused on BOIs induced in presence of visual information, excluding therefore the somatic versions of BOIs and similar body illusions induced with auditory cues (Tajadura-Jiménez et al., 2012). Nevertheless, similar principles to those proposed here have been revealed: e.g., temporal constraints in visuotactile integration (Ehrsson et al., 2005a) and negligible effects of tactile quality (White et al., 2010). In addition, we did not address the important contribution of interoceptive signals in the sense of body ownership (Seth, 2013), although this has recently shown to influence different aspects of BOIs (Crucianelli et al., 2013; Lloyd et al., 2013; van Stralen et al., 2014).

Moreover, our theoretical proposals based on computational principles that combine and integrate exteroceptive and proprioceptive signals for explaining the induction of BOIs, do not imply that the emergence of the sense of body ownership relies on a strictly deterministic computation. For example, interoceptive signals and emotional states are fundamental in our sense of embodiment (Carruthers, 2008; Seth, 2013). Nevertheless, we consider that formulating and experimentally validating computational models, even if these are approximate and not exhaustive, can be a first step toward deciphering the mechanisms underlying BOIs. These approaches can be extended to include further contributions and to account for a more holistic view of our own body-perception.

Beside the necessity for experimental validation of such theoretical models, future studies are needed to investigate whether and how the contribution of spatial, temporal, and semantic characteristics of crossmodal stimuli changes once BOIs are experienced. That is, while we discussed the experimental principles in the context of inducing the illusions, there is the possibility that these spatial, temporal, and semantic constraints are adapted after the onset of the illusion—a possibility discussed above as part of the causal model. The study of Hohwy and Paton (2010) points certainly in this direction: once the rubber hand illusion was induced with a standard paradigm, the illusion could be sustained even when suddenly introducing semantic or spatiotemporal violations in the crossmodal stimuli. The result of this intervention was the elicitation of unusual experiences such as tactile sensations originating from a stroked cardboard, or supernatural tactile sensations generated by an elevated finger that was not in contact with the rubber hand. Similarly, in the study

of Kilteni et al. (2012) the gradual introduction of semantic violations in terms of body proportions did not abolish but sustained the ownership illusion toward a very long fake arm. The same question could be also applied to the temporal aspects of visuotactile integration; for example, does the illusion persist if the administered visuotactile stimuli progressively change from synchronous to asynchronous? Indeed, there is evidence suggesting that a full BOI triggered by seeing a realistic virtual body in spatial coincidence with the physical body, could be sustained during asynchronous visuotactile stimulation (Maselli and Slater, 2013).

Last but not least, the present review leaves the question of why somatoparaphrenic patients perceive their body parts as not belonging to themselves, unanswered. Although outside the scope of the present review, recent studies have started to explore the induction of BOIs with somatoparaphrenic patients (Jenkinson et al., 2013; van Stralen et al., 2013; Bolognini et al., 2014). Investigating whether or not the principles on multimodal triggers and semantic information mentioned here for healthy subjects, apply also for these patients, could provide a possible strategy to grasp the link between delusions and illusions of body ownership.

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CHAPTER 6

SLIDING PERSPECTIVES: DISSOCIATING OWNERSHIP FROM SELF-LOCATION DURING FULL BODY ILLUSIONS IN VIRTUAL REALITY

Related publication:

Sliding perspectives: dissociating ownership from self-location during full body illusions in virtual reality.
Maselli, A., and Slater, M.
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ABSTRACT

Bodily illusions have been used to study bodily self-consciousness and disentangle its various components, among other the sense of ownership and self-location. Congruent multimodal correlations between the real body and a fake humanoid body can in fact trigger the illusion that the fake body is one's own and/or disrupt the unity between the perceived self-location and the position of the physical body. However, the extent to which changes in self-location entail changes in ownership is still matter of debate. Here we address this problem with the support of immersive virtual reality. Congruent visuotactile stimulation was delivered on healthy participants to trigger full body illusions from different visual perspectives, each resulting in a different degree of overlap between real and virtual body. Changes in ownership and self-location were measured with novel self-posture assessment tasks and with an adapted version of the cross-modal congruency task. We found that, despite their strong coupling, self-location and ownership can be selectively altered: self-location was affected when having a third person perspective over the virtual body, while ownership toward the virtual body was experienced only in the conditions with total or partial overlap. Thus, when the virtual body is seen in the far extra-personal space, changes in self-location were not coupled with changes in ownership. If a partial spatial overlap is present, ownership was instead typically experienced with a boosted change in the perceived self-location. We discussed results in the context of the current knowledge of the multisensory integration mechanisms contributing to self-body perception. We argue that changes in the perceived self-location are associated to the dynamical representation of peripersonal space encoded by visuotactile neurons. On the other hand, our results speak in favor of visuo-proprioceptive neuronal populations being a driving trigger in full body ownership illusions.

1. INTRODUCTION

A large body of experimental research in cognitive neuroscience has exploited bodily illusions to study bodily self-consciousness. This work has established a tight link between self-consciousness and the processing of multisensory bodily signals performed in specific brain areas (Makin et al., 2008; Ehrsson, 2011; Blanke, 2012). It further allowed disentangling distinct components of bodily self-consciousness and their candidate neural representations (Longo et al., 2008; Blanke and Metzinger, 2009; Tsakiris et al., 2010).

The present study focuses on the mutual relation between two important components of bodily self-consciousness: the feeling of owning a body (*body ownership*) and the experience of the body occupying a given portion of space in the environment (*self-location*). Although in normal conditions *ownership* and *self-location* are tightly tied, recent experimental work has shown that these two components are, at least partially, separable (Longo et al., 2008). However, so far it has not been explored whether these two components are intrinsically coupled or are rather dissociable despite their strong coupling (Serino et al., 2013). In this article we present a study performed with the support of virtual reality (VR) technology, and designed to specifically test the hypothesis that, under specific experimental conditions, *ownership* and *self-location* can be selectively altered. The rationale behind the current study is based on a series of previous studies that are reviewed in the following.

1.1. EXPERIMENTAL MANIPULATIONS OF THE SENSE OF SELF-LOCATION

Self-location has been mainly investigated through experimentally induced out-of-body experiences (OBE). The experimental paradigm to induce an OBE in healthy subject consists in participants wearing a head-mounted display (HMD) occluding the physical body and displaying the back of their own body -or that of a mannequin- as filmed from a distance of roughly two meters. The visual perspective then coincides with the location of the real body and is dissociated from the location of the virtual body seen through the HMD. The illusion is then triggered through congruent visuotactile stimulation on the real and fake body. When synchronous visuotactile stimulation is delivered on the back (Lenggenhager et al., 2007), most participants experience the illusion of looking at their body from the outside, similarly to what is reported in OBEs of neurological origin (Blanke and Mohr, 2005). This illusion is associated with illusory changes in *self-location*, with a systematic shift from the participant's visual perspective toward the seen body. Such a drift has been consistently found throughout a variety of assessments: the "walking task" (Lenggenhager et al., 2007) and the "mental ball dropping" task (Lenggenhager et al., 2009) provided explicit measures of the perceived *self-location* in external and body-centered reference frames respectively, while the crossmodal congruency task (CCT) was used to implicitly assess *self-location* through the localization of tactile events in the external space (Aspell et al., 2009).

Functional magnetic resonance imaging (fMRI) revealed that these illusory changes in *self-location* correlate with activity in the temporo-parietal junction (TPJ) and the extrastriate body area (EBA) (Ionta et al., 2011). The implication of the TPJ was consistently found in lesion studies on neurological

patients suffering aberrations in *self-location* (Blanke et al., 2004). Focal electrical stimulation of the TPJ was further shown to systematically trigger OBE (Blanke et al., 2002).

In a similar experimental setting, OBE illusions have been alternatively triggered by delivering synchronous visuotactile stimulation on the chest while displaying the visual stimuli at the location of the occluded physical body (Ehrsson, 2007). In contrast to what found in the “back stroking” case, participants tended to feel located at the position of the physical body; this was implicitly assessed by asking participants to rate how much they felt at the location where they saw their body or at the camera’s (i.e., the physical body’s) location (Guterstam and Ehrsson, 2012). The difference is probably due to the fact that, in the “chest stroking” case there is no spatial conflict between visual and tactile cues. In the “back stroking” case, it probably the spatial misalignment of visual and tactile synchronous cues that induces a recalibration in the perceived *self-location*.

1.2. EXPERIMENTAL MANIPULATIONS OF THE SENSE OF OWNERSHIP

The sense of ownership toward a full body has been largely studied making use of the full body ownership illusion (FBOI), defined as the continuous and consciously impermeable feeling that a virtual/fake full body, including all its body parts, belongs to us in its integrity.

Built up on the rich experimental literature on the rubber hand illusion (Botvinick and Cohen, 1998), the experimental paradigm to elicit a FBOI consists in outfitting participants with an immersive HMD that occludes the real body and displays in its place a fake humanoid body, which may be a filmed mannequin (Petkova and Ehrsson, 2008) or a virtual character (Slater et al., 2010). Unlike the case of OBE, participants have thus a first person perspective (1PP) of the fake body usually displayed in the same posture as the real body. This setup provides participants with congruent visuo-proprioceptive cues, i.e., visual information about the virtual body’s spatial configuration are congruent with perceptual cues about the body posture delivered by muscle spindle and joint receptors. In the case of a static filmed mannequin, synchronous visuotactile stimulation was found to be the necessary trigger for eliciting the illusion (Petkova and Ehrsson, 2008). However, it was shown that other modalities of multisensory/multimodal correlations could trigger the illusion with no need for synchronous visuotactile stimulation. In particular, visuomotor correlations are extremely efficient in eliciting a FBOI (Slater et al., 2010; Kokkinara and Slater, 2014), thanks to the rich information processing involved in the sensorimotor control loop. On the other hand, if the fake body has a highly realistic humanoid appearance, the illusion may be elicited by congruent visuo-proprioceptive cues alone, with no need for further multimodal correlations (Maselli and Slater, 2013).

Healthy subjects experiencing a FBOI report that the seen fake body was perceived as if it was their own body and as if perceptual experiences, e.g., tactile events, were generated from the fake body. Apart from self-reports and questionnaires, the FBOI is indeed evaluated by monitoring autonomic responses to events threatening the fake body. For example, when attacking or threatening the integrity of the fake body during a FBOI, significant increases in skin conductance response (Petkova

and Ehrsson, 2008) and in heart rate deceleration (Slater et al., 2010; Maselli and Slater, 2013) have been found. Importantly, the measured change in autonomic responses is positively correlated with the intensity of the illusion inferred from questionnaire scores. By monitoring brain activity with fMRI during a FBOI, it was found that the illusion correlates with activity in bilateral ventral premotor cortex (vPMc), left intraparietal cortex and left putamen (Petkova et al., 2011a). Interestingly, the ventral premotor cortex activation was found to be particularly associated with the construction of the unitary experience of a full body, ensuing from the merging of the sense of ownership of different body parts. No implication of the TPJ during a FBOI has been reported.

An alternative approach to explore the sense of ownership, complementary to the FBOI, is the “chest stroking” OBE illusion described in the previous section (Ehrsson, 2007; Guterstam and Ehrsson, 2012). Autonomic responses to threat events have shown how, in this illusion, the sense of ownership is “attached” to the not visible real body located at the position of the visual perspective (Ehrsson, 2007; Guterstam and Ehrsson, 2012), while the sense of ownership toward the body seen in the extra-personal space is disrupted (Guterstam and Ehrsson, 2012).

1.3. DO OWNERSHIP AND SELF-LOCATION HAVE DIFFERENT NEURAL REPRESENTATIONS? HINTS FROM FULL BODY ILLUSIONS

When comparing results from the OBE and FBOI experiments discussed above, several hints emerge suggesting that *ownership* and *self-location* might have different origins and neural representations (Maselli and Slater, 2013; Serino et al., 2013).

First, as discussed above, fMRI studies revealed that OBE and FBOI are associated with the activation of different brain areas (Ionta et al., 2011; Petkova et al., 2011a). Second, the experimental paradigms used for inducing OBE and FBOI were developed to explicitly assess either changes in *self-location* or in *ownership*, and not both at the same time.

In 1PP FBOI, self-location is not altered at all as the real and virtual body are collocated. On the other hand, the OBE experiments reviewed above have been mainly designed to accurately measure changes in the perceived *self-location*. The concurrent feeling of *ownership* toward the body seen in the extra-personal space was mainly assessed through questionnaire and free reports. When pooled together, data from questionnaires and self-reports in “back stroking” OBE show that illusory changes in *self-location* are not systematically associated with the sense of *ownership*: self-reports from some participants (Ionta et al., 2011) suggest that this illusion is associated with self-recognition rather than with the experience of owning the virtual body (e.g., “*I had the impression of being touched by the stick as if I was between two mirrors and I could see my back*”; “*I had the impression of watching a photo of myself...*”). So it is possible that questionnaire data also reveal an enhanced sense of self-recognition rather than ownership toward the virtual body (Petkova et al., 2011b; Maselli and Slater, 2013). This possibility is further supported by the fact that participants score higher to the question “*It felt as if the virtual body/mannequin was my body*,” when they see their own body rather than a mannequin filmed from the back (Lenggenhager et al., 2007). This modulation with the appearance of the virtual

body is not found instead in 1PP illusion, in which the virtual body could importantly differ from the real in terms of age, gender and race, without reducing the illusion (e.g., Slater et al., 2010; Peck et al., 2013).

Only with few studies attempted so far to assess *ownership* in the “back stroking” OBE paradigm through autonomic measures: widespread decrements in body temperature associated with this OBE illusion have been recently reported (Salomon et al., 2013) and, based on previous RHI analogous results (Moseley et al., 2008), interpreted as a shift of the sense of ownership from the real to the virtual body. However, these results are not conclusive, as the effects found were smaller than the thermometer’s resolution. Pomés and Slater (2013) measures instead heart rate deceleration (HRD) and movements in responses to a threat to the virtual body. Although no significant modulation of the HRD was found, their multivariate analysis suggests that the sense of *ownership* can positively contribute to sensations of drifting toward the virtual body. Still, these results do not provide any direct evidence for modulations of ownership being systematically driven by an altered sense of *self-location*.

Upon direct comparison between 3PP and 1PP conditions, it has been systematically found that *ownership* is significantly suppressed in 3PP with respect to 1PP (Slater et al., 2010; Petkova et al., 2011b; Maselli and Slater, 2013). Results from the “chest stroking” OBE illusions further support these finding, showing how, in this full body illusion the sense of ownership toward the real body seen from a 3PP is disrupted (Guterstam and Ehrsson, 2012).

In summary, no direct experimental evidence is currently available for effective changes in *self-location* driven by OBE illusions to imply systematic changes in *ownership*. This scenario yields the motivation for the present study. In fact, the current experimental evidence suggests that *ownership* and *self-location* may have different neural representations and that they may be -at least to some extent- dissociated from each other. In this study we explicitly tested this hypothesis and further addressed the issue of how *ownership* and *self-location* interact when both are simultaneously altered in controlled experimental setups. The study is based on a set of three independent experiments conducted with the support of immersive virtual reality.

2. THE CROSS-MODAL CONGRUENCY TASK AS A MEASURE OF SELF-LOCATION

An important part of the results presented in this work relies on the use of the cross-modal congruency task (CCT). In this section we give a short introduction to clarify the principles that validate the CCT, under specific configurations, as a tool to measure *self-location* in external space

The CCT is a standard psychophysics test that has been designed to study interactions between vision and touch (Spence et al., 2008). The task consists of discriminating the elevation of perceived target vibrations in the presence of visual distracter stimuli (Driver and Spence, 1998b). In the

classical configuration an array of four vibrators and four light emitting diodes are arranged on the participant's hands (two on the indexes and two on the thumbs). On each trial a vibration and a light flash are presented and the participant has to make a rapid judgment on whether the vibration was up (on the index) or down (on the thumbs), irrespectively of the side and of the location where the flashing light switched on. A large number of studies have consistently shown that vibrotactile discrimination is delayed and less accurate when the distracting visual cue is incongruent in elevation with the target vibration. The effect is quantified in terms of the cross-modal congruency effect (CCE), defined as the difference in performances (e.g., response times or error rates) between incongruent and congruent trials. Because visuotactile interactions are stronger when the visual cue is presented closer to the target tactile stimulation, i.e., on the same side/hand, CCE values are typically larger when computed for trials with visual and tactile cues on the same side with respect to the opposite side (Spence et al., 2004).

Three different processes have been proposed as responsible for the observed visuotactile interaction: cuing of exogenous spatial attention, multisensory integration (MSI), and response competition (light distracters priming the response) (Spence et al., 2004). These different mechanisms may dominate the CCE or contribute to it in combination with others, depending on the time separation, i.e., the stimulus onset asynchrony (SOA), between the target and the distracter stimulus. MSI mechanisms dominate the CCE for SOA smaller than 100 ms (irrespectively of the stimuli order), while for SOAs outside this range the effect is mainly driven by exogenous attention or priming effects (Shore et al., 2006).

Using an appropriate SOA, the CCT can be therefore used as a tool for detecting the MSI of visual and tactile stimuli. The crossmodal effect found in a variety of spatial configurations can be indeed explained on the basis of the known spatial properties of bimodal visuotactile (VT) neurons found in the human and non-human primate's brain: the effect is preserved when the hands are crossed (Driver and Spence, 1998a; Maravita et al., 2003), showing how visual distracters are processed in the corresponding hand-centered reference frame, rather than in retinotopic coordinates. An analogous modulation is found in VT neural populations having visual receptive fields (vRFs) that shift in space along with body movements (Graziano and Gross, 1993; Duhamel et al., 1998; Lloyd et al., 2003; Brozzoli et al., 2012). Interestingly, crossmodal interactions were found also when the visual distracters were located on tools that have been actively manipulated (Maravita et al., 2002). This provided an additional behavioral counterpart for the properties of parietal VT neurons in the macaque monkey whose vRFs extend outwards after active tool manipulation (Iriki et al., 1996).

All these results are crucial in pointing out how the CCT can be exploited to infer the location of tactile events as perceived in external space. Following this rationale, previous studies used the CCT to test the spatial recalibration of the limb position occurring during a rubber hand illusion (RHI): effective crossmodal interactions were found despite the fact that vibrators and visual distracters (located on the rubber hands) were not aligned in external space (Pavani et al., 2000; Zopf et al., 2011), but only when the illusion was experienced. These results showed a recalibration of the perceived location the tactile stimuli, hence of real hands, toward the location of the rubber hands.

Similarly, the CCT has been adopted to infer shifts in the perceived location of the whole body, i.e.,

to test *self-location*, during OBEs (Aspell et al., 2009), with the arrays of lights and vibrators located on the back of the virtual and physical bodies respectively. An effective crossmodal interaction was found during the experienced OBE illusion, but only adopting a SOA of 233 ms, which falls in the regime in which crossmodal congruency effects are dominated by exogenous spatial attention rather than by MSI (Shore et al., 2006). No effect was found however for SOA range dominated by MSI effects, thus the interpretation of Aspell et al.'s results as due to illusory change in *self-location* is not straightforward.

3. MATERIALS AND METHODS

3.1. PARTICIPANTS

A total of 51 subjects were recruited for the study. Experiment 1 involved 15 naïve participants (12 females) with average age 21.6 years (± 3.7 years SD); Experiment 2, 17 naïve participants (8) with average age 20.4 years (± 2.3 years SD); Experiment 3, 19 naïve participants (10 females) with average age 22.7 years (± 5.0 years SD). Participants in all the three groups had little or no previous experience in virtual reality (scores to the question “*Have you ever experienced virtual reality before?*” on a Likert scale from 1 to 7 had a median of 1 and interquartile range (IQR) of 1 for all the three experiments). All participants had normal or corrected to normal vision and had no history of neurological or psychiatric disorders. Participants signed an informed consent form before taking part to the experiment, and received a compensation of €10 after completion. The experimental protocol was approved by the “Comité Ético de Investigación” of the University of Barcelona, in line with the institutional ethics and national standards for the protection of human participants. In accordance with ethical commitments, all participants were contacted by email within 3–6 weeks after the experiment, and were asked whether they had any positive or negative thoughts about their experience in the experiment. None of the participants reported negative post-experimental sensations.

3.2. MATERIALS

Experiments were implemented and conducted with the support of VR technology. The virtual environment was a faithful reproduction of the laboratory in which the experiments took place, modeled in 3D Studio Max by a graphics artist (Figure 1). The environment was controlled with the Unity¹ platform. Participants entered the virtual environment through a stereo NVIS nVisor SX111² HMD (dual SXGA displays with 76°H $\times$ 64°V field of view (FOV) per eye, with 50° (66%) of overlap in the horizontal axis, resulting in a total field of view of 102° horizontal and 64° vertical; image resolution: 1280 $\times$ 1024 per eye; frame rate: 60 Hz). Head tracking was performed by a six degree of freedom (DoF) Intersense IS-900 device based on a coupling of infrared monitoring and

1 <http://unity3d.com/>

2 <http://www.nvisinc.com/index.php?id=48>

inertial technology³. The tracked data were streamed in real time using the Virtual Reality Peripheral Network⁴ (VRPN) protocol to the Unity project.

Figure 1. Experimental setup.

The virtual environment (B) was a replication of the laboratory in which the experiment took place (A). Participants experienced the environment through a stereo wide field-of-view head mounted display. Four vibrators, controlled by an Arduino board, were fixed on the participant legs for the cross-modal congruency task. A cardboard tube was used to deliver continuous visuotactile stimulations symmetrically on the two legs in some of the experimental conditions.

Visuotactile stimulation was delivered on the participant legs with a tracked cardboard tube, 70 cm in length and 5 cm in diameter. The tube's movements were tracked using the Tracking Tools toolkit of Optitrack⁵, a system for object motion tracking that uses 12 infrared cameras. Data from a 3D optical marker attached to the physical tube were streamed in real time (via the VRPN) to the Unity

3 <http://www.intersense.com/pages/20/14>

4 <http://www.cs.unc.edu/Research/vrpn/index.html>

5 <http://www.naturalpoint.com/optitrack/products/tracking-tools/>

project and were used to control the movements of a virtual tube. Two optical markers were used to register the exact position of the knees of the participants with those of the virtual avatar, and other two were used in Experiment 3 for monitoring the position of the two hands. The length of the avatar's legs was scaled so to match the actual legs length for each participant. This allowed a precise colocation of the physical and virtual bodies in the 1PP condition, an exact spatial overlap of the vibrators arranged on the real legs and the virtual light distracters (LD), and further an accurate displacement of the virtual tube, which assured it to be displayed at exactly the same location on the real and virtual legs.

A set of four small vibrating motors⁶ was used for the CCT. The motors (3 V, 100 mA, 50 Ω , 1200 $\pm$ 300 r.p.m.) were controlled through an Arduino board connected to the Unity project. Participants used an Intersense joystick to give responses in the CCT and in the "Tube Task" described below.

3.3. RESPONSE VARIABLES: MEASURES, DATA PROCESSING AND STATISTICAL METHODS

3.3.1 CROSSMODAL CONGRUENCY TEST (CCT)

The CCT was used in our experiments to test possible shifts in the perceived self-location toward the virtual body. The rationale for this choice has been exposed in details in Section 2. The array of LDs/vibrators used for the CCT was arranged on the virtual/physical legs. This novel configuration had been set to detect effects of multisensory integration of tactile events on the real body and visual events on the virtual body, while having different visual perspectives of the virtual body. The four vibrators were positioned on the participant's legs using elastic bands: two on the thighs, 10 cm above the knees, and two on the external side of the shins (on the tibialis anterior muscle), 10 cm below the knees. Four virtual LDs (round red lights with ~ 120 mm² surface) were located in the corresponding positions on the virtual body. Each trial of the CCT consisted of a visual cue switching on during 33 ms and followed, after a 50 ms SOA, by a target vibration of 100 ms. Due to different delays in the video stream to the HMD and in the vibrators' activation (measured in the laboratory with an oscilloscope device), the effective SOA was about 20 ms with the light stimuli leading vibrations. Participants were instructed to keep their gaze on a fixation point (a blue dot in the middle of the LDs array) and, for each trial, to indicate as fast and as more accurately as possible whether the delivered target vibration was above (i.e., on the thighs) or below (i.e., on the lower legs), irrespectively of the side and of the LD's location. Participants gave responses using the upper (for above) and lower (for below) buttons of a joystick held in their right hand.

Each CCT run consisted of 180 trials: 160 experimental trials, 40 for each of the four possible combinations of LD and vibration locations, plus 20 "no-go" trials. In the "no-go" trials the fixation point changed color (from blue to fuchsia) and participants were instructed to stop giving responses even if target vibrations were released. "No-go" trials were included in order to make sure that participants kept their eyes open and focused on the fixation point throughout the whole duration of the task (Zopf et al., 2010); subjects that responded to more than 30% of the no-go trials were

⁶ Flat motor, model C1034-50L, by Shenzhen Linglong Electronics Co., Ltd

excluded from the CCT data analysis. The 180 trials were presented in a random order.

The CCT data were initially processed to extract the average response time (RT) and error percentage (EP) for each participant as a function of *side* (left leg vs. right leg), *congruency* (in elevation) and experimental *condition*. Trials with incorrect responses or with RT larger than 1500 ms or smaller than 200 ms, were discarded. The two measures were then combined into the inverse efficiency (IE) score, defined as the ratio between the reaction time and the percentage of correct responses [$IE = RT / (1 - EP)$], which provides the most informative summary of the data available and compensate for possible speed-accuracy trade-offs (Townsend and Ashby, 1983; Kennett et al., 2001; Spence et al., 2001).

We chose to perform the statistical analysis on the IE data because of the better informative content of this variable with respect to the more commonly used RT (Bruyer and Brysbaert, 2011). The IE data were first analyzed in a Three-Way repeated measures ANOVA ($3 \times 2 \times 2$) with interactions, with factors *condition*, *side* and *congruency*. This can detect the cross-modal interactions in terms of a main effect of congruency -because of the longer response times and the higher error rate in incongruent trials- and any interaction between *congruency* and *side* -which shows that the cross-modal interaction is stronger for stimuli close in space-. A significant interaction among the three factors would detect critical differences among the various experimental. Pairwise comparisons were then performed running a One-Way repeated measurement ANOVA on CCE-IE (the CCE calculated on the performance variable IE) with the single factor *side*: as discussed above, a significant modulation of the CCE by *side* gives hints for a perceived spatial alignment between the arrays of vibrators and LDs, and in turns provides a proxy for the perceived *self-location*.

3.3.2. THE “TUBE TASK” (TT)

The “Tube Task” (TT) is a novel test designed to gather measures of *ownership* and *self-location*. Participants were instructed to use a joystick to adjust the size (Experiment 1) the size plus the later position (Experiment 2) of a virtual tube, so to match with its extremities the perceive locations of their external ankles.

During the task no virtual body was displayed and a blue virtual tube was the unique visible object in the environment. The tube was displayed horizontally so to pass through the participant’s ankles locations. At the beginning of the task the tube was centered on the middle point of the participant’s ankles, had length of 114 cm and a fixed 5 cm diameter. Participants performed the task immediately after entering the virtual environment through the HMD. This measure provided the subject’s baseline. The task was then repeated after each experimental condition

According to the variant used in the experiment, the task returned one or two measures: $\Delta TubeSize$, defined as the difference between the size of the tube set after each condition and its baseline value, provided a measure of changes in the perceived posture (i.e., the legs separation relative to the midline). $\Delta TubeShift$, defines as the difference between the position of the tube set after each condition and its baseline value, provided instead an estimate for the perceived drift of the body midline, thus for *self-location*.

In the specific experimental design adopted in this study, we propose to assess *ownership* by looking at the effects of the strong visuo-proprioceptive coupling between the real and virtual body that is established during a FBOI (Maselli and Slater, 2013). The TT was then designed as tool for detecting such visuo-proprioceptive coupling: the experimental manipulations adopted included a change in posture of the virtual body whose legs spread apart while participants stayed still in the initial posture. Significantly positive values of $\Delta TubeSize$ will then be a proxy for an effective visuo-proprioceptive coupling between the real and virtual bodies, able to affect proprioception just via visual cues, and thus a proxy for the ownership illusion. Before applying this new method for testing the experimental hypotheses under study, the validity of the TT was tested in Experiment 1.

In Experiment 1, in which participants were asked to adjust only the tube's size, TT data were analyzed using One-Way repeated measures ANOVA with the single factor *condition* applied on the $\Delta TubeSize$. In Experiment 2 the same analysis was applied separately to $\Delta TubeSize$ and $\Delta TubeShift$. Pairwise comparisons between experimental conditions were then performed running paired t-tests.

3.3.3. THE “ANKLES POINTING TASK” (APT)

This task was designed -through pilot studies- as an alternative to the TT for *ownership* assessments. As discussed in Section Discussion of the Results, we found that, while the TT is a sensitive test for *ownership* (via posture assessments) when only the length of the tube is controlled, it loses such sensitivity when combining *ownership* and *self-location* assessments and giving participants the possibility to change the tube's size and concurrently its lateral position. By comparing results from Experiments 1 and 2, it was indeed clear that tube's shifting option deteriorated the sensitivity in the feet separation estimate. For this reason we introduced the APT and designed it so that it could provide veridical estimates of the legs separation in a body centered reference frame, irrespectively of the visual perspective that participants were given in the different experimental conditions.

In this case participants were asked to point with the two hands the perceived location of the external ankles. Participants performed the task in complete darkness. They were instructed to first extend both arms out and then to progressively move them in, with the palms facing each other, until each hand would point the outer ankle on the correspondent side (see Movie SOM⁷). The corresponding distance between the two hands was recorded through the tracking system (see Section Materials). As for the TT, the measure of interest was the changes in the hands' separation set after each condition with respect to its baseline value, ΔHS .

As ΔHS data from the APT Experiment 3 were not normally distributed, a Wilcoxon matched pairs test was adopted to compare the ΔHS distributions in the two experimental conditions.

3.3.4. QUESTIONNAIRE

A 12-items questionnaire (reported in Table 1) was used in Experiments 2 and 3 to assess the subjective level and quality of the illusory experience. *Ownership* toward the virtual body was assessed explicitly (*my-body*) and implicitly through responses related to the legs spreading event

7 The movie is available at <https://www.frontiersin.org/articles/10.3389/fnhum.2014.00693/full> when clicking on the “Open Supplemental Data” link on the right side

(*legs-x*) as well as via the *clothing* statement that has been previously shown to positively correlate with the explicit subjective report of ownership illusion (Slater et al., 2010; Maselli and Slater, 2013). A further item was included to contrast the sense of ownership toward the virtual body with the sense of looking at another person (*s-else*). Changes in *self-location* were assessed with explicit items related to drifting sensations. Two items were included to validate the delivery of synchronous visuotactile stimulation. Each questionnaire item was scored at the end of each experimental block on a Likert scale from 1 (not at all) to 7 (completely agree) to express the level of agreement. For each item, scores given for different experimental conditions were compared pairwise via the non-parametric Wilcoxon matched pairs test.

Item statement	Item tag	Illusory component
I felt that the body I saw was my own body	<i>my-body</i>	Ownership
I felt that I was wearing different clothing than when I came to the laboratory	<i>clothing</i>	
I felt as if the body I saw belonged to someone else	<i>s-else</i>	
I felt as if I had two bodies	<i>two-bodies (C)</i>	Self-location
During the experiment, I felt as if my real body was drifting to the left	<i>drift-left</i>	
During the experiment, I felt as if my real body was drifting to the right	<i>drift-right</i>	
It seemed as if I was at two places at the same time	<i>two-places (C)</i>	
When I saw the virtual legs separating I felt as though my real legs were moving	<i>legs-moving</i>	Response to legs separation
I felt a weird sensation in my legs when I saw the virtual legs separating	<i>legs-weired</i>	
When I saw the virtual legs spreading apart, I felt as the instinct to spread apart my real legs	<i>legs-instict</i>	
It seemed as though the touch I felt was caused by the carton tube that I was seeing moving on the virtual body	<i>touch-tube</i>	Visuo-tactile implementation
It seemed as tough I felt the touch in the location where the carton tube touched the virtual legs	<i>touch-loc</i>	

Table 1. Questionnaire.
 Each questionnaire item was scored on a Likert scale from 1 (not at all) to 7 (completely agree) to express the level of agreement. The (C) label denotes control items

Figure 2. Different visual perspectives. According to the experimental conditions, participants had three different visual perspectives on the virtual body: a first person perspective with total overlap of the real and virtual bodies (1PP-TO); a third person perspective with partial overlap between the two bodies (3PP-PO); a third person perspective with no overlap between the two bodies (3PP-NO). In the Body and Body+VT conditions of Experiment 1, the visual perspective was the same as in 1PP-TO.

3.4. EXPERIMENTS: DESIGNS AND PROCEDURES

For the three experiments a within-subjects design was adopted. Each experimental condition was presented within one experimental block. Participants went through the different conditions in a counterbalanced order across participants, so that each condition was presented in the first experimental block the same number of times.

Participants wore a pair of comfortable trousers prepared so to easily arrange the four CCT vibrators held in direct contact with the skin by elastic bands. They sit on an armchair with their foot resting on a footstool and their hands on armrests, holding a joystick with their right hand (Figure 1). The separation between the feet was adjusted by the experiments at 18 cm. Participants were instructed to not make any movement, apart from head movements, for the whole duration of each experimental block. Before starting, the experimenter provided full instructions on how to perform the CCT and the TT or APT. All experiments started with an initial training session, preceding the experimental blocks: after a brief (about 10 s) exposure to the virtual environment, with a gender-matched virtual avatar displayed from a 1PP, participants were asked to perform the TT or APT; this initial measure was stored and used as the participant's baseline. Immediately afterwards, the virtual body appeared again and a CCT training session of 30 trials was initiated.

3.4.1. EXPERIMENT 1

Three experimental conditions were included: in the *noBody* condition the virtual body was not displayed and participants saw an empty armchair when looking down. In the *Body* condition the virtual body was displayed to be spatially coincident with the physical body, i.e., from a first person perspective with total overlap between the real and virtual bodies (as in the upper panel of Figure 2). The *Body + VT* condition was the same as the *Body* one, but with the addition of continuous synchronous visuotactile stimulation via the tracked tube. In the *noBody* condition the visual perspective was the same as the first person perspective given in the two *Body* conditions, just the virtual body was not visible.

After completing the training phase, participants went through the three experimental blocks, each having an average duration of 10 min. In the initial phase (~1 min) participants were asked to first explore the virtual scene moving the head around and then to focus on the virtual body (*Body* conditions) or on the chair (*noBody*). Only in the *Body + VT*, synchronous VT stimulation was delivered: the experimenter slowly moved the tracked tube on both legs, simultaneously and symmetrically, from the feet to the thighs (see Movie in the SOM⁸). The CCT was then started (~8 min). In the *Body + VT* condition, during the CCT the tube's stroking continued symmetrical and simultaneous on both legs but was restricted to the lower part of the calf and the feet (i.e., outside the region delimited by the CCT array). At CCT completion participants were again instructed to observe the scene and focus their attention on the virtual body or the chair (~1 min), as in the initial phase. In the two *Body* conditions, the avatar's legs moved apart after about 1 min, with the virtual feet reaching a distance of 55 cm in 3 s; in the *noBody* condition participants just looked at the empty chair for the same period of time. The "Tube Task" was then performed and terminated the experimental block: as the visual perspective was not manipulated, participants were instructed and only had the possibility to

⁸ The movie is available at <https://www.frontiersin.org/articles/10.3389/fnhum.2014.00693/full> when clicking on the "Open Supplemental Data" link on the right side

control the length of the tube, not its position. The HMD was removed and participants rested from 5 to 10 min before starting the next block.

The experiment was designed to test the response variables to be adopted in Experiments 2 and 3. The three main objectives were: (1) to show that the novel version of the CCT with vibrators and visual distracters arranged on the legs is equivalent to classical version (on the hands) and thus a valid tool for *self-location* assessments (see Section The Cross-Modal Congruency Task as a Measure of Self-Location); (2) to show that this novel version of CCT is still sensitive for detecting visuotactile integration processes on the self-body even when irrelevant visuotactile stimulation is concurrently delivered; (3) to validate the TT as a novel objective proxy for a full body ownership illusion.

In order to validate the first two points CCT's performances should reveal strong visuotactile interactions— i.e., a CCE significantly larger on the same side, with respect to opposite side— in both *Body* conditions. Note that we needed to validate point (2) in order to apply the CCT in the 3PP perspectives conditions of Experiments 2 and 3: in these conditions, in fact, it is necessary to keep providing visuotactile stimulation to sustain the full body illusion during the CCT, which is too long for a previously induced illusion to be sustained otherwise

In the two *Body* conditions in fact, participants have a 1PP over a highly collocated realistic virtual body, a condition that has been shown to be sufficient for experiencing a high sense of ownership toward the virtual body (Maselli and Slater, 2013). We then expected that the TT would be able to corroborate the sense of *ownership* by revealing an increase in the perceived separation between the legs at the end of both *Body* condition with respect to the baseline value: because participants remained in static posture throughout each experimental block, such an increase would be driven by the just seeing the virtual legs spreading apart and indeed would reveal the strong visuoproprioceptive coupling between the real and the virtual body that is established during ownership illusions. In summary, in order to validate point (3), the distance between the feet estimated through the TT should be larger than the baseline value in both *Body* conditions and should not vary in the control *noBody* condition, in which no visual cues about body posture was available.

3.4.2. EXPERIMENT 2

Experiment 2 was designed to test the experimental hypotheses proposed in the introduction. The specific aim of the experiment was to show that it is possible to experience illusory changes in *self-location*, as in OBEs, with little if any illusion of *ownership* over the seen virtual body. At the same time, we expected that if *ownership* is induced over a dislocated body the perceived *self-location* should be strongly affected.

As in Experiment 1, we adopted a within-subjects design with three experimental conditions, in all of which the real and virtual bodies had the same posture. In *1PP-TO* condition, participants saw the virtual body from a 1PP with a total overlap (TO) between the real and virtual bodies. In the *3PP-PO* condition the visual perspective was shifted laterally with respect to the virtual body, while keeping a partial overlap (PO) between the two; the lateral shift was set *ad-hoc* for each participant

so that the right leg of the avatar coincided in external space with the left leg of the participant (average later shift of 25 cm). In the third condition, the visual perspective was shifted laterally 80 cm to the right of the virtual body, with no overlap (NO). The three different visual perspectives over the virtual body are shown in Figure 2. In all the three conditions synchronous visuotactile stimulation was delivered symmetrically on both legs via the tracked tube, in exactly the same way as in Experiment 1. Note to the *Body + VT* condition of Experiment 1 and the *1PP-TO* condition of Experiment 2 were exactly the same.

The procedure was the same as that described for Experiment 1. Participants went through all experimental blocks (one for each condition) after completing the training phase. Each block had an average duration of 10 min: the initial phase of tube's visuotactile stimulation (~1 min) was followed by the CCT (~8 min), a second phase of VT stimulation only (~1 min), the virtual legs spreading event (few seconds) and finally the TT. At the end of each block participants gave their scores to all questionnaire items while resting on the armchair.

The aim of the experiment was to test how *ownership* and *self-location* are modulated in FBI by shifting the visual perspective progressively away from the virtual body. Because we were interested in eliciting full body illusion we adopted the legs stroking as a trigger for the bodily illusions. The choice of the legs instead of, e.g., the chest, relays on several reasons: (i) first the legs and feet are visually prominent when looking down at our own body (if hands gesture is limited), particularly when laying in a resting posture; (ii) looking down at the chest requires a more targeted intention and is particularly uncomfortable in VR due to the HMD weight; (iii) stroking the legs allowed the stimulation of a wide portion of the whole body -from the feet to the thighs- and during the CCT to perform the stimulation while avoiding the region delimited by the CCT arrays; (iv) finally the legs separation could be easily manipulated without implying major changes in the overall resting posture.

3.4.3. EXPERIMENT 3

Experiment 3 was planned and designed as a follow up of Experiment 2, because of the failure of the TT in assessing changes self-posture when combined with self-location assessments (see discussion in Section The "Ankles Pointing Task" (APT) and Discussion of the Results). A within-subject design was adopted with two conditions: the *1PP-TO* and the *3PP-NO* of Experiment 2. The procedure was exactly the same of Experiment 2 with two differences. First the APT substituted the TT. Second, before starting each experimental block, participants were outfitted with headphones streaming white noise. This latter modification was introduced to avoid the potential inhibitory effect that conflicting visuo-auditory cues may have in the *3PP* condition, in which a spatial mismatch was present between the sound produced by the real tube stroking the participant's legs and the virtual tube's location on the virtual body.

4. RESULTS

The analysis reported in this Section was performed excluding outliers from the distributions under test; outliers were identified via the schematic boxplot introduced by Tukey (1977). The degrees of freedom reported for each test give information about the number of outliers excluded. Requirements for normality were always checked with the Shapiro-Wilk test (Shapiro and Wilk, 1965) and reported with its p-value (p_{sw}). We avoided the debated practice of correcting for multiple comparisons (Perneger, 1998), and instead report effect sizes together with the true p-value for each performed test.

The average RT, EP and IE extracted from the CCT data and averaged across participants are given in Table 2 as a function of side, congruency, and condition, for all the three experiments.

4.1 EXPERIMENT 1

4.1.1 CCT

An average of 11% of responses were given for no-go trials across participants, none of which exceeded the 30%. Figure 3A shows the bar chart for the full body CCE-IE. In all conditions the effect is larger when the LD is on the same side with respect to opposite. Three-Way ANOVA with interactions showed a significant main effect of *congruency* [$F_{(1,13)} = 90.8$, $p < 0.0001$, partial $\eta^2 = 0.39$] and *condition* [$F_{(2,13)} = 8.7$, $p = 0.0003$, partial $\eta^2 = 0.11$], and a significant interaction term between *side* and *congruency* [$F_{(1,13)} = 24.4$, $p < 0.0001$, partial $\eta^2 = 0.15$]. Normality of the residuals was borderline ($p_{sw} = 0.053$).

Pairwise comparisons of the CCE-IE between same and opposite side showed a significant difference for all conditions [*noBody*: $F_{(1,12)} = 7.7$, $p = 0.017$, partial $\eta^2 = 0.39$; *Body*: $F_{(1,12)} = 48.1$, $p = 0.0001$, partial $\eta^2 = 0.80$; *Body + VT*: $F_{(1,12)} = 28.1$, $p = 0.0002$, partial $\eta^2 = 0.72$]. Residuals were normally distributed for all comparisons ($p_{sw} > 0.3$).

4.1.2 TUBE TASK (TT)

Figure 3B shows the bar plot for the $\Delta TubeSize$ distributions in the three conditions. All were normally distributed ($p_{sw} > 0.85$). $\Delta TubeSize$ is clearly larger than zero in the two *Body* conditions, as confirmed by one-sample one-tailed t-tests [*Body*: $t_{(14)} = 3.17$, $p = 0.003$, Cohen's $d = 0.82$; *Body + VT*: $t_{(14)} = 2.36$, $p = 0.017$, Cohen's $d = 0.61$]. This indicates a recalibration of the perceived posture. This was not the case for the *noBody* (control) condition. This result shows that, when the perceived posture was not affected by visual cues from the virtual body, participants reliably replicated the initial baseline estimation of their legs separation. It is important to stress that, despite the within-subjects design, the body posture's estimate did not retain aftereffects or biases from previous exposure to the conditions in which the virtual body was seen changing its posture.

Target-distractor congruence	Position of distracters	Reaction time (RT) [ms]	Error percentage (EP) [%]	Inverse efficiency IE = RT/(-EP) [ms]	Target-distractor congruence	Position of distracters	Reaction time (RT) [ms]	Error percentage (EP) [%]	Inverse efficiency IE = RT/(-EP) [ms]
EXPERIMENT 1					EXPERIMENT 3				
NoBody					1PP-TO				
Congruent	same	600 (23)	1.0 (0.5)	606 (23)	Congruent	same	705 (33)	4.0 (1.2)	734 (38)
	different	632 (22)	2.0 (0.9)	644 (20)		different	735 (33)	6.8 (1.9)	789 (44)
Incongruent	same	690 (28)	7.7 (1.2)	750 (33)	Incongruent	same	818 (36)	8.2 (1.6)	887 (43)
	different	680 (20)	3.7 (1.1)	707 (20)		different	792 (32)	8.1 (2.0)	863 (44)
Body					3PP-NO				
Congruent	same	609 (29)	0.4 (0.2)	613 (31)	Congruent	same	724 (30)	3.5 (0.9)	753 (38)
	different	650 (29)	1.0 (0.4)	656 (29)		different	719 (28)	5.7 (1.6)	765 (36)
Incongruent	same	723 (32)	4.8 (1.3)	764 (38)	Incongruent	same	791 (34)	10.4 (2.1)	890 (53)
	different	665 (28)	3.9 (0.5)	692 (30)		different	783 (30)	7.1 (1.2)	841 (36)
Body + VT					Table 2. Experiments 1–3: Means (standard errors) from CCT performances. The reported values for reaction time, error percentage and inverse efficiency index are averages across participants. The variables are reported as a function of visual distracter side, congruency between vibrotactile and visual cues, and experimental condition.				
Congruent	same	637 (32)	1.3 (0.6)	648 (35)					
	different	682 (36)	3.6 (1.3)	707 (36)					
Incongruent	same	738 (32)	9.2 (2.2)	823 (50)					
	different	712 (31)	4.8 (1.4)	748 (30)					
EXPERIMENT 2									
1PP-TO									
Congruent	same	638 (28)	2.2 (0.7)	653 (28)					
	different	684 (30)	5.3 (1.1)	723 (57)					
Incongruent	same	752 (30)	15.2 (3.3)	910 (31)					
	different	713 (26)	7.3 (2.0)	776 (36)					
3PP-PO									
Congruent	same	647 (19)	2.7 (1.0)	665 (20)					
	different	694 (21)	4.0 (1.6)	726 (27)					
Incongruent	same	751 (23)	13.8 (4.8)	977 (147)					
	different	702 (20)	7.1 (2.0)	765 (35)					
3PP-NO									
Congruent	same	656 (21)	4.7 (1.2)	691 (26)					
	different	687 (23)	5.8 (1.1)	732 (58)					
Incongruent	same	734 (23)	15.7 (3.6)	900 (28)					
	different	745 (23)	12.7 (2.4)	860 (32)

Figure 3. Results from Experiment 1. (A) Means and standard errors of the cross-modal congruency effect in inverse efficiency (CCE-IE) measured on the same side and on the opposite side, for the three experimental conditions (noBody, Body, and Body+VT). Ranges for the p-values from One-Way repeated measures ANOVA between same and other side are reported. (B) Differences (means $\pm$ standard errors) between the tube size estimation from the “Tube Task” (TT), performed after and before each of the experimental conditions: noBody, Body, and Body+VT. Positive values of Δ TubeSize indicate that participants experienced a recalibration of their perceived legs separation as a consequence of seeing the virtual legs spreading apart. Ranges for the p-values are reported for distributions with a mean significantly larger than zero (from one sample one-tailed t-test) and for paired comparisons across conditions (One-Way ANOVA). *0.01 < p < 0.05, **0.001 < p < 0.01, ***0.0001 < p < 0.001.

One-Way repeated ANOVA revealed a significant effect of condition on $\Delta TubeSize$ [$F_{(2, 14)} = 6.5$, $p = 0.005$, partial $\eta^2 = 0.26$], with the residual being normally distributed ($p_{SW} = 0.24$). Pairwise comparisons revealed that $\Delta TubeSize$ was significantly larger for both *Body* conditions with respect to the *noBody* condition [*Body* vs. *noBody*: $t_{(14)} = 3.4$, $p = 0.002$, Cohen's $d = 0.67$; *Body* + VT vs. *noBody*: $t_{(14)} = 2.37$, $p = 0.016$, Cohen's $d = 0.53$]. No difference between the two *Body* conditions was found [$t_{(14)} = 0.56$, $p = 0.58$].

4.2. EXPERIMENT 2

One subject was excluded from the analysis because he did not understand correctly the experiment instructions and another because the vibrators array stopped working during one of the conditions.

4.2.1. CCT

An average of 11.8% of responses were given for no-go trials across participants, none of which exceeded the 30%. Three-Way ANOVA with interactions revealed a significant main effect of *congruency* [$F_{(1, 12)} = 68.4$, $p < 0.0001$, partial $\eta^2 = 0.34$], a significant interaction term between *side* and *congruency* [$F_{(1, 12)} = 20.0$, $p < 0.0001$, partial $\eta^2 = 0.13$], and a trend for interaction of *side*, *congruency* and *condition* [$F_{(1, 12)} = 2.7$, $p = 0.071$, partial $\eta^2 = 0.04$]. The requirement for normality of the residuals was satisfied ($p_{SW} = 0.08$).

Pairwise comparisons (Figure 4A) revealed a significantly higher CCE-IE on the same side with respect to opposite in *1PP-TO* [$F_{(1, 12)} = 27.7$, $p = 0.0002$, partial $\eta^2 = 0.70$] and *3PP-PO* [$F_{(1, 12)} = 74.2$, $p < 0.0001$, partial $\eta^2 = 0.86$], but not in *3PP-NO* [$F_{(1, 12)} = 1.13$, $p = 0.31$]. Residuals were normally distributed for all comparisons ($p_{SW} > 0.26$). Because we expected a significant difference between the CCE on same and other side also in *3PP-NO*, we repeated the test with the CCE computed for the RT data (CCE-RT). In this case we found CCE-RT to be higher in the same than in the other side [$F_{(1, 14)} = 4.57$, $p = 0.0507$, $\eta^2 = 0.051$, $p_{SW} = 0.17$], in line with our expectations.

It was interesting to specifically inspect performance on the *3PP-PO* trials with the target vibration on the left leg of the participant. In fact, for these trials, the light distracters on the “opposite side” were located, in external space, in exactly the same positions of the vibrators (the virtual right leg overlapped in external space with the participant's left leg), while those on the “same side” were spatially incongruent. Despite this, the average CCE-IE was much higher on the same side than on the opposite (see inset in Figure 4A). A significant difference between same and opposite side was detected in this subsample with a matched-paired Wilcoxon test ($z_{13} = 3.1$, $p_{13} = 0.002$, $PS_{dep} = 0.92$), as when running an One-Way ANOVA the resulting residuals were not normally distributed.

4.2.2 TUBE TASK

Due to technical recording problems, the TT data were missing from three subjects of the 15 subjects under analysis. The Shapiro Wilk test revealed normal distributions for both $\Delta TubeSize$ and $\Delta TubeShift$ ($p_{SW} > 0.24$). Two outliers (one in *1PP-TO* and one in *3PP-NO*) were found and excluded from the analysis.

Figure 4. Results from Experiment 2. (A) Means and standard errors of the cross-modal congruency effect in inverse efficiency (CCE-IE) measured on the same side and on the opposite side, for the three experimental conditions (1PP-TO, 3PP-PO and 3PP-NO). The inset shows the same for the 3PP-PO subset of trials in which the target vibration was on the real left leg that overlapped in external space with the right virtual leg. Ranges for the p-values from One-Way repeated measures ANOVA between same and other side are reported. (B) Differences (means $\pm$ standard errors) between the tube lateral position set in the Tube Task (TT) after and before each experimental condition. Positive values of Δ TubeShift indicate that participants experienced a recalibration of their self-location to the left, which is toward the virtual body. Ranges for the p-values are reported for distributions with a mean significantly larger than zero (from one sample t-test) and for paired comparisons across conditions (One-Way ANOVA). (C) Differences (means $\pm$ standard errors) between the tube size estimation from the Tube Task (TT), performed after and before each experimental condition. The Δ TubeSize distributions match the zero mean distribution in all the three conditions. (D) Box plots showing the comparison of questionnaire data across conditions: only items for which significant differences among conditions have been found are shown. Ranges for the p-values from matched pairs Wilcoxon tests are reported. * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $0.0001 < p < 0.001$, **** $0 < p < 0.0001$.

Figure 4B shows the bar chart for the $\Delta TubeShift$ distributions. For all conditions the distributions were normal ($p_{SW} > 0.20$). One-sample one-tailed t-test analysis revealed a distribution mean significantly larger than zero for both the 3PP-PO [$t_{(11)} = 7.59, p < 0.0001$, Cohen's $d = 2.19$] and 3PP-NO [$t_{(10)} = 2.8, p = 0.0097, d = 0.84$], but not for 1PP-TO [$t_{(10)} = 1.5, p = 0.086, d = 0.44$].

One-Way repeated ANOVA revealed a significant effect of condition on $\Delta TubeShift$ [$F_{(2,9)} = 13.66, p = 0.0002$, partial $\eta^2 = 0.60$], with normally distributed residuals ($p_{SW} = 0.99$). Pairwise comparisons revealed that $\Delta TubeShift$ was significantly larger in both 3PP conditions with respect to 1PP-TO [3PP-PO vs. 1PP-TO: $t_{(10)} = 5.4, p = 0.0002$, Cohen's $d = 2.62$; 3PP-NO vs. 1PP-TO: $t_{(9)} = 2.2, p = 0.029, d = 0.92$]. Interestingly, $\Delta TubeShift$ in the 3PP-PO condition was found to be significantly larger than in 3PP-NO [$t_{(10)} = 3.4, p = 0.0036$, Cohen's $d = 1.79$].

The $\Delta TubeSize$ values were normally distributed in all conditions ($p_{SW} > 0.24$). Contrary to our expectations the TT did not detect significant changes in the perceived posture for any of the conditions (see Figure 4C). One-sample t-test performed on the three distributions revealed indeed no difference from the zero-mean distribution ($p > 0.29$). One-Way repeated ANOVA also revealed no significant difference between conditions [$F_{(2,11)} = 1.73, p = 0.2$].

This unexpected outcome may be due to the interaction between the tube size adjustment and the additional lateral shift. In fact the 1PP-TO condition in this experiment is exactly the same as the *Body + VT* condition in Experiment 1, with the only difference being instructions given for the TT. The fact that in Experiment 1 the distribution of $\Delta TubeSize$ has a mean significantly larger than zero, while in Experiment 2 its mean is statistically equal to zero suggests that having the possibility to shift the tube laterally, and actually doing it, has a detrimental effect on the TT's measure of perceived body posture. The only difference between the two groups was in fact that in the latter participants had the possibility to shift the tube's laterally a part from adjusting its size.

4.2.3 QUESTIONNAIRE

Median values and interquartile ranges are reported in Table 3 for all items. The results from matched pairs Wilcoxon tests are given in Table 4 (items for which none of the three comparisons was significant were omitted). Effect sizes are given in terms of the probability of superiority of dependent measures, PS_{dep} , defined as the probability that the score from the condition that most frequently has the higher score will be greater than the score from the condition that most frequently has the lower score (Grisand Kim, 2012). The table highlights all significant comparisons as shaded cells. Boxplot corresponding to the significant comparisons are shown in Figure 4D.

Table 3 | Experiment 2: Medians and interquartile ranges of the questionnaire scores.

Item	1PP-TO		3PP-PO		3PP-NO	
	Median	IQR	Median	IQR	Median	IQR
<i>my-body</i>	6	3	5	3	3	4
<i>clothing</i>	6	4	5	5	4	3
<i>s-else</i>	3	3	4	3	6	2
<i>two-bodies</i>	2	2	3	4	4	4
<i>drift-left</i>	1	0	5	6	2	4
<i>drift-right</i>	1	0	1	4	1	1
<i>two-places</i>	3	2	3	4	3	4
<i>legs-moving</i>	4	4	4	3	2	3
<i>legs-weird</i>	5	5	4	3	2	4
<i>legs-instinct</i>	6	2	5	3	3	5
<i>touch-tube</i>	7	1	7	1	7	1
<i>touch-loc</i>	7	0	7	0	7	1

4.3. Experiment 3

4.3.1. CCT

Three-Way ANOVA with interactions revealed a significant main effect of congruency [$F_{(1,13)} = 94.4, p < 0.0001$, partial $\eta^2 = 0.51$] and a significant interaction between side and congruency [$F_{(1,13)} = 6.3, p = 0.014$, partial $\eta^2 = 0.06$]. Importantly, the three-way interaction between congruency, side and condition was not significant, indicating that visuotactile interactions were comparable in both conditions. The requirement for normality of the residuals was satisfied ($p_{\text{SW}} = 0.97$). Pairwise comparisons between CCE-IE on same side and opposite side (shown in Figure 5A) revealed a significant difference in both the 1PP-TO [$F_{(1,15)} = 15.7, p = 0.0012$, partial $\eta^2 = 0.51$] and the 3PP-NO [$F(1, 15) = 5.79, p = 0.029$, partial $\eta^2 = 0.28$]. Residuals were normally distributed ($p_{\text{SW}} > 0.19$).

4.3.2. ANKLES POINTING TASK (APT)

Data from two subjects were missing due to recording problems. Another two data sets were discharged because of the participant having misinterpreted the task instructions. A total of 15 subjects were included in the analysis. It is notable that the ΔHS estimates from these two subjects were “extreme” outliers (Tukey, 1977) in the ΔHS distribution from 3PP-NO.

The ΔHS distribution extracted from the APT was not normal, but resembled a bimodal distribution

with one cluster around zero and one another at positive values. This was particularly the case for the 1PP-TO distribution. The cluster around zero was probably a biased from participants that based their measure on the knowledge that their feet did not move, as explicitly reported by one of the two excluded participants.

A matched-pairs Wilcoxon rank test revealed a significant difference between the two experimental conditions ($z_{14} = 2.42$, $p_{14} = 0.016$, $PS_{dep} = 0.71$), indicating that participants perceived a significantly larger distance between their own ankles in the 1PP-TO than in the 3PP-NO. The box plot of the two distributions is shown in Figure 5B.

Table 4 | Experiment 2: Paired comparisons of the questionnaire scores. 1PP-TO

Item	1PP-TO vs. 3PP-PO			1PP-TO vs. 3PP-NO		
	<i>z</i>	<i>p</i>	PS_{dep}	<i>z</i>	<i>p</i>	PS_{dep}
<i>my-body</i>	0.52	0.60		2.05	0.040	0.73
<i>s-else</i>	0.82	0.42		-2.71	0.007	0.87
<i>drift-left</i>	-2.98	0.003	0.8	-2.63	0.009	0.73
<i>legs-moving</i>	0.12	0.91		1.94	0.052	0.70
<i>legs-weired</i>	0.58	0.56		2.29	0.023	0.73
<i>legs-instinct</i>	0.44	0.66		2.28	0.022	0.73
<i>touch-loc</i>	0.44	0.66		2.23	0.026	0.67

Item	3PP-PO vs. 3PP-NO		
	<i>z</i>	<i>p</i>	PS_{dep}
<i>my-body</i>	2.03	0.02	0.80
<i>s-else</i>	-2.63	0.009	0.87
<i>drift-left</i>	1.66	0.097	
<i>legs-moving</i>	2.55	0.011	0.80
<i>legs-weired</i>	2.08	0.037	0.70
<i>legs-instinct</i>	2.68	0.007	0.80
<i>touch-loc</i>	2.23	0.026	0.67

Reported *p*-values are from matched pairs Wilcoxon tests; effect size is reported in terms of the probability of superiority of dependent measures (PS_{dep}). Only results from comparisons revealing a significant difference across conditions are reported. Shaded cells highlight comparisons that revealed a significant difference across conditions.

Figure 5. Results from Experiment 3. (A) Means and standard errors of the cross-modal congruency effect in inverse efficiency (CCE-IE) measured on the same side and on the opposite side, for the two experimental conditions (1PP-TO and 3PP-NO). Ranges for the p -values from One-Way repeated measures ANOVA between same and other side are reported. (B) Box plot of the differences between the hands separation measured in the “Ankles Pointing Task,” after and before each experimental condition. Positive values of ΔHS indicate that participants experienced a recalibration of their perceived legs separation as a consequence of solely seeing the virtual legs spreading apart. ΔHS values were significantly larger in 1PP-TO than in 3PP-NO, showing that a proprioceptive recalibration occurred in the first condition but not in the latter. The p -value from matched pairs Wilcoxon test is reported. (C) ΔHS values are plotted against the scores to the mybody questionnaire item. A strong statistical trend ($p = 0.055$) for a positive correlation between the two variables was found. (D) Box plots showing the comparison of questionnaire data across conditions: only items for which significant differences among conditions have been found are shown. Ranges for the p -values from matched pairs Wilcoxon tests are reported. $*0.01 < p < 0.05$, $**0.001 < p < 0.01$, $***0.0001 < p < 0.001$.

4.3.3. QUESTIONNAIRE

Questionnaire results are summarized in Table 5 and shown in Figure 5D. The results are consistent with those from Experiment 2, apart from the *drift-left* item. Scores were in fact significantly higher in 1PP-TO than in 3PP-NO for the items *my-body* ($z = 3.27$, $p = 0.001$, $PS_{dep} = 0.89$) and the three items assessing the response to the legs separation event (*legs-moving*: $z = 3.18$, $p = 0.001$, $PS_{dep} = 0.86$; *legs-weird*: $z = 2.65$, $p = 0.008$, $PS_{dep} = 0.78$; *legs-instinct*: $z = 2.29$, $p = 0.022$, $PS_{dep} = 0.72$). On the other hand, scores *s-else* were significantly higher in 3PP-NO than in 1PP-TO ($z = 2.9$, $p = 0.004$, $PS_{dep} = 0.78$). Differently from Experiment 2, no significant difference was found for *drift-left*, although a weak trend for scores to be higher in 3PP-NO than in 1PP-TO was found ($z = 1.52$, $p = 0.13$). This was due to the extremely low scores given to this item in the 3PP-TO condition across all participants, which was not the case in Experiment 2.

Table 5 | Experiment 3: Medians, interquartile ranges and paired comparisons of the questionnaire scores.

Item	1PP-TO		3PP-NO		MP Wilcoxon test		
	Median	IQR	Median	IQR	z	p	PS_{dep}
<i>my-body</i>	6	2	2.5	3	3.27	0.001	0.92
<i>Clothing</i>	4	3	3.5	4	1.02	0.31	
<i>s-else</i>	3	2	4	4	-2.90	0.004	0.78
<i>two-bodies</i>	3	2	2.5	4	-0.84	0.40	
<i>drift-left</i>	1	0	1	1	-1.52	0.13	
<i>drift-right</i>	1	0	1	0	0.51	0.61	
<i>two-places</i>	3	2	2.5	3	0.11	0.91	
<i>legs-moving</i>	5	3	2	3	3.18	0.001	0.86
<i>legs-weird</i>	5	5	3	5	2.65	0.008	0.78
<i>legs-instinct</i>	5.5	2	3.5	4	2.29	0.022	0.72
<i>touch-tube</i>	7	1	7	1	-0.28	0.78	
<i>touch-loc</i>	7	0	7	0	-0.58	0.56	

Reported p -values are from matched pairs Wilcoxon tests and effect size is reported in terms of the probability of superiority of dependent measures (PS_{dep}). Shaded cells highlight comparisons that revealed a significant difference across conditions.

4.3.4. Correlation analysis

We tested the correlation between the level of ownership as assessed from questionnaire scores to the *mybody* item and the changes in the perceived legs separation measured with the APT (ΔHS). The Spearman's rho was showing a close to statistical significant positive correlation between the two measures ($\rho = 0.34$, $p = 0.055$), also shown in the scatter plot in Figure 5C. It is remarkable that

despite the cognitive bias discussed above (participants knew that their feet did not move), which introduces extra variance in the APT data hindering correlation analysis, a positive correlation was found. This result further corroborates the validity of APT method as measure for ownership illusions.

5. DISCUSSION OF THE RESULTS

5.1. EXPERIMENT 1

Results from Experiment 1 validated the methods used in the study. It was shown that the new proposed version of CCT, with the LEDs/vibrators arranged on the legs, is a valid tool to detect effective integration of visuotactile (VT) bodily signals, and thus to detect changes in the perceived *self-location* during full body illusions (see discussion in Section *Materials and Methods*). The CCT revealed in fact effective visuotactile interactions in both the *Body* conditions, in which participants experienced a fully collocated virtual body from a 1PP, a condition shown to be sufficient for eliciting a FBOI (Maselli and Slater, 2013). Importantly, the effective SOA was 20 ms, so that effective VT interactions can be primarily attributed to effective VT integration (Shore et al., 2006). In a similar setup, Aspell et al. (2009) had instead to increase the SOA to 233 ms in order to detect effective VT interactions when additional visuotactile stimulation was delivered during the CCT; however, as a drawback, the observed interaction was mainly dominated by exogenous attention rather than MSI (Shore et al., 2006). This difference may be due to the fact that, in our study, the visuotactile stimulation was delivered outside the region delimited by the CCT lights/vibrators array.

Interestingly, effective VT integration was detected also in the *noBody* condition. In previous studies, a similar condition was implemented, but with the array of visual distracters shifted with respect to the vibrators: in the “rubber hands absent” condition of Pavani et al. (2000) the vibrators were located on the unseen hands and the LEDs array was shifted 20 cm upward; similarly, in the “body not visible” condition of Aspell et al. (2009) the vibrators, located on the back while the distracters, were seen in the far extra-personal space. In both studies no significant visuotactile interaction was detected when the body was not visible. A significant CCE effect has instead been reported for an object condition in Salomon et al. (2012); however, as suggested by the authors, it is not straightforward to interpret this results because of the experimental design adopted, in which “object” trials where intermixed at a fast pace with “body” trials (Salomon et al., 2012). The fact that we did find evidence for visuotactile interaction also when the body is not visible is most probably due to the fact that LED distracters and vibrators were in spatial register. The result shows that the spatial information about the body provided solely by proprioception is sufficient to have a robust stored localization of body parts that contribute to the multisensory integration of visual and tactile information. This is consistent with the previous findings of the CCE modulation associated with various degree of visuo-proprioceptive spatial mismatch (Spence et al., 2008).

Experiment 1 further validated the TT/APT as novel tools for objective assessments of full body ownership illusions. The TT data showed that in the two *Body* conditions (in which ownership was

experienced toward the virtual body) after seeing the virtual body moving the feet apart and getting into a new posture, participants estimated a larger distance between their feet even if the physical body did not move at all. This outcome relays, as expected, on the strong coupling of visual and proprioceptive cues from the virtual and real bodies that is established during an ownership illusion (see Section 4.4 in Maselli and Slater, 2013). In this respect, the validation of the TT as a tool to assess full body ownership through assessments of illusory changes in posture driven by movements of the virtual body only extends to the APT. In fact, in the latter differs from the TT only in the way in which participants indicated the perceived distance among their feet, which was design ad-hoc to provide estimates of the legs separation in a body centered reference frame. The validity of the APT as a proxy for the FBOI was further corroborated by the positive correlation found between ownership measures from questionnaire (scores to the mybody item) and the illusory change in body postures measured with the APT (ΔHS), found in Experiment 3.

5.2. EXPERIMENTS 2 AND 3

The outcome of Experiments 2 and 3 supports our main experimental hypotheses. We first discuss the set of results that show how ownership and self-location can be manipulated independently from each other, during FBOI and OBE illusion respectively. We do this by comparing data from the 1PP-NO and 3PP-NO conditions. We then discuss results that show how simultaneous changes in ownership and self-location can be induced, and do interact, when having a third person visual perspective of a virtual body that partially overlaps with the physical body, as in the 3PP-PO condition.

5.2.1. FBOI AND OBE CAN OCCUR INDEPENDENTLY OF EACH OTHER

As expected we found evidence for FBOI to occur in the 1PP-TO but not in the 3PP-NO in both questionnaire and APT data. Scores to the my-body item, as well as to all the three legs items, were significantly higher in 1PP-TO than in 3PP-NO, showing that ownership toward the virtual body was experienced consistently across participants, only in the 1PP-TO condition. The APT data from Experiment 3 corroborated this finding. A significantly larger change in the perceived feet separation was in fact found in the 1PP-TO condition with respect to 3PP-NO. This showed that a tight coupling between vision and proprioception, characteristic of ownership illusions, is established in the 1PP-TO but not in the 3PP-NO condition. In both Experiments 2 and 3, scores to the s-else item were significantly higher in 3PP-NO than in 1PP-TO. This complementary result shows that the virtual body seen in the far extra-personal space was experienced as the body of another person rather than as one's own body, supporting the finding that no ownership is generally experienced toward the virtual body seen in the far extra-personal space. Despite this, both TT and CCT performances consistently show that actual changes in the perceived self-location took place in 3PP-NO. The distribution of $\Delta TubeShift$ in 3PP was found to be significantly larger than zero (indicating a perceived lateral shift in the perceived position of the whole body) and significantly larger than the $\Delta TubeShift$ measured in 1PP-TO (which was compatible with no lateral shift). This finding is consistent with results from previous studies of experimentally induced OBEs, which measured similar shifts of the perceived self-location toward the virtual body using methods akin, e.g., the walking task (Lenggenhager et al., 2007) and the mental ball dropping task (Lenggenhager et al., 2009; Ionta et al., 2011). Notwithstanding the evidence provided by questionnaire and TT data for an altered self-location in 3PP-NO, the CCT

data from Experiment 2 in this condition did not provide clear evidence for integration of visual cues on the virtual body and tactile cues from the correspondent body locations on the physical body (the CCE-IE was not significantly dependent on side). This was indeed contrary to our expectation. However, it is worth noting that a strong trend ($p = 0.052$) for a significant cross-modal interaction was found in the CCE-RT data (CCE measured on response times). Additionally, only a weak trend for a significant difference across conditions was found in the CCE-IE ANOVA ($p = 0.07$), which shows that the data do not provide clear evidence for CCT performance to be different in 3PP-NO than in the other two conditions, where a strong VT interaction was detected. The lack of a significant CCE-IE effect in 3PP-NO may be due to fact that visual distracters were far on the left side of the visual field, with a loss of sensitivity. In this case a larger sample would be needed. Also, conflictive visuo-auditory cues in 3PP-NO (from the tube stroking) may have acted as additional confounders making the task more difficult, and/or contributing negatively to the OBE illusion itself. These speculations are supported by CCT performances in Experiment 3, in which white noise was introduced to mask visuo-auditory incongruences on a larger sample of participants. A significant difference in the CCE-IE across same and different sides was indeed found in both 1PP-TO and 3PP-NO. This indicates that, during an OBE illusion, visual events experienced on the virtual body and tactile events experienced on the real body are integrated despite the dramatic spatial separation between them. It is important to notice that the feeling of another person to be present that may arise in our 3PP-NO condition (and generally in all experimental setups inducing full body illusion from a 3PP), may induce social mechanisms that affects self-processing (Serino et al., 2008), and in turns hinder the FBI. In any case, joint evidence from questionnaire (drift-left item), the CCT and the TT in the 3PP-NO condition speaks in favor of an actual shift of the perceived self-location toward the virtual body.

Summarizing, results from Experiments 2 and 3 provided the first experimental evidence that OBE and FBOI are two diverse perceptual illusions affecting different aspect of body self-consciousness. This was established by showing that both could occur independently of each other and that the two manifest themselves in different perceptual phenomena. In the general discussion we provide arguments for the different neural correlates that may be predominantly involved in each of the two illusions.

5.2.2 FBOI DURING OBES: EVIDENCE FOR A STRONG INTERACTION OF OWNERSHIP AND SELF-LOCATION

Experiment 2 provided novel evidence on how the sense of ownership and the sense of self-location influence each other when they are concurrently manipulated. All data collected show that this was the case for the 3PP-PO condition, in which the visual perspective was dislocated from the eyes of the virtual avatar (3PP) while preserving a substantial overlap between the two bodies: participants in this condition experienced a strong FBOI over the virtual body with a concurrent significant change in the perceived self-location.

Apart from the drift-left item, questionnaire scores in this condition were statistically equal to those given in 1PP-TO. At the same time, the comparison between this condition and the 3PP-NO condition revealed the same significant differences found in the 1PP-TO vs. 3PP-NO comparison. This indicated that a strong FBOI occurred similarly in both 1PP-TO and 3PP-PO. On the other hand, TT data showed that participants experienced a strong drift in the perceived self-location.

Furthermore, the drift was significantly stronger than that experienced in 3PP-NO, despite the fact that the actual displacement among the virtual and real bodies was much greater in the latter.

Analogously, the CCT data from the 3PP-PO condition support a significant shift in the perceived self-location. The highly significant cross-modal interaction found in 3PP-PO clearly showed that vibrotactile cues were indeed processed in an updated spatial register in which tactile events on the real body and visual events on the virtual body are associated according to a precise bodily-based topological correspondence. This result is even more remarkable when considering that, in this condition, the vibrotactile cues on the real left leg of participants were exactly collocated with the LEDs on the right leg of the virtual body, so that if no shift in the perceived self-location occurred we should have observed a strong interaction among these visuotactile cues, which was instead not observed (see inset in Figure 4B).

Summarizing, the experimental manipulation in the 3PP-PO condition induced concurrent changes in ownership and self-location. Most importantly, the latter was much stronger than the analogous change experienced in the 3PP-NO condition, indicating a strong interaction between ownership and self-location. Despite the fact that the two can be dissociated from each other, it seems that the sense of ownership experienced over a dislocated virtual body can importantly boost the experienced drift in the perceived self-location.

6. GENERAL DISCUSSION

The experimental study here presented provides direct experimental evidence that the sense of ownership and the sense of self-location can be selectively manipulated in full body illusions. It was shown that it is possible to experience illusory changes in the perceived self-location during OBEs when no sense of ownership is experienced toward the virtual body. On the other during FBOI experienced toward a fully collocated virtual body, the perceived self-location was (obviously) not altered, as no conflict in the location of the two bodies was present.

The fact that OBE illusions can occur without changes in the sense of ownership and that OBE and FBOI are indeed two different perceptual illusions was previously suggested (Petkova et al., 2011b; Maselli and Slater, 2013), but to date it was not supported by experimental data.

Previous studies on OBE illusions have been primarily designed to manipulate and measure illusory changes in self-location. Despite this OBE illusions are often considered and discussed as belonging to the wider class of full body ownership illusions (e.g., Blanke, 2012; Limanowski et al., 2013). Having here shown that FBOI and OBE are different perceptual illusions is thus particularly important, because the lack of a clear distinction between the two illusions often resulted in interpreting observed changes in self-location as evidence for a sense ownership experienced toward a body seen in the far extra-personal space (Lenggenhager et al., 2007; Aspell et al., 2012).

As a second important outcome, the present study showed that when seeing a virtual body that

overlaps only partially with the space occupied by the physical body, a strong FBOI is experienced together with a significant shift in the perceived self-location toward the virtual body. This is indeed the first explicit experimental evidence for a FBOI experienced while having a third person visual perspective over a fake full body. Our data further show a positive interaction between the two components of body self-consciousness: in this “partial overlap” configuration, the experienced shift in self-location is in fact significantly larger than the one experienced in an OBE illusion. It seems then that, when both ownership and self-location are affected during a full body illusion, it is the sense of ownership that drives the sense of self-location toward the owned body.

Although our study does not provide any direct evidence for the existence of distinct neuronal correlates for FBOI and OBEs, in the following we propose plausible candidates for the sets of neuronal structures that are likely involved in the two illusions.

6.1. On the Neuronal Correlates of Experimentally Induced OBEs and Peripersonal Space

It has been recently proposed (Blanke, 2012) that the best neural candidates for encoding the perceived shift in self-location experienced during experimentally induced OBEs are the populations of bimodal visuotactile (VT) neurons hosted in cortical and subcortical areas of the primates brain.

Bimodal visuotactile populations are characterized by tactile receptive fields that can cover small patches or large portions of the body surface, and by visual receptive fields (vRF) anchored to the body part mapped in the tactile modality (Graziano and Gross, 1993; Duhamel et al., 1998; Brozzoli et al., 2012; Huang et al., 2012). For these characteristic properties bimodal VT populations have been suggested to encode the peripersonal space (Fogassi et al., 1996): through their vRFs these populations define in fact the region of space surrounding the body in which visual stimuli may trigger somatic sensations. The main functional role of this dynamic representation of the external space in body-parts centered coordinates is to guide movements for defensive purposes and for efficient interaction with external objects (Graziano and Cooke, 2006; Sereno and Huang, 2014).

Results from single cell recording in the monkey have further shown that the vRF of bimodal visuotactile neurons is highly plastic and can expand after the active manipulation of tools (Iriki et al., 1996). This groundbreaking result provided the first robust experimental evidence that the peripersonal space is highly plastic and can be reshaped in relatively short time scales. The plasticity of bimodal VT neurons has been then advocated as the mechanism that allows healthy humans to embody external objects, like tools, in their body schema (Maravita and Iriki, 2004).

As discussed thoroughly in Section The Cross-Modal Congruency Task as a Measure of Self-location, the cross-modal congruency task (CCT) has been shown to be a powerful psychophysical test to detect dynamic modulations of the peripersonal space during active tool use (Maravita et al., 2002), as well as during a rubber hand illusion (Pavani et al., 2000; Zopf et al., 2010). In line with these results, CCT performances in our study showed that, during experimentally induced OBEs, an actual extension (or shift) in the vRF of proximal visuotactile neurons occurs. This modulation can

be interpreted as a modulation of the peripersonal space likely triggered by VT neural populations that maps large portions of the body, such as the legs. It is worth noting that neuronal populations with such properties have been identified in the human posterior parietal cortex (PPC) (Huang et al., 2012), and that the PPC has been shown to play a crucial role in mapping bodily signal into external space (Azañón et al., 2010).

In line with the original proposal from Blanke (2012), we argue that the dynamical changes in the vRF of visuotactile neurons with large receptive field on the body surface, is responsible for the perceived changes in self-location. We further argue that the same mechanisms may be regarded as the minimum common denominator of all OBEs. This proposal is not in conflict with the well-known implication of the TPJ in OBEs, which has been revealed in lesion analysis of patients suffering from recurrent OBEs (Blanke and Arzy, 2005), in electro-stimulation studies showing that OBEs can be systematically induced by direct stimulation of the TPJ (Blanke et al., 2002), and with fMRI performed during experimentally induced OBEs (Ionta et al., 2011). The latter study showed in fact that activity in the TPJ seems to encode the perceived elevation of the whole body -rather than its position in extra-personal space- and thus it is plausible that the TPJ implication in OBEs occurs at higher level in the hierarchical processing of sensory signals, in which a further integration is operated to combine visuotactile cues with vestibular and auditory information (Lopez et al., 2008).

6.2. DIFFERENT REPRESENTATIONS FOR THE SENSE OF OWNERSHIP AND SELF-LOCATION

Our study has shown that OBEs can occur with or without an associated ownership illusion. This implies that the dynamic changes in the peripersonal space associated with OBEs may be coupled or not with the activity of a larger and more complex network of neuronal populations that give rise to the sense of ownership during FBOI. Imaging studies have shown that the illusion of ownership for both body parts (RHI) and full bodies involves a complex network of brain areas that is still not well established and controversial. Depending on the experimental design and the imaging technique adopted, the ownership illusion has been found to correlate with activity in several brain areas: ventral premotor cortex (vPMc) and posterior parietal cortex (PPc) (Ehrsson et al., 2004; Petkova et al., 2011a), primary somatosensory cortex (Limanowski et al., 2013; Shokur et al., 2013), the extrastriate body area (EBA) (Limanowski et al., 2013); and, at subcortical level, the insula (Tsakiris et al., 2007; Limanowski et al., 2013). Recent theoretical accounts for body ownership have stressed the role of multimodal hierarchical processing of sensory and motor signals from the body (e.g., Hohwy, 2007; Ehrsson, 2011; Moseley et al., 2012; Limanowski and Blankenburg, 2013). Although a review of these works is beyond the scope of the present work, we want to stress here the potential contribution that our results may bring about.

The present study has highlighted, in particular, the fundamental role of visuo-proprioceptive correlations in driving FBOI. In a previous study we showed how congruent visuo-proprioceptive correlations from a (realistic) virtual body and the physical body could be sufficient to elicit a FBOI with no need for additional multimodal correlations (Maselli and Slater, 2013). The current

study provides more stringent evidence for the effective coupling of visual signals from the virtual body and proprioceptive signals from the real one, that is established during FBOI. It was in fact shown that proprioceptive information about the body posture can be significantly modulated by seeing a change in the posture of the virtual body, even when the physical body does not move. Furthermore, we found that if visual and proprioceptive cues about the body are not in severe conflict (i.e., when a partial spatial overlap of the virtual and real bodies is preserved) a strong FBOI can be experienced. We additionally found that in this case the FBOI has the effect of strengthening the recalibration of tactile sensations toward the virtual body, which is characteristic of OBEs. These results strongly support the earlier proposals (Moseley et al., 2012; Maselli and Slater, 2013) suggesting that a fundamental node of the complex network of brain areas involved in ownership illusions is the neural population homologous to the one hosted in area 5 of the monkey parietal cortex, that integrates visual and proprioceptive signals to encode limb position (Graziano et al., 2000).

7. SUMMARY

We have presented an experimental study conducted with the support of virtual reality, with the aim of exploring the relation between two of the important components of body self-consciousness: ownership and self-location. Our results provide direct experimental evidence that the sense of ownership and the sense of self-location can be selectively manipulated in experimentally induced full body illusions. It was shown that FBOIs and OBEs could occur independently of each other, affecting ownership and self-location respectively. It was also shown that the two illusions could co-occur affecting concurrently ownership and self-location; our results suggest that in these cases illusory changes in ownership and self-location have a synergic interaction.

We discussed how our results support the recent proposal suggesting that self-location is strictly related with a reshaping of the visual receptive field of proximal visuotactile neurons mapping large portions of the body's surface. On the other hand, we discussed how our results support the need for a driving activation of visuo-proprioceptive neuronal populations in full body ownership illusions.

Finally, our results moderate previous conclusions about the role of the visual perspective in ownership illusions. It was in fact shown that a FBOI could be experienced from a 3PP when the virtual body preserved a partial spatial overlap with the physical body.

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CHAPTER 7

ALLOCENTRIC AND EGOCENTRIC MANIPULATIONS OF THE SENSE OF SELF-LOCATION IN FULL-BODY ILLUSIONS AND THEIR RELATION WITH THE SENSE OF BODY OWNERSHIP

Related publication:

Allocentric and egocentric manipulations of the sense of self-location in full-body illusions and their relation with the sense of body ownership.

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ABSTRACT

Self-location refers to the experience of occupying a given position in the environment. Recent research has addressed the sense of *self-location* as one of the key components of self-consciousness, together with the experience of owning the physical body (*ownership*). Experimentally controlled full-body illusions proved to be valuable research tools to study these components and their interaction, and to explore their underlying neural underpinning. The focus of this manuscript is to provide a close look into the nuances of different illusory experiences affecting the sense of *self-location* and to examine their relation to the concurrent experienced sense of body *ownership*. On the basis of previous reviewed studies, it is proposed that the sense of *self-location* may be regarded as the blending of two parallel representations: the abstract allocentric coding of the position occupied in the environment, mainly associated with *visual-perspective*, and the egocentric mapping of somatosensory sensations into the external space, mainly associated with peripersonal space. Open questions to be addressed by future research are further addressed.

1. INTRODUCTION

SPATIAL AND BODILY ASPECTS OF SELF-LOCATION

Two main spatial components are contemplated in recent accounts of *self-consciousness*: *self-location*, intended as the perceived position of the body in space, and the *visual-perspective*, defined as the point from which visual information from the environment is gathered (Blanke and Metzinger 2009). In normal conditions, both *self-location* and *visual-perspective* coincide with the position of the physical body. This tight coupling can be temporally disrupted during neurological or experimentally induced out-of-body experiences, in which subjects report the sensation to be located outside their body and to perceive the world from a *visual-perspective* incongruent with the position of the physical body (Blanke 2012).

In out-of-body illusion experiments, the *visual-perspective* is decoupled from the position of the seen body by using stereo goggles that project an immersive view of the environment from an arbitrary location. In the presence of environmental landmarks, such as walls or furniture, the mere manipulation of *visual-perspective* could engender an abstract allocentric representation of *self-location* within the seen room (Barry and Burgess 2014), as demonstrated during navigation in virtual environments (Hassabis et al. 2009).

Manipulations of the *visual-perspective* in out-of-body illusion experiments entail a third-person view of the real body within the experimental room, or of a fake body in a virtual environment. Furthermore, visuotactile stimulation is delivered through a moving rod. The processing of similar semantic and multisensory information can trigger modulations in the activity of bimodal visuotactile populations and other visuotactile subpopulations responding also to proprioceptive, semantic (Graziano et al. 2000) or vestibular (Bremmer et al. 2002) stimuli. These multisensory populations establish a somatosensory connection to visual stimuli in the environment and are regarded as the main encoders of peripersonal space (Graziano and Gross 1993; Fogassi et al. 1996).

Within the context of full-body illusions, it shall thus be advantageous to consider the sense of *self-location* as the blending of two parallel representations: the abstract allocentric coding of the position occupied in the environment, mainly associated with the *visual-perspective*, and the egocentric mapping of somatosensory sensations into the external space, mainly associated with peripersonal space.

MANIPULATIONS OF SELF-LOCATION IN OUT-OF-BODY ILLUSIONS

Experimental out-of-body illusions allow investigating the multisensory and neurophysiological basis of *self-location*. Two main paradigms have been exploited hitherto. Here I review the most relevant studies rationalizing them on the basis of the multisensory and neurophysiological processes involved. Common to the two paradigms is the use of immersive goggles to prevent direct vision of the real body and provide participants with a third-person *visual-perspective* over their own body (filmed from a distance; e.g. Ehrsson 2007) or over a virtual body (Lonta et al. 2011). This *visual-perspective*'s

manipulations can be modulated by providing or not environmental landmarks: when participants see their body as filmed from a different position within the experimental room, they have a new egocentric visual-perspective over the known environment that automatically triggers mechanisms of allocentric remapping of *self-location* (Barry and Burgess 2014). In the case in which no landmark is present, like the case in which the avatar is the only visible element (Ionta et al. 2011), there are no spatial cues for activating allocentric remapping of *self-location*.

Another common ingredient is the delivery of visuo-tactile stimulation through a moving object. The difference between experimental paradigms concerns the spatial congruence of such stimulation. In one case, a rod is used to stroke the real hidden body on the front, while a similar rod is seen moving in temporal synchrony and with spatial patterns that match the felt touch in the egocentric *visual-perspective* (Ehrsson 2007). Alternatively, the touch is delivered on the back of the participant that sees the stick moving synchronously on the back of the body in front, thus in spatial incongruence with the felt touch (Lenggenhager et al. 2007). Accordingly, in the front-stroking there is no visuotactile conflict: the touch is seen where it is felt, even if empty space is seen instead of the real body (Ehrsson 2007), or the latter is replaced by a fake one (Guterstam et al. 2015). The back-stroking involves instead a spatial conflict: no visual counterpart of the felt touch is seen where expected; nevertheless, the precise temporal synchronicity and the corresponding spatial patterns in body-centred coordinates may trigger an aberrant coupling among somatosensory sensations from the real body and visual cues on the seen body, similarly to the case of tool incorporation (Maravita and Iriki 2004).

NEURAL CORRELATES OF SELF-LOCATION IN OUT-OF-BODY ILLUSIONS

Which are the neurophysiological and perceptual correlates of front-stroking and back-stroking paradigms?

A recent imaging study adopting the front-stroking paradigm revealed the implication of a set of brain regions including hippocampus, posterior cingulate cortex (PCC), retrosplenial cortex (RSC) and intraparietal sulcus (IPS; Guterstam et al. 2015). The induced changes in *self-location* seem thus to be mostly related to the recalibration of the allocentric representation of *self-location* in the environment, triggered as the artificial *visual-perspective* is nourished with congruent visuotactile signals. The hippocampus hosts in fact neural populations that encode mnemonic allocentric representations (Hassabis et al. 2009), while the PCC and RSC are involved in the translation of egocentric-to-allocentric spatial representations (Vann et al. 2009). In the altered self-location experience, the role of PCC and RSC would be to translate body-centred, head-centred and retinotopic spatial representations encoded in the IPS, into allocentric spatial representations stored in the hippocampus (Guterstam et al. 2015 and references therein). Subjective scores to *self-location* assessments support this view, revealing that the illusory *self-location* corresponds to the position of the *visual-perspective* (Guterstam and Ehrsson 2012; Guterstam et al. 2015).

In back-stroking out-of-body experiments, *self-location* is altered in a more subtle fashion. The temporally synchronous but spatially incongruent visuotactile stimulation can in fact induce a spatial dissociation between *visual-perspective* and *self-location*, with the latter shifted towards the seen body. This was found in both allocentric (Lenggenhager et al. 2007) and egocentric

(Lenggenhager et al. 2009) representations and is associated with strengthened interactions of visual cues on the fake body with tactile cues on the real one (Aspell et al. 2009; Maselli and Slater 2014). The remapping of the visual receptive field of visuotactile populations, which would extend or shift to encompass the seen body, has been proposed as the origin of the detachment of *self-location* from *visual-perspective* (Blanke 2012). However, although this proposal is grounded in several behavioural and neurophysiological data (Maravita and Iriki 2004), there is no direct evidence in its support.

Results from brain-recording studies are still fragmented. When applying the back-stroking paradigm to supine participants, TPJ activation patterns suggest the encoding of the perceived elevation (Ionta et al. 2011), while TPJ's connectivity patterns reveal the dominance of right-hemispheric networks in modulating *self-location* and *visual-perspective's* direction (Ionta et al. 2014). These results are consistent with the multisensory nature of TPJ populations (integrating vestibular, visual, tactile and auditory signals) and the well-known implication of this region in neurological out-of-body experiences (Blanke and Mohr 2005). No major involvement of the TPJ was instead found when inducing the illusion in standing participants, as no elevation sensations were triggered. In this configuration, changes in *self-location* were correlated with decreased activity in the medial-prefrontal cortex (Lenggenhager et al. 2011), suggesting that the processing of visuotactile conflicts may be sufficient for detaching *self-location* from *visual-perspective*, independently of anomalous vestibular activity.

THE SENSE OF BODY OWNERSHIP DURING OUT-OF-BODY ILLUSIONS

Body ownership refers to the experience that the physical body belongs to the self. Experimental manipulations similar to those adopted for out-of-body illusions can project the sense of *ownership* to fake bodies (for a review see Kilteni et al. 2015). While ownership illusions are easily experienced when seeing the fake body in spatial overlap with the real body (Maselli and Slater 2013; Petkova and Ehrsson 2008), the extent to which *ownership* can be experienced over a body seen from a detached *visual-perspective* is under debate (Serino et al. 2013; Maselli and Slater 2014).

As for *self-location*, different out-of-body paradigms have different impacts on the sense of *ownership*. In front-stroking setups, subjects experience disownership of their body seen from a distance (Guterstam and Ehrsson 2012): it is as if the processing of visuotactile cues congruent with the novel *visual-perspective*, locks *self-location* to *visual-perspective* and deprives the seen body of accessible somatosensory experiences. Complementing the altered *visual-perspective* with the view of a spatially congruent fake body may further bind *self-location* to *visual-perspective* and enhance disownership of the self-body seen from outside (Guterstam et al. 2015).

In the back-stroking case, the multisensory coupling between the real and the seen body can elicit some degree of ownership over the latter, even if not systematically (Serino et al. 2013). In fact, changes in *self-location* are not sufficient to trigger *ownership* over the fake body, even when involving a remapping of tactile cues towards distant external space, i.e. on the seen fake body (Maselli and Slater 2014). Interestingly, when the fake body is displaced from the real one while keeping partial spatial overlap with it, synchronous visuotactile stimulation triggers changes in both *self-location* and body *ownership*, with reciprocal synergic interactions among the two (Maselli and Slater 2014). This result speaks in favour of the major role of visuoproprioceptive populations in driving the sense of

body ownership (Maselli and Slater 2013).

CONCLUSIONS AND FUTURE DIRECTIONS

In this manuscript I have argued that, in the context of full-body illusions, *self-location* can be advantageously regarded as the blending of two parallel spatial representations: an abstract allocentric representation, mainly associated with *visual-perspective*, and the egocentric mapping of somatosensory sensations into the external space, mainly associated with peripersonal space. According to the specific experimental paradigm adopted to induce out-of-body illusions, these representations can be selectively or simultaneously altered, with different implications for the sense of *ownership*.

Future studies are needed to establish how the two representations are integrated to results in the subjective experience of being located in a given position in space. In fact, the two resonance imaging studies conducted to date have explicitly focused on either one or the other aspect. In Guterstam et al. (2015) *self-location* was locked to the *visual-perspective*, and the latter was manipulated so to provide anomalous visual cues on environmental landmarks and thus to trigger an allocentric remapping of *self-location*. In Ionta et al. (2011) no landmarks were available and changes in *self-location* mainly relied on the presentation of conflicting multisensory bodily cues, detaching *self-location* from *visual-perspective* through anomalous visuotactile correlations.

Another important missing piece of the puzzle is a direct evidence in support of the proposal that the reshaping of visual receptive field of visuotactile populations may be responsible for decoupling *self-location* from *visual-perspective*. It would be further interesting to assess whether the suggested involvement of visuotactile subpopulations responding also to vestibular signal is necessary (Blanke 2012) or optional (Maselli and Slater 2014) for eliciting illusory changes in *self-location*. Finally, experimental paradigms for out-of-body illusions always included visuotactile stimulation. Nevertheless, the novel design proposed in Guterstam et al. (2015) suggests the possibility to investigate illusory changes in *self-location* while eliminating confounds associated with visuotactile processing. In their design, the altered *visual-perspective* over the scanning room was complemented with the view of a spatially congruent fake body. This configuration was shown to be sufficient for eliciting full-body ownership illusions (Maselli and Slater 2013), which in turn could drive *self-location* to the position of the *visual-perspective* with no need for visuotactile triggers.

Addressing these among other questions in future studies will provide important advances in the fields of self-consciousness and spatial cognition.

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CHAPTER 8

GENERAL DISCUSSION

GENERAL DISCUSSION

The research presented in this thesis aimed at providing new insights and a comprehensive view of the multisensory underpinning of full-body illusions. Multisensory integration has been addressed as the causal root of bodily illusions since the first report of the rubber hand illusion (Botvinick and Cohen, 1998). Since then, experimentally induced bodily illusions have been endowed with the status of unique tools for studying the otherwise elusive neural and multisensory basis of self-body perception (Botvinick, 2004; Graziano and Botvinick, 2002). Indeed, a large number of studies provided important insights into the relation between the processing of body-related sensory and semantic stimuli on one hand, and self-perception with its different facets and corresponding neural underpinnings on the other. Despite this collective effort, results from independent studies were not always consistent with each other, and a common framework able to encompass the outcome of the numerous and diverse studies carried out during more than ten years of research was still missing.

The work presented in this thesis tackled some of the open-issues emerging from controversial results in the literature. We directly faced questions like: Which is the role of visuotactile stimulation in ownership illusion? Are congruent visuotactile information a necessary ingredient to experience ownership over a fake body? If not, which are the alternative mechanisms that can trigger such illusions? On a different side: Which is the role of visual perspective? Is it possible to experience ownership over a fake body or body-part seen from a 3PP? If this is not the case, why? Which are the different multisensory mechanisms that set apart full body ownership illusions from illusory out-of-body experiences? Although some of these questions may seem naïve, an astonishing lack of consensus was there. We have addressed these and other related questions for the specific case of full-body ownership illusions (FBOs), with particular focus on how different experimental manipulations used to elicit full-body illusions have an impact on the experienced sense of body ownership and self-location. Our approach was mainly based on experimental setups integrating Immersive Virtual Reality, motion capture systems, physiological measures and psychophysical assessments. This experimental work, together with a thoughtful effort for modelling and encompassing results from the relevant literature in a coherent overall framework, provided several new insights in the field. The present chapter reviews and discusses the most relevant findings.

THE KEY ROLE OF VISUOPROPRIOCEPTIVE BINDING IN OWNERSHIP ILLUSIONS

In the attempt to pinpoint the minimal combinations of multisensory components contributing to the sense of body ownership and analyze their mutual interaction, the work presented Chapter 2 brought about several noticeable results. First, we showed for the first time that the mere exposure to a static view on a realistic collocated virtual body could elicit FBOs. This confirmed that, differently from what previously stated (Petkova and Ehrsson, 2008), synchronous visuotactile stimuli are not necessary for eliciting ownership over a fake body, but could be replaced by other forms of dynamic multisensory stimuli, like spatiotemporally congruent visuovestibular or visuomotor stimuli (González-Franco et al., 2010; Sanchez-Vives et al., 2010; Slater et al., 2010). As a novelty, it implied that a much simpler form of multisensory manipulation, static congruent visuoproprioceptive stimuli, could be an effective trigger by itself. This provided a novel evidence for the crucial role of visuoproprioceptive integration in building up the sense of body ownership.

The role of visuoproprioception binding in establishing the illusion was largely overlooked in previous studies, probably due to the intrinsic limitation of experimental setups alike to the one used in classic rubber hand illusion (RHI), in which the physical object used as surrogate body part had to be necessarily placed aside the corresponding body part. Under similar configurations visual and proprioceptive information about the body are incongruent, so that visuotactile (and/or visuomotor) congruent stimulations were actually necessary triggers for the illusion. A general view got therefore established that considered the multisensory processing of trains of multimodal stimuli as the key mechanisms for triggering changes in the sense of ownership. In this view, once triggered, the sense of ownership over the fake body would have an impact on proprioception, driving the spatial coding of the self-body towards its seen surrogate (e.g. Makin et al., 2008), an effect robustly assessed via the proprioceptive drift measure. In this respect, our result brought a discontinuity in the narrative, shedding light on the primary role of visuoproprioceptive binding in shaping the sense of body ownership. Not only we showed that seeing a fake body exactly where the real hidden body is can by itself elicit ownership illusions, but we point at visuoproprioceptive binding as the key minimal component underlying the illusory experience of ownership towards external objects.

This finding has been replicated in following independent studies, and/or taken as the basis for novel experimental setups exploiting the possibility to induce ownership illusions while avoiding the possible interference of dynamic stimulation like visuotactile triggers (Martini et al., 2015; Nierula et al., 2017; Tieri et al., 2015). Building on this result, in a later study (presented in Chapter 6), we introduced a novel behavioral task to test illusory ownership over a fake body. The task consisted in a proprioceptive assessment about the self-body posture (in our case in pointing to the position of the ankles) in absence of vision, to be done before and after the experimental manipulation. Right before the second proprioceptive assessment and after the experimental manipulation, participants viewed the virtual body slightly moving into a new posture while instructed to not move. The rationale was that, for those participants who experienced ownership over the virtual body, the induced visuoproprioceptive binding between the real and the virtual body would induce a recalibration of the felt position when seeing the virtual body moving, even in absence of actual movement (Maselli and Slater, 2014). Results supported this prediction, on the one hand confirming that a tight visuoproprioceptive binding is established during body ownership illusions, and on the other proving the proposed test to be a reliable behavioral assessment for illusory ownership.

The study presented in Chapter 2 provided further relevant contributions. As from our main aim to pinpoint the “building blocks” of the ownership illusion, it provided a novel view on how the different multisensory components contributing to the illusion interact reciprocally. The most relevant findings were the following: 1) when a FBOI is established via visuoproprioceptive binding, further exposure to multisensory stimulations modulates the strength of the illusion, with a reinforcing or damping effect depending on their congruency; 2) the level of realism of the virtual body modulates the strength of the illusion; 3) having a 1PP over the fake body is a necessary condition for ownership illusions to occur. In discussing these results, we proposed a “basic model” for ownership illusions, in which we pinpointed the basic constraints that should be satisfied when combining different multisensory and semantic information about the body, from the real body and its fake counterpart, in order for illusory ownership to emerge. In a later study, presented in

Chapter 5, these ideas were further elaborated, presented more systematically in the context of the relevant literature, and further formulized within a proposal of a causal inference computational model.

A CAUSAL INFERENCE MODEL FOR OWNERSHIP ILLUSIONS

The model presented in Chapter 5 has been worked out in the Bayesian inference framework and for the representative case of the classic RHI. Our approach was to look for a conceptual framework for modelling how our nervous system differentiate between external objects, including others bodies, and the self-body with its body parts. According to the model, the illusion would take place depending on the probability that all the sensory information available (visual from the rubber hand and somatosensory from the real hand) is assumed to have the same one origin, the own hand, in contrast to the case of having two independent origins, the real hand and the rubber hand. This probability could be estimated in terms of the likelihood of the available sensory information under the assumption of a common origin, and the prior belief about the existence of more than one hand. Beside the details of the formulation, the model allows to account for the effect of different types of multisensory and semantic components potentially contributing to the illusion, also accounting for their mutual interaction. Importantly, the contribution of each factor could be modeled at different degrees of semantic and spatiotemporal congruency, and not simply in the more classical dichotomous fashion (e.g., synchronous vs asynchronous). Samad and colleagues independently proposed a similar Bayesian inference model for the classic RHI, including visual, proprioceptive and tactile components (Samad et al., 2015). They further implemented the model and compared its predictions with data collected from ad-hoc performed experiments, showing a good agreement among the two. Noticeably, they showed how this class of inference models is able to predict that ownership illusion can occur also based on visuoproprioceptive information alone, corroborating in this way our earlier result.

An alternative computational framework proposed for the study of self-processing, including the sense of body ownership, is predictive coding (Apps and Tsakiris, 2013; Seth, 2013). In general predictive coding accounts are based on the Helmholtzian view that the brain needs to infer the hidden causes of the sensory signals, and that it does so by minimizing the error between predictions from its internal causal model and the available sensory information (Rao and Ballard, 1999; Srinivasan et al., 1982). Applied to the case of the RHI, predictive coding proposals hold that the illusion results from minimizing the prediction error arising from seeing the touch on the rubber hand and feeling it on the real hand. To minimize the error the brain could adopt several “strategies”, for example recoding the position of the real hand towards the location of the seen touch and updating its prior beliefs about the one’s own hand appearance (Apps and Tsakiris, 2013), and/or by attenuating the somatosensory processing from the real hand (Zeller et al., 2014). Although these proposals provided interesting insights and can potentially account for several observed correlates of ownership illusions, their actual implementation is still missing. Bayesian inference models similar to our proposal, are easier to implement. In fact, as we proposed, implementations like the one presented in Samad et al. (2015), could be extended to include other factors (e.g., semantic and visuomotor information), and further interfaced with neural network models able to simulate processes like the multisensory integration

of visuotactile stimuli on the hand (Magosso, 2010; Magosso et al., 2010).

OWNERSHIP ILLUSIONS RELAXES TEMPORAL CONSTRAINTS FOR VISUOTACTILE INTEGRATION

The study presented in Chapter 2 brought, among the other results discussed above, a serendipitous finding. When the ownership illusion was established, in our case through visuoproprioceptive coupling, asynchronous visuotactile stimuli were not perceived as wrong, which was instead the case when the illusion was not experienced. Building up on this result, in the study presented in Chapter 3, we designed an experiment to formally test the hypothesis that, when undergoing an ownership illusion, the temporal constraints for visuotactile integration are relaxed as a result of the established causal binding between the real and the fake body. The study provided a robust support in favor of this hypothesis. These results provided the first evidence for the impact of ongoing body ownership illusions on the processing of multisensory information, and fit consistently with several effects highlighted by previous research on multimodal integration.

It was previously shown that vision of the hand facilitates visuotactile integration by extending the temporal window in which two independent, tactile (vibration on the hand) and visual (flashing led) stimuli (Ide and Hidaka, 2013). This effect was found only if the hand image was shown in an anatomically plausible position, indicating that the effect was linked to some aspect of self-body processing. Nevertheless, differently from what we did, that study did not address any effect of ownership, as the design consisted in just showing a drawn hand image on a screen placed in front on the participants, far in space from the hand receiving the touch.

Interestingly, a more recent study reported complementary findings that apparently contradict our results. Keys and colleagues showed that modulating the sense of ownership towards a rubber hand, by controlling the plausibility of its anatomical posture, do not affect the detection of visuotactile asynchrony (Keys et al., 2018). A substantial difference with respect to our study that may explain the different outcome is rooted in the causal relationship between the visual and tactile stimuli to be integrated. In testing multisensory interaction, Keys and colleagues adopted the classical choice of a flashing LED presented next to the finger receiving the tactile stimuli. We instead adopted a visual stimulus semantically congruent with the delivered touch, namely the brief rotation of a geared wheel seen in touch with the virtual finger corresponding to the one receiving the touch. This is a crucial difference because while a LED flash, however close to the body, cannot generate by itself a mechanical vibration resulting in a tactile sensation, this is the case for the case of a geared wheel sliding on a finger. It is the causal binding established during ownership illusions, between events seen on the virtual body and semantically congruent somatosensory stimuli on the real one, that does relax constraints for multisensory integration, not the illusion itself.

In support of our view, previous research reported consistent evidence for how the perceived temporal relationship between stimuli and/or events is flexible and dependent on their implicit causal association. This is the case of the intentional-binding effect, in which a willed action and its associated sensory feedback are perceived closer in time than they actually are (Haggard et al., 2002; Moore and Obhi, 2012). Expansions of the temporal window of integration similar

to the one we found, have been attributed to the causal binding of audiovisual stimuli in speech perception (Vatakis et al., 2008; Vatakis and Spence, 2007). Another effect in line with our finding is the simultaneity constancy effect. In this case, flexible temporal windows for the integration of multisensory stimuli associated to the same events are considered as a compensatory mechanism for the intrinsic differences in the transduction and/or transmission times of the different sensory channels, and for the fact that such differences are modulated by environmental conditions like illumination and temperature (Harrar and Harris, 2005; Kopinska and Harris, 2004). Cast within this wider framework, our results indicate that the sense of body ownership involves predictive cause-effects mechanisms that shape the processing of bodily signals during interactions with the environment.

THE SENSE OF OWNERSHIP OVER A SEMI-TRANSPARENT BODY INCREASES PAIN SENSITIVITY

The results presented in Chapter 4 provide novel insights into how, during ownership illusions, the appearance of the surrogate body modulate pain perception. In particular, we showed that when experiencing an ownership illusion over a semi-transparent body, higher levels of experienced ownership resulted in an increased pain sensitivity. Previous studies have shown that the analgesic effect of having direct view of one's own body while receiving painful stimuli (Longo et al., 2009), holds true when looking at a collocated virtual body during ownership illusions (Martini et al., 2014; Nierula et al., 2017). Considering this evidence, our finding could seem to contradict the naïve expectation that analgesic effects would fade away together with the vision of the body and with the associated diminished sense of ownership. Nevertheless, to a closer inspection our intriguing findings could be accounted by at least two alternative explanations. They may reflect a top-down modulation of pain in which body transparency is interpreted as a form of weakness and increased vulnerability. This is in line with independent evidences for the increased pain sensitivity associated with the view of a negatively-valued body, e.g., injured, reddened, or swollen (Martini et al., 2013; Osumi et al., 2014b, 2014a). Alternatively, the trend we found could be related to the interference of body semi-transparency with lower level mechanisms underlying pain modulation. Pain perception was in fact linked with the intracortical excitability in the primary somatosensory cortex (Longo et al., 2012). Accordingly, the impact of body vision on pain sensitivity was associated with an increased intracortical inhibition within the somatosensory cortex, and with a reorganization of somatosensory maps consisting in sharpened neurones receptive fields, both inhibiting the perception of painful stimuli (Haggard et al., 2013). Along these lines, we speculated that when the "owned" body appears to be semi-transparent, these mechanisms of sharpening and reorganization may be not as effective. Nevertheless, as we did not foresee the actual outcome of our study, our design was not optimal to formally test these speculative interpretations. Despite this, having shown that the apparent level of body transparency does modulate pain sensitivity, our work paved the way to future studies that could investigate potential clinical application of IVR protocols for pain treatment.

THE SENSE OF OWNERSHIP AND SELF-LOCATION ARE SELECTIVELY DISSOCIABLE IN BODILY ILLUSIONS

Self-location and body ownership are considered to be two fundamental components of self-consciousness (Blanke and Metzinger, 2009). However, the extent to which these two aspects can be selectively altered during full-body illusions has been, and still is, an important matter of debate.

Numerous studies consistently reported that ownership towards a filmed or a virtual body is experienced together with changes in self-location during illusory out-of-body experiences (OBEs) induced with the back-stroking paradigm (Blanke, 2012; Ionta et al., 2011; Lenggenhager, 2007; Serino et al., 2013). On the other hand, an independent branch of studies consistently reported that in order to experience ownership towards a surrogate body a first person perspective over the body is a must (Maselli and Slater, 2013; Petkova et al., 2011; Petkova and Ehrsson, 2008). How to reconcile these two opposite lines of evidence? In our previous study (see discussion in Chapter 2), we proposed that a possible explanation to the puzzle is linked to the fact that what in OBEs experiments is reported to be ownership is rather a form self-identification similar to the case of recognizing oneself in a mirror (Maselli and Slater, 2013). In our view, the main difference between ownership and self-identification is that the latter lacks the key visuoproprioceptive coupling that characterizes illusory ownership. In fact, the reports of ownership from OBEs studies are exclusively based on questionnaire data and self-reports in debriefing sessions, assessments that cannot test this difference. The study presented in Chapter 6, tested the hypothesis that manipulations of self-location and body ownership in FBOs and OBEs rely on different and dissociable, although interacting, multisensory processes. The study was designed ad-hoc for testing the following hypothesis. While changes in the sense of ownership are rooted in the visuoproprioceptive coupling of visual stimuli from the surrogate body and somatosensory stimuli from the real body as we previously suggested (Maselli and Slater, 2013), changes in the perceived self-location are rooted in the expansion of the visual receptive fields of visuotactile neuronal populations. Our results clearly demonstrated the validity of this hypothesis with objective measures from behavioural postural tasks and psychophysical tests (Maselli and Slater, 2014).

To our knowledge our study is still now the only experimental work that simultaneously tested how both the sense of ownership and self-location are altered during full bodily illusions with different conditions of visual perspective over the fake body. Additional studies with a similar approach are needed to corroborate and extend our results. In fact, numerous studies still overlook the important point of disentangling genuine alterations of the sense of ownership from actual changes in the sense of self-location during full body illusions triggered from a third person perspective. In particular, neuroimaging studies are needed to shed more light into the different brain processes associated with the different patterns of alterations in the sense of ownership and self-location corresponding to different types of bodily illusion. In fact, while there is a rich literature of imaging studies focusing selectively in one of the two components of self-consciousness (see Section 1.2.3 for references), a deeper and more comprehensive look on how these the two components interact and/or can be dissociated is still missing.

ALLOCENTRIC AND EGOCENTRIC MANIPULATION OF SELF-LOCATION IN ILLUSORY OBEs

In the thorough analysis of the relevant literature carried out to inspect the differences that tease apart alterations of ownership and self-location (Maselli and Slater, 2014), we further emphasized important aspects that differentiate illusory OBEs triggered via the back-stroking paradigm from front-stroking induced OBEs. In both, a third-person-perspective over a distant body seen from behind is given and the illusion is triggered by synchronous visuotactile stimulation. However, in the front-stroking case, seen and felt touch are spatially coincident in the disembodied empty space,

as seen through the visor, where the real body is located but occluded (Ehrsson, 2007). In the back-stroking case seen and felt touch are instead in spatial conflict (Lenggenhager, 2007). These different experimental paradigms correspond to important differences in the resulting illusory experience. As largely discussed in Chapters 1 and 7, far from being subtle, such differences encompass all aspects of the corresponding illusory experience, from subjective reports, to behavioral and neuronal correlates. Despite this, in the literature there is to date an utter lack of discussion and inquire about the issue.

In Chapter 7 a detailed overview of the key differences characterizing illusory changes in self-location induced by back-stroking and front-stroking OBEs is presented along with a thoughtful analysis of the possible implications for a comprehensive understanding of the sense of self-location as a constitutive component of self-consciousness. As a new proposal, it is suggested that the sense of self-location may be regarded as the blending of two parallel representations. An abstract allocentric coding of the position occupied in the environment, and the egocentric mapping of somatosensory sensations into the external space. Although future experimental work is needed to corroborate this speculative view, this work represents an important example of the effort for comparing in a comprehensive and constructive approach different brunches of experimental research. To pursue crucial advances in our current understanding of the complex brain machinery underlying self-perception, it is desirable that this type of approach will spread out, inspiring further novel experimental practices.

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