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5 Neural Mechanisms of Bodily Self-Consciousness and the Experience of Presence in Virtual Reality

Abstract: Recent neuroscience research emphasizes the embodied origins of the experience of the self. This chapter shows that further advances in the understanding of the phenomenon of VR-induced presence might be achieved in connection with advances in the understanding of the brain mechanisms of bodily self-consciousness. By reviewing the neural mechanisms that make the virtual reality experience possible and the neurocognitive models of bodily self-consciousness, we highlight how the development of applied human computer confluence technologies and the fundamental scientific investigation of bodily self-consciousness benefit from each other in a symbiotic manner.

Keywords: Bodily Self-consciousness, Presence, Virtual Reality, Out-of-body Experience, Agency, Body Ownership, Self-location.

5.1 Introduction

The ultimate goal of virtual reality (VR) is to produce the authentic experience of being ‘present’ in an artificial environment. To achieve this, VR technologies have been classically conceived within a cybernetic approach, placing the human subject at the core of a feedback control loop where multi-media technologies substitute all interaction with the external world. Pioneers of VR began to describe this ‘presence’ as the “illusion of non-mediation” (Lombard & Ditton, 1997) or the “suspension of disbelief” (Slater & Usoh, 1993), which occurs when the subject reports a transfer of presence from reality to the immersive virtual environment. This is directly linked to the mechanisms by which our experience of being a self in the world, termed bodily self-consciousness, is constructed using multisensory information.

The study of bodily self-consciousness has been based on the findings from altered experiences of the self, such as out of body experiences (OBE). During an OBE, a subject (or self) experiences states in which he/she feels as though he/she occupies a spatial location separated from that of his/her own physical body and perceives the world from a disembodied perspective. Alterations in bodily self-consciousness, whether of neurological origin or induced experimentally, shed light on the components and mechanisms that structure our natural and typical sense of presence. We suggest here that the presence in VR relies on these mechanisms, and as such, one should consider scientific insights about bodily self-consciousness and its neural origins in order to understand how presence in a virtual environment can be achieved.

This chapter aims to bridge the VR development and the neuroscience of self-consciousness by showing that VR profits from concepts and knowledge developed in cognitive neuroscience, which help us understand and perfect the technology that gives rise to presence in VR environments. Additionally, it highlights that cognitive neuroscience benefits from the unique opportunities offered by VR technologies to manipulate perception and consciousness and study the brain mechanisms underlying self-consciousness.

We first illustrate the close association of the origins of tele presence technologies with altered forms of self-consciousness. We then discuss attempts to establish models of presence in virtual reality and neurocognitive models of bodily self-consciousness. Finally, we conclude by examining the reciprocal relationship between these fields and consider the direction of future interactions.

5.2 Tele-Presence, Cybernetics, and Out-of-Body Experience

The possibility to experience tele-presence in a distant or even an artificial reality was first realized when the technologies of video transmission and computer graphics allowed individuals to wear displays mounted on the head and see pictures of a world captured at another location – or through fully generated by a mathematical computer model. Howard Rheingold experimented with this idea in Dr. Tashi's Laboratory (Tsukuba, Japan, in 1990) with a remotely controlled robotic head and head mounted displays (HMD). At one point, turning his head as he was looking through the robot's eyes, the cameras installed inside the robot caused the robot to turn toward his physical body. Speaking of the body he saw, Rheingold said; "He looked like me and abstractly I could understand that he was me, but I know who me is, and me is here. He, on the other hand, was there. It doesn't take a high degree of verisimilitude to create a sense of remote presence" (Rheingold, 1991). Rheingold concluded, "What you don't realize until you do it is that tele-presence is a form of out-of-the-body experience."

It may not come as a surprise that we owe the invention of the head-mounted graphical displays in 1963 to a brilliant engineer and scientist Marvin Minsky who had an out of body experience. He indeed revealed, "One day, at age 17, I was walking alone at night during a snowstorm in a singularly quiet place. I noticed that the ground looked further away than usual, and then it seems that I was looking down from a height of perhaps 10 meters, watching myself crossing the field" (reported in Grossinger, 2006). Minsky, a pioneer in cybernetics and artificial intelligence, was a highly influential thinker since the invention of tele-presence and immersion systems. Following the cybernetic principles in which a person can be considered an 'entity' reacting to 'inputs' through 'output' channels, it was hypothesized that an ultimate and total mediation of all the input-output channels would lead to a replacement of what a person perceives as being their environment. In other words, a person could be fooled into believing that the experienced situation is real if his/her mind cannot detect any discrepancy between the expected and the mediated outcome of their actions (e.g., the head-camera feedback-loop that Rheingold experienced). Using VR systems, which consider the human "senses as channels to the mind" and the "body as a communication device" (Biocca, 1997), it became possible to explore cyberspace and to contemplate a generalization of Minsky's idea of tele-presence in a distant location (Minsky, 1980) to the broader concept of presence in an immersive virtual environment. Pioneers in VR soon observed that users of virtual reality systems "are in a world other than where their real bodies are located" (Slater & Usoh, 1992) and that they experience the troubling "sense of being" in a non-existing environment (Heeter, 1992). Interestingly, these accounts resemble Rheingold's reference to an artificial form of "out-of-the-body experience" (Rheingold, 1991).

What exactly are out-of-body experiences (OBE) of neurological origin? An OBE is an autoscopic phenomenon during which people have the impression of having left their body, of floating above it, and of observing it from outside. During an OBE, one is subjected to a displacement of their point of view out of the boundaries of the physical body. OBEs may occur during epileptic seizures, but they have also been observed in other neurological or psychiatric conditions. They may also occur in neurologically healthy individuals. OBEs have even been directly evoked by administering electrical stimulation to the brain during the treatment of an epileptic patient, specifically at the right angular gyrus (Blanke, Landis, Spinelli, & Seek, 2002). Blanke and colleagues proposed that an OBE involves an alteration in bodily self-consciousness (BSC) caused by selective deficits in integrating multisensory body-related information into a coherent neural representation of one's body and of its position in extrapersonal space (Blanke, Landis, Spinelli, & Seek, 2004; Blanke, 2012). In the normally functioning brain, self-consciousness arises at different levels, ranging from the "the very simple (the automatic sense that I exist separately from other entities) to the very complex (my identity, complete with a variety of biographical details)" (Damasio, 2003). Blanke and Metzinger (2009) described a low-level account of the bodily self and termed it minimal phenomenal selfhood. Focusing on the experience of the bodily self, minimal phenomenal selfhood comprises three main components, (i) self-identification with the body as a whole (rather than ownership of body parts), (ii) self-location, and (iii) the first person perspective (1PP). Using this concept, an OBE can be described as an incoherence in the integration of 1PP, self-identification, and self-location. Interestingly, the alteration of the three components of BSC also applies to the description of tele-presence phenomenon reported by Rheingold. A similar parallel can also be drawn between autoscopic hallucinations (the experience of viewing one's own body in extracorporeal space) and multimedia setups (an example of which is "Video Place", an interactive installation created by Krueger in 1985 where people play with interactive video silhouettes of themselves).

Apart from pathological cases of altered bodily self-consciousness, such as OBE and autoscopic hallucinations that may strike us as rather strange phenomena (see also heautoscopy and feeling-of-a-presence; Lopez et al., 2008; Heydrich, Blanke, & Brain, 2013), it might seem quite astonishing that in most instances, we experience a presence inside a body and rarely question how this is achieved. Similarly, the experience of being in the world that is perceived from the perspective of the body (1PP) is rarely challenged in reality. It is only under the artificial mediation of perception induced by VR technologies that a subject questions the limits of the natural and usual experience of self-consciousness. What makes the condition of tele-presence induced by VR interesting as a phenomenon is the intangibility of those limits, with an experience of presence (almost) as authentic as that experienced in reality on the one hand and an unusual experience closer to an actual OBE on the other hand. As such, trying to understand the presence in virtual reality is similar to investigating the ability of the brain to integrate artificial perceptions into a coherent representation. As such, presence might better be described “as an immediate feeling produced by some fundamental evaluation by the brain of one’s current circumstances” (Slater, 2009) or as the “neuropsychological phenomenon evolved from the interplay of our biological and cultural inheritance” (Riva, Waterworth, & Waterworth, 2004).

5.3 Immersion, Presence, Sensorimotor Contingencies, and Self-Consciousness

In the previous section, we highlighted similarities between the experience of tele-presence in VR and the neurological phenomenon of OBEs, suggesting a stronger link between VR research on presence and neuroscientific research on self-consciousness. In the next section, we first consider more recent developments regarding the experience of presence in the context of VR and then focus on neuroscience research elucidating its neural mechanisms.

As mentioned in Lombard and Jones (2007), various terms have been used to discuss the concept of presence in the 1800 articles, which the authors reviewed over more than twenty years. Today, the terminology benefits from these decades of refinement based on which several terms have been distinctively identified. In particular, Slater defined ‘immersion’ as the ability of a VR system to induce an experiential displacement of a person inside what is called an immersive virtual environment (Slater, 2003). Presence should be distinguished from immersion and considered more correctly as “a ’response’ to a system of a certain level of immersion” (Slater, 2003). Compared to Lombard and Ditton’s (1997) original conception of presence as the “perceptual illusion of non-mediation” or to the previous definition “suspension of disbelief” proposed by Slater and Usoh (1993), this distinction between immersion and presence disuntangle the concept of presence as an experience from the technological and artificial substrates that are used to generate it.

Later, Slater introduced two concepts with an aim to establish two levels of presence (Slater, 2009), the place illusion (PI) and the plausibility illusion (Psi). The PI phenomenon is arising directly from the integration of multiple cues from the virtual environment, whereas the Psi is the result of higher-level cognitive processes accepting a virtual scenario as plausible and therefore potentially real. The PI may therefore be more closely related to different bottom-up levels of sensorimotor immersion generated by VR, whereas the Psi acts on specific cognitive mechanisms. These distinctions are fundamental for engineers to evaluate the immersive power of their systems and for researchers to target how to generate a more substantial experience of presence. Importantly, it is generally accepted that the key mechanism for generating the PI is the implementation of a set of sensorimotor contingencies (SCs) supported by the virtual environment. Thus, the corresponding set of valid actions available to the user corresponds to a given sensory feedback, and it is implemented as action-effect feedback loops. It is useful for programmers of VR simulation systems to understand that the feedback loop is not simply a design pattern but a necessary condition for SCs, as the richness and extent of the SCs contribute to the experience by augmenting the PI level in response to the subject's exploration of the virtual environment.

To explain with greater concision its separate experiential states, Riva and Waterworth described the presence in VR as a three-level hierarchical process (Riva, Waterworth & Waterworth, 2004); (i) the proto-presence, i.e., an embodied presence related to the level of perception-action coupling, (ii) the core presence emerging from conscious and selective activity in order to integrate sensory occurrences into coherent percepts, and (iii) the extended presence linking the current core-presence to the past experience in a way that challenges the significance of the lived experience. Riva and Waterworth's different levels of presence in VR closely correspond to the 'layers of the self' proposed by Damasio (1999), i.e., the proto-self (to which the proto-presence corresponds), the core-self (the core-presence in VR), and the autobiographical self (the extended presence in VR). To situate these levels of presence within the general picture of VR, Riva and Waterworth introduced additional dimensions of focus, locus, and sensus (Riva, Waterworth & Waterworth, 2004; see also Waterworth & Waterworth, 2001). "Focus can be seen as the degree to which the three layers of presence are integrated toward a particular situation" and is maximal "when the three levels are working in concert", i.e., proto, core, and extended presence are coherent. The locus dimension or "the extent to which the observer is attending to the real world or to a world conveyed through the media" is more about contrasting the virtual to the physical world. Finally, sensus (defined as "the level of consciousness or attentional arousal of the observer") denotes one's awareness of 'feeling present' during immersion, and it is also referred to as the sense of presence (SoP). Estimations of SoP through questionnaire have been proposed as a mean to quantify presence (see review Herbelin, 2005). However, in the same way in which "participants know that nothing is 'really' happening, and they can consciously decide to modify their automatic behavior accordingly" (Slater, 2009), participants are made aware of the artificial nature of their feeling of presence in VR and evaluate it in comparison with what they think it should be in reality. To avoid this bias, a direct approach based on low-level bodily experience, as studied in cognitive science of self-consciousness, seems preferable.

This refinement of the concept of presence highlights its experiential nature and thus its link to aspects of consciousness, particularly bodily self-consciousness. To address this link further, we review selected findings on bodily self-consciousness and its neural underpinnings.

5.4 Presence and Bodily Self-Consciousness

A system based purely on sensory-motor contingencies cannot account for the experiential nature of presence. The experience of ‘being here’ (in a physical reality or in VR) implies that a *subject* is having this experience. According to Damasio (1999), the minimal level of experience, also defined as the “core consciousness”, arises at the interplay between two components, “the organism” and “the object”. Thus, a pre-reflexive, non-verbal representation of the “organism” as the subject of experience, which Damasio conceptualized as the Self (i.e., the “core Self”), precedes any experience. Recent research in neuroscience has suggested a systematic relationship between the subject of experience and the specific representations of the body in the brain. We experience the world from the physical location and with an egocentric perspective of the body, which we feel as our own. The concept of minimal phenomenal selfhood corresponds to such a proposal of the embodied self (Blanke and Metzinger, 2009) and of bodily self-consciousness (Blanke, 2012).

According to a prominent view in neuroscience, the embodied self is characterized by two major aspects of bodily experience, i) the sense of agency, i.e., the subjective experience of being the author of one’s own actions, and ii) the sense of ownership, the feeling that this body is mine (Gallagher, 2000; van den Bos & Jeannerod, 2002). Both may be selectively impaired by neurological and psychiatric disorders. For example, in somatoparaphrenia (typically occurs following right parietal brain damage), patients feel that their contralesional hand is not their own (Vallar & Ronchi, 2009). In the ‘Anarchic Hand’ syndrome, patients feel a loss of volitional control over their hand while maintaining ownership (Della Sala, 1998). The double dissociations observed in these disorders support the notion that agency and ownership rely on separate brain mechanisms. On the one hand, the brain seeks correspondence between internally generated motor commands and the re-afferent sensory feedback caused by their consequences. Some neuroscientists believe that this correspondence is crucial for generating the experience of being the agent of the movement. On the other hand, our brain also constantly receives and integrates multisensory information from different parts of our body, and the integration of these different multisensory body-related signals is assumed an important mechanism for generating body ownership.

Recent developments in VR have captured these basic mechanisms of bodily self-consciousness and used them to introduce a new and potentially more powerful account of VR experience, the sense of embodiment. Kilteni, Groten, and Slater (2012) defined it as “the ensemble of sensations that arise in conjunction with being inside, having, and controlling a body”. Accordingly, the sense of embodiment is generated in conjunction with the sense of agency, the sense of body ownership, and the sense of self-location. The latter is defined as a position in space where the self is experienced to be, according to the model of bodily self-consciousness by Blanke and Metzinger (2009). Kilteni and colleagues suggested that, “self-location refers to one’s spatial experience of being inside a body, and it does not refer to the spatial experience of being inside a world”; thus, it may be that self-location does not entirely correspond to the place illusion. Although different, sense of presence and sense of embodiment certainly share most mechanisms described above. It has even been proposed that the sense of embodiment “potentially includes the presence subcomponent” (Kilteni, Groten, & Slater, 2012).

Research on cognitive neuroscience has shown that critical concepts in the VR field, such as presence and sense of embodiment, are better understood in terms of neural mechanisms of bodily self-consciousness. Critical components of bodily self-consciousness are associated with integrated sensorimotor and multisensory body-related signals, generating agency, body ownership, self-location, and the first person perspective (see Blanke & Metzinger, 2009; Blanke, 2012). In the next sections, we will review major achievements in neuroscience that support this view, starting with studies on agency and following with research on body ownership and self-location.

5.4.1 Agency

The predominant model that reflects our sense of agency is often referred to as the “forward model”. Following the original idea of Von Helmholtz (1866), it posits that when we make a movement, our sensorimotor systems generate an “efferent copy” of that movement, i.e., an internal representation of the sensory consequences of the planned movement (Wolpert, Ghahramani & Jordan, 1995). This internal representation is compared to the actual re-afferent sensory inputs related to the action (e.g., visual, proprioceptive). Under normal conditions, the sensory feedback matches signals predicted by the efferent copy, and such a match generates the attribution of the action to oneself, i.e., the sense of agency (Blakemore & Frith, 2003; Jeannerod, 2006). To experimentally test the sense of agency, neuroscientists have introduced systematic perturbations of the sensory (mostly visual) feedback for movements (Georgieff & Jeannerod, 1998). Early experiments on agency used ingenious manipulations, employing mirrors to achieve visuo-motor discrepancies, such as in the classical paradigm proposed by Nielsen (1963), which indicated, for the first time, the dissociation between the unconscious monitoring of our hand motor actions and our sense of agency for them.

While mirror based paradigms contributed to our initial understanding of the sensorimotor mechanisms underlying the sense of agency, the advent of computer and video technology gave rise to novel possibilities to test sensorimotor mismatch. As the control of digitally represented outcomes (such as cursor movements) entered many research laboratories, several paradigms utilizing these new sensorimotor contingencies appeared. The use of computers allowed the introduction of precise and well controlled deviations between motor actions and their visual outcomes and made it possible to precisely test the effect on the attribution of those actions to the self (David et al., 2007; Salomon, Szpiro-Grinberg & Lamy, 2011). For example, Farrer and colleagues (2007) joined such conflicts with functional magnetic resonance imaging (fMRI) to study brain activity in participants while controlling the movement of a circle along a T shaped path. In some trials, the participants had full control over the movement of the circle while in other trials, the computer controlled the shown trajectory. The results showed that when the participants felt in control over the reproduced movement, this was associated with the activation of the insular cortex, an area that processes and integrates several bodily-related signals (Craig, 2009; Tsakiris et al., 2007). When the participants felt no control over the movement, a different region was activated, specifically, the right inferior parietal cortex. This region has been related to many spatial functions, particularly to self-attribution of actions (Salomon, Malach, & Lamy, 2009; Tsakiris, Longo & Haggard, 2010) and awareness of one's own actions (Lau et al., 2004; Sirigu et al., 2004). Moreover, lesions to this region may lead to loss of agency, as in the anarchic hand syndrome (Bundick & Spinella, 2000). These and other findings are consistent with the observation that the inferoparietal cortex is responsible (together with areas not reviewed here, such as the supplementary motor area and the cerebellum) for capturing discrepancies between the efferent copy and the actual sensory consequence of actions, thus for monitoring action attribution (Chaminade & Decety, 2002; David, Newen, & Vogeley, 2008; Farrer et al., 2003; Farrer et al., 2007).

Other paradigms based on live and recorded video images of movements have also been employed to study the mechanisms underlying self-attribution of actions (Farrer et al., 2008; Sirigu et al. 1999; Tsakiris et al., 2005). In a classic experiment, Van de Bos and Jeannerod asked participants to make one of several possible hand gestures and showed them, by means of a video setup, their own hand or that of an experimenter making the same or a different gesture. Additionally, the presented hands were also rotated, such that the participants or experimenter's hand could appear to be facing down, up, left or right (van den Bos & Jeannerod, 2002; see also Kannape et al., 2010, 2012). Their results indicated that when the participant and experimenter made different actions, almost no self-attribution errors occurred. However, when the actions were identical, the spatial orientation of the hand served as a strong cue for self-attribution of that action to the self or the other – that is when the hand of the experimenter was shown in the same posture and from the same perspective as one's own hand, participants more frequently misattributed that hand to themselves. Thus, although action-based self-attribution related to the forward model, proprioceptive and spatial cues strongly affected self-judgments of the depicted actions when dynamic cues were non-informative.

Technological advances allowing more controlled manipulation of sensorimotor contingencies, such as computer-based control of the visual consequences of actions and real time video presentations, have increased our understanding of the sense of agency. The advantages inherent in these methods have now been combined with those of VR. Modern VR, including full body motion tracking and realistic avatar modeling, offer an optimal environment to study the sense of agency and body ownership as well as their effect on presence. For instance, Salomon and colleagues (2013) used a visual search task with multiple full body avatars animated in real time, with one avatar mimicking the participants' movements precisely while the others movements are spatially or temporally deviated. The participants had to find the avatar moving in accordance with their own movements among the distractor avatars when their movements were self-initiated or when being moved passively by the experimenter. The results showed that during self-initiated trials, the participants detected the self-avatar more rapidly, even when more distractor avatars were present.

Finally, VR has allowed studies to be extended beyond specific limb representations into full body representations of action in space. In a full body version of Nielsen's and Jeannerod's agency experiments, Kanappe and colleagues used full body tracking and avatar animation to test agency of locomotion. The results showed that we have limited conscious monitoring of our locomotive actions, indicating the limits of agency for full body motion (Kannape et al., 2010; see also Mentzer et al., 2010 for a related paradigm using auditory-motor conflicts). Once again, the relationship between technological advances in video and VR and the study of the sense of agency highlights the symbiosis between the study of the self and the emulation of self-related processes in virtual environments.

5.4.2 Body Ownership and Self-Location

The findings of the sense of agency over one's own movements, however, does not sufficiently account for the experience of the embodied self, in particular of body ownership. Simply consider the example that another person is lifting your arm. You perceive no sense of agency, but a preserved sense of body ownership. Research has shown that the subjective feeling that this hand and body is mine originates from the integration of different sensory cues. This is difficult to test experimentally because of the complexity of manipulating the experience of one's own body. In research on the awareness for external events, researchers can manipulate the sensory features of external stimuli and then measure the effects of such manipulations on perceptual and neural mechanisms. In the case of body ownership, however, such a classical experimental approach is much more difficult for the simple reason, which is that the body is always present to the subject, as William James noticed. Some of the first insights on bodily self-consciousness arose from Ambroise Paré's description in 1551 of the illusory presence of a missing limb, i.e., the 'phantom limb' experience frequently reported by amputee patients. Phantom limb phenomenon shows that the brain can generate the experience of a limb and body ownership (because phantom limbs generally are experienced as own limbs) even if the respective body part is absent. Neuroscientists, more than 400 years later, were able to experimentally reproduce an analogous phenomenon, i.e., extending the sense of bodily ownership to an artificial object. In the so-called "rubber hand illusion", synchronous stroking of a seen fake hand and of one's own unseen (real) hand cause the fake hand to be attributed to the subject's body ("I feel like it is my hand"; Botvinick & Cohen, 1998; Ehrsson et al., 2007; Tsakiris & Haggard, 2005). The rubber hand illusion is also associated with a misperception of the position of the participant's own hand relative to the fake hand and even with changes in the physiology of one's own hand. For instance, if a harmful stimulus suddenly approaches the rubber hand while the illusion occurs, subject's skin conductance response increases (neurophysiological marker of increased arousal to a threat, see Armel & Ramachandran, 2003; Ehrsson et al., 2007). Others have reported a reduction in temperature of the real limb 'perceptually' substituted by the rubber hand (Moseley, Olthof et al., 2008). Sanchez-Vives and colleagues demonstrated the rubber hand illusion in VR by showing that illusory ownership of an artificial hand could be obtained when a virtual hand, instead of a rubber hand, is presented in a virtual environment (Sanchez-Vives et al., 2010). VR provided Evans and Blanke (2012) with the ability to induce illusory hand ownership in a systematic and computer-controlled manner, thus allowing for the simultaneous recording of high-density EEG, revealing that illusory ownership and motor imagery share the same neural substrates in fronto-parietal areas of the brain. Neuroimaging techniques, such as fMRI (Ehrsson et al., 2007; Tsakiris et al., 2007), transcranial magnetic stimulation (TMS; Kammers et al., 2009; Tsakiris et al., 2008), and electroencephalography (EEG, Kanayama et al., 2007), have been applied to study the neural correlates of the rubber hand illusion, pointing to a fronto-parietal network of brain areas involving the premotor cortex and the posterior parietal cortex, which normally integrate multisensory stimuli (somatosensory, visual, auditory) occurring on or close to the body. The experience of ownership of the rubber hand is also associated with activity in the (predominantly right) insular cortex, an area receiving multiple sensory inputs from 'exteroceptive' senses as well as from 'interoceptive' channels monitoring internal body states (Craig, 2009). These neuroimaging results are important in showing that body ownership is obtained though activation of brain regions that integrate multisensory body-related signals to construct multiple representations of one's own body.

The paradigm generating the rubber hand illusion has also been extended to face perception. In the so-called 'enfacement' illusion, viewing another person's face being touched while feeling touch on one's own face results in perceiving the other person's face as similar to one's own (see Apps & Tsakiris, 2013 for a review; Sforza et al., 2008; Tsakiris et al., 2008). Showing a change in the perception of one' own face following such short sensory stimulation is particularly interesting, as one's own face is the part of the body that most strongly defines one's own visual identity and is shown to others during social interactions (Rochat & Zahavi, 2011). Self-face recognition is considered an important component of self-consciousness, such that self-face recognition in the mirror-test is considered a hallmark of self-consciousness in non-human species and in human infants (see, e.g., Gallup, 1970; Povinelli, 2001). A recent fMRI study investigating the neural correlates of the enfacement illusion has shown that it is generated by modulation of activity in the right temporo-parietal junction and intraparietal sulcus, areas that normally integrate multisensory body-related information (Apps et al., 2013).

Thus, an abundance of evidence from both the rubber hand illusion and enfacement illusion has contributed to the establishment of some of the mechanisms which allow manipulating BSC. Specifically, synchronous multisensory inputs related to a part of the real body and to an artificial replacement of that body part activate brain areas, which normally integrate multisensory information related to one's own body. Such stimulations induce an extension of the limits of BSC from the physical body to its artificial or virtual replacement. However, although these studies have important contributions to the understanding of BSC, they focus on separate (body part centered) representations of the body. On the contrary, a fundamental feature of self-consciousness is that it is characterized by the experience of a single and coherent whole body rather than of multiple separated body parts. For this reason, Blanke (2012) proposed the concept of self-identification in order to reflect full-body ownership, as opposed to the feeling of ownership of single body parts. Lenggenhager and colleagues (2007) used VR technology to study this global aspect of BSC experimentally. In what it is referred to as the full body illusion, subjects see a virtual body (avatar) placed 2 meters in front of them while being stroked on their back (Lenggenhager et al., 2007). When the viewed and felt stroking is synchronous, participants report perceiving the virtual body as their own (change in self-identification) and feel displacement toward the virtual body (change in self-location). Other variants of the full-body illusion have been reported. For instance, in the so-called body swap illusion, participants observe, via head-mounted display and the first-person perspective, a mannequin being stroked on its chest, which is congruent with a stroking of their own chest (Ehrsson, 2007; Petkova & Ehrsson, 2008). When interviewed about such experience, participants scored high on questions such as, "I had the impression that the fake body was my own body", and they physiologically reacted strongly to harmful stimuli approaching the fake body (Petkova & Ehrsson, 2008).

Ionta, Heydrich, and colleagues (2011) used fMRI to study the neural mechanism of the full body illusion. They showed that self-location induced by synchronous stroking of the virtual body and of one's own body activated the temporo-parietal junctions (TPJ). Interestingly, the focus of TPJ activity found in fMRI was close to the area of brain damage in nine patients suffering OBEs of neurological origin. Further, functional connectivity analyses of the fMRI data showed that right and left TPJ are bilaterally connected to the supplementary motor area, ventral premotor cortex, insula, intraparietal sulcus, and occipito-temporal cortex and that changes in self-location modulated brain activity among right TPJ, right insula, and right supplementary motor area and between left TPJ and right insula (Ionta, Martuzzi et al., 2014). These recent data, together with the previously reviewed neuroimaging studies (see also Serino et al., 2013), point to an extended network of multisensory areas underlying BSC, which involve premotor and posterior parietal cortices as well as the temporal parietal junction and the insula, predominantly in the right hemisphere.

5.5 Conclusion

The early VR developments were based on the concepts from cybernetics, that is, an artificial system which would be capable of emulating sensory inputs, thus removing the person from his/her true environment and placing him/her into an artificial one. This view initiated the quest for fully immersive systems, which would surround entirely the human body and its senses, transporting people into 'cyberspace'. These technological developments in sensing, display, and immersion technologies have since evolved symbiotically with research on the cognitive mechanisms of presence.

The present selective review of recent literature in neurology and neuroscience of bodily self-consciousness crucially highlights how new technologies have enabled experimental manipulations that contribute to the understanding of bodily self-consciousness and therefore of presence itself. In particular, these technologies offer novel methodological approaches, and they have provided researchers in neuroscience with unprecedented experimental opportunities for approaching high level and complex mechanisms of self-consciousness, such as agency, body ownership, and self-location. Research on these aspects of embodiment and bodily self-consciousness, and the neural underpinnings of both, have been investigated in the last 15 years, and are beginning to contribute to our understanding of the mechanisms of presence in VR. For instance, although the VR community has highlighted sensorimotor contingency as the prominent factor for presence, neuroscience research shows that multisensory integration of bodily signals is also critical for the presence, embodiment, and related aspects of bodily self-consciousness.

As illustrated throughout this chapter, research on the cognitive neuroscience of bodily self-consciousness is gradually merging with the investigation of presence in VR. Neurological observations of altered bodily self-consciousness (employing VR technologies) might eventually lead to a better understanding of self-consciousness in its most basic form, arising when the "I" of the conscious self declares to be present at a given place. While a definitive model of presence is yet to be achieved, cognitive neuroscience has enriched the field with novel paradigms, allowing qualification and quantification of the multisensory integrative mechanisms with which bodily self-consciousness is constructed. This model of how the mind gives rise to our presence in the world promises to introduce original perspectives for approaching immersive embodiment systems.

When observing the increasing complex nature of human-computer confluence technologies, it appears that the evolution of research on the presence in VR can be seen as a precursor of how interactions within the digital world should be considered using a neurological perspective and how they may eventually shape our bodily self.

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