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Neurological Basis of Bodily Self-Consciousness and Related Psychopathologies

Bedensel Öz-Bilincin Nörolojik Temelleri ve İlişkili Psikopatolojiler

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Abstract

Self-consciousness is based on dynamic processing of sensory information coming from different bodily sources and leads to differences in body awareness. According to recent studies, this sensory information (i.e. vestibular, somatic-sensory), seems to be a fundamental requirement for the formation of bodily self-consciousness. In this context, based on the compatibility between different sensory inputs there are striking changes occurs in both limb and whole body perception. The basic assumption of the previous research that has been carried out in this area is to test the validity of these different consciousness experiences which will lead to a better understanding of the sensory-integration processes. The aim of this article is to review the neuroscience and psychiatry literature on bodily self-consciousness and to discuss the experimental settings and underlying sensory processes. In addition to that, the limitations of the previous experimental studies are discussed further.
Keywords: Consciousness, body image, illusions, somatosensory discrimination disorder

Öz

Bedenden gelen farklı duyusal bilgilerin dinamik bir şekilde işlenmesine bağlı olarak insanların bedensel farkındalıklarının değişmesi, bedensel öz-bilinç yaklaşımının ortaya çıkmasına neden olmuştur. Son yıllarda yapılan çalışmalara göre farklı duyu sistemlerinden gelen bu duyusal bilgilerin (örn. vestibüler, bedensel-duyusal) birlikte işlenmesi ve yorumlanması, bedensel öz-bilincin oluşması için temel bir gereksinim olarak gözükmektedir. Bu bağlamda duyusal sinyallerin uyumlu ya da uyumsuz olması sonucunda hem uzuv hem de tüm beden algısında çarpıcı değişimler gözlenmektedir. Bu alanda yürütülen çalışmaların temel varsayımı, bedensel deneyimlerin farklı duyulardan gelen sinyallerin tümleştirilerek birlikte işlenmesi sayesinde olduğu yönündedir. Bu makalede bedensel öz bilincin deneysel olarak nasıl çalıştığını incelenmesi ve altında yatan duyusal süreçlerin tartılması amaçlanmıştır. Buna ek olarak, daha önce yapılan deneysel çalışmaların kısıtları tartışılmıştır.
Anahtar sözcükler: Bilinçlilik, beden imajı, illüzyonlar, bedensel-duyusal ayrımsama bozukluğu

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HOW do we distinguish our own body from others' bodies or objects? What is the relationship between the self and the body? For centuries, many philosophers had enormous interest in such questions regarding the body and the self, which they addressed from different perspectives. Recent neurological studies have examined the following two questions (i) how our brain processes our body and (ii) what type of conscious states of mind create this ownership.

According to previous research, the brain needs to evaluate certain sensory information in order to create a sense of self. The source of this information is not always caused by an external stimulus, but often comes either from one's own mind, or from the body. Therefore, bodily self-consciousness is defined as a state of mind related to dynamic interpretation of internal (e.g. proprioceptive) and external (e.g. tactile or visual) sources. A unique sense of body ownership arising from the subjective perception and process of bodily sensations refers to a key feature of this mental state. Previous research has led researchers to investigate how sensory and motor signals from the body construct the basis of the sense of self, and to explore the role of bodily self-consciousness for the sense of self (Gallagher 2000, Tsakiris 2006). Recent studies have revealed that body representation in the brain is elicited through integration of multisensory information, such as vestibular, visual and tactile inputs (Metzinger 2003). The studies have suggested that several brain regions constantly process multisensory bodily signals in order to create bodily self-consciousness (Gallagher 2000, Arzy et al. 2006). According to these studies, multisensory brain regions are not dependent on high-level cognitive processes such as memory, thinking and reasoning when forming the basis for bodily self-consciousness, and consequently create the sense of self we experience (Blanke 2012).

In normal circumstances, a musician is able to distinguish auditory stimuli in detail. Likewise, previous studies have shown that healthy individuals can successfully dissociate multisensory signals from their own limbs to full-body, and then associate these signals with their sense of self. However, impairments in the ability to process internal and external bodily signals can induce altered states of consciousness, such as those experienced in neurological disorders. For example, it has been observed that the sense of ownership over both whole-body, and individual body-parts such as hand or foot, becomes altered due to brain lesions (Blanke and Metzinger 2009). As in the above example, these brain lesion studies provided a basis for further research on the flexibility of body perception. More recently, a consensus over the concept that multisensory integration creates a body representation has emerged due to new experimental paradigms in the field of cognitive psychology and neuropsychology. In general, these studies examined how the sense of body and the sense of self can be manipulated through the use of multisensory conflicts, although the first research in this area mostly focused on changes in perception of body-parts (Botvinick and Cohen 1998, Ehrsson et al. 2004). However, the fundamental element of bodily self-consciousness became characterized by the perception of body as a single and a whole after suggestion that the brain combines the neural signals from multiple body parts generating holistic sense of the body (Blanke and Metzinger 2009). Therefore, recent studies have led researchers to study the whole-body perception (Ehrsson 2007, Lenggenhager et al. 2007, Petkova and Ehrsson 2008).

The aim of this review is to explain the relationship between multisensory inputs and the sense of self based on a bodily self-consciousness-based approach, and to examine new experimental paradigms developed in the light of neurological observations.

Role of multisensory integration in body representation

We exist through our body in the real world, and perceive this world through it, highlighting the importance of the body for the sense of self. In a daily life, we regard our body as a means of communication with our environment and define that body within which we believe we live as our own body. In a cycling experience, for example, the stimulations from the wheel of the bicycle will be transmitted to the tactile senses. The bike will be increaingly integrated into the pre-existing body representation as we continue to ride (Metzinger 2003). Recent studies have pointed out the importance of multisensory processes that play a critical role in constructing this highly flexible body representation (Makin et al. 2008, Blanke 2012). It has been shown that the representation of body is dynamically updated via integration of multisensory information (Botvinick and Cohen 1998, Lackner 1988). Studies conducted in this context have often focused on the ownership over body-parts aspect of bodily self-consciousness (Ehrsson et al. 2004, Tsakiris and Haggard 2005).

Over the past two decades, neuroscientists showed that several areas of the brain play a crucial role in integration of multisensory signals (Stein et al. 2009, Perrault et al. 2012), even including primary areas, such as the primary visual and somatosensory cortical regions involved in processing of multisensory integration (Calvert et al. 2007, Stein and Stanford 2008). In an electrophysiological study by Rizzolatti and colleagues, monkeys were presented with a visual stimulus either close to or far away from their hand with a simultaneous tactile stimulus on their hand while the activity of premotor cortex were recorded (Makin et al. 2008). The results of this experiment showed that the premotor neurons responding to the tactile stimulus also respond to the visual stimulus. Crucially, these neurons only responded to tactile and visual stimuli applied to the hand, and not to those approaching other parts of the body.

Further studies showed that receptive fields of these neurons that respond to visual and tactile stimuli to the monkeys' hand were anchored to the arm position (Graziano et al. 1997). In a fMRI study by Graziano et al. (1997), monkeys' right arms were placed on a table in front of them and then visual stimuli approaching the hand presented along several trajectories. It was observed that the sensory neurons in the premotor cortex had greater response when the visual stimulus approached directly to the location of the hand. The same neurons respond the visual stimulus approaching the new location of the monkeys' hand when the hand moved (see Figure 1). The change of the receptive fields of these neurons depends on the position of the hand, suggesting that these neurons operate within a hand-centered coordinate system.

Integration of visual and tactile information from the space around the body is considered as an indicator of an intermediate layer between the body and the outside world (Rizzolatti et al. 1981). Based on electrophysiological studies with monkeys, this intermediate layer, defined as a peripersonal space, originates from neurons that combine signals from different senses, especially from the visual-tactile neurons. Accordingly, neurons responding to visuo-tactile stimulation at a distance accessible to the arms of monkeys (5-50 cm) supports the view that there is a specific neural network representing the personal space. These results support the existence of a multisensory mechanism that combines different stimulations oriented towards the limbs (Llyod 2007).

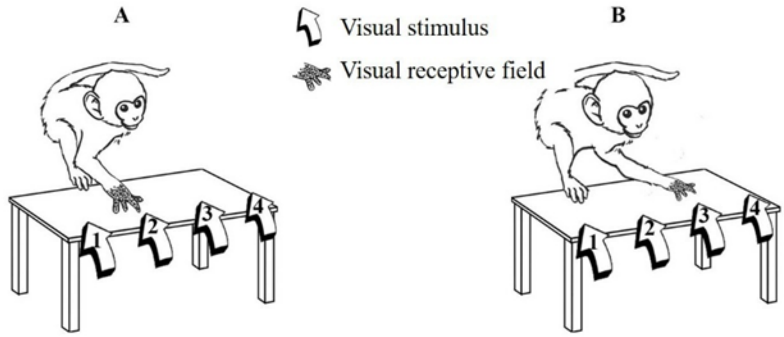

Figure 1. Illustration of the experiment by Graziano at al. (1997).
1-4 (arrow) represents paths of visual stimuli. (A) Neurons mostly respond to the visual stimulus approaching to the pathway 2 when the monkeys' right arm placed to right side. (B) Neurons responded best to the visual stimulus approaching to pathway 3 when the monkeys' arm located at the left side.

Brain imaging studies with humans revealed that this multisensory integration mechanism in monkeys is also found in humans (Makin et al. 2007, Làdavas and Farnè 2004). Functional magnetic resonance imaging (fMRI) studies have found that the premotor cortex and intraparietal cortex respond to both visual and tactile stimuli in respect to certain limbs (Lloyd et al. 2003, Makin et al. 2007). For example, Llyod et al. (2003) showed an increased activation in the ventral premotor cortex and some parts of the intraparietal cortex when subjects' hand was touched, depending on the position of the arm. Similar to this study, another experiment has shown that visual stimuli presented closer to the hand lead to increased activity in the intraparietal cortex, compared to a stimulus presented further away (Makin et al. 2007). The existence of the mechanism for multisensory processing is supported by studies on patients with extinction (Brozzoli et al. 2010). Most studies on sensory extinction have been conducted with patients with right hemisphere damage, thus, neglecting their left side (Driver and Vuilleumier 2001). However, this neurological disorder affects not only the visual modality but also other sensory modalities (Mattingley et al. 1997). In another study, it was shown that patients are able to detect a visual stimulus presented to their right side, but have difficulty in detecting a tactile stimulus applied to their left side (Làdavas et al. 1998, Moro et al. 2004). On the basis of these results, it has been suggested that there is a mechanism for integration of bodily signals in peripersonal space.

In summary, physiological studies conducted with both animals and humans emphasize the importance of integrating information across sensory systems in peripersonal space for sense of bodily self (Makin et al. 2008). Based on this, Ehrsson (2009) defined the sense of bodily self as a layer between the external world and the mind, suggesting the important role in body-part ownership.

Flexibility of body-part representations

Full-body illusions elicited by different sensory and motor inputs have shown that the body perception changes dynamically (Lackner 1998, Ramachandran and Hirstein 1997). One of the first studies using tendon vibration induced proprioceptive motion illusion (Goodwin et al. 1972). This suggests that the tendon vibration produces the impression of a change in size of the body. In another study, if the tendon of bicep muscle was vibrated in blindfolded subjects touching their nose, and they reported an illusory sense of elongation of their arm or their nose (in the literature known as illusion of Pinocchio; Lackner 1998). In this case, interaction of vibrated body part with another body part leads the subjects to feel change in size of stationary body-part. In a similar illusion called the phantom nose, blindfolded participants touch the nose of the person sitting in front of them. As a result of this illusion, participants experienced an illusory change in location or length of their own nose (Ramachandran and Hirstein, 1997). Despite the different methods, these illusions provided evidence that our body perception, which previously seemed to be unchangeable, could in fact easily be manipulated with conflicting information (tactile and proprioceptive) from different senses.

Pathological body-part representations

In addition to the bodily illusions induced in experimental settings, damage to certain parts of the brain and some pathological disorders can also lead to striking changes in the body perception. For example, amputees or individuals born without certain limbs continue to feel the presence of the missing-limbs, and in some cases, can feel real pain, known as phantom limb syndrome (Ramachandran 1993, Ramachandran and Hirstein 1998, Brugger et al. 2000). In the literature, this pathological syndrome, which causes people to experience pain from the missing limb (phantom pain) is cited as the foremost example of the association between sensation and perception. Likewise, patients with damage to basal ganglia, thalamus or frontal areas also experience altered sensations, such as having one or more extra limbs (Kim et al. 2017). It has been argued that the common characteristic of these pathologies is the incompatibility between the inputs from visual and proprioceptive system (Halligan et al. 1993, Ramachandran and Hirstein 1998).

In contrast to the pathological syndrome in which the presence of the missing-limb is felt, it has been observed that physical perception is impaired in the opposite direction in patients with focal brain injury. For example, in a body awareness disorder called somatoparaphrenia, individuals generally reject their own hand and describe it as someone else's (Vallar and Ronchi 2009). This disorder is also defined as a body representation disorder due to abnormalities in sensory-motor feedback, since it occurs simultaneously with neglect syndrome or a limb paralysis after parietal region damage (Daprati et al. 2000).

Rubber hand illusion

The most well-known experiment which allows to study the changes in body representation in a controlled manner is the rubber hand illusion. The rubber hand illusion creates an illusion of ownership over an object that does not belong to the body. In an experiment designed by Botvinick and Cohen (1998), participants' real hand was placed behind a screen out of their view and a rubber hand was placed to appear where the real hand was supposed to be. Then, both the rubber and the real hand were stroked synchronously by paintbrushes. After watching this process for a while, participants reported that they began to feel the strokes they saw on the rubber hand, which they perceived as their own. Additionally, when asked to close their eyes and point out the position of their real hand, the participants mislocalized their real hand closer to the rubber hand (proprioceptive drift). Drift in perceived location of the participants’ hand is considered as an objective assessment of the rubber hand ownership. The stronger sense of ownership over the rubber hand has been found to associated with larger drift in location their hand towards the rubber hand (Botvinick and Cohen 1998). However, when the strokes on the rubber and the real hand are not synchronous (Botvinick and Cohen 1998), or when another object replaces the rubber hand (Tsakiris and Haggard 2005), or when the location of the rubber hand is anatomically incompatible with the position of the person, the illusion either disappears or decreases in strength (Llyod 2007).

Another objective measure used to support the ownership of the rubber hand is the autonomic physiological responses generated against a threatening stimulus approaching the rubber hand. For example, bending a finger on the rubber hand backwards (Armel and Ramachandran 2003) or approaching it with a needle (Ehrsson 2009) has been shown to lead an increase in the skin conductance responses. These results were interpreted in two different ways. First, it has been proposed that the real hand was replaced with the rubber hand, or the rubber hand was included into the boy representation as an additional third hand (Ehrsson 2009). However, the subjective reports from the participants support the view that the rubber hand paradigm is an illusion in which the real hand disappears, and is replaced by the rubber hand. Additionally, in another rubber hand illusion study, a decrease in the temperature of the participants' real hand (Moseley et al. 2008) was accepted as another indicator that the real hand was replaced by the rubber hand.

During a rubber hand illusion, visual stimulus seen on the rubber hand and tactile stimulus felt on the real hand is perceived as a single visuo-tactile stimulus, as long as the rubber hand is in anatomically appropriate location with participants' posture (Makin et al. 2008, Constantini and Haggard 2007). Moreover, visual and proprioceptive information of the hand position plays important role during the rubber hand illusion. For example, the illusion was not observed when the position of the rubber hand was implausible (Llyod 2007). Considering these anatomical constraints, it has been shown that the strength of the illusion is significantly reduced, or not induced at all when the rubber hand is replaced with a wooden hand or non-hand object (Tsakiris and Haggard 2005). Despite these limitations, Armel and Ramachandran (2003) who support the theories of perception based on Bayesian inference, claim that synchronous visuo-tactile stroking is sufficient to create the illusion. In their study, the participants experienced the illusion while a table was stroked synchronously, but their subjective evaluations about the illusion effect and the skin conductance responses were diminished compared to the humanoid-rubber hand condition (Armel and Ramachandran 2003).

Brain imaging studies using functional magnetic resonance imaging (fMRI) and Positron emission tomography (PET) have revealed neural correlates of the rubber hand illusion. Synchronous stroking of the rubber hand and real hand has been shown to be associated with the activity in the insular cortex, cingulate cortex, premotor and occipital cortex (Ehrsson et al. 2004, Limanowski et al. 2014). On the other hand, ownership-related increase in the premotor and occipital cortex activity was observed when participants' real hand and the rubber hand have the same posture. The proprioceptive drift in felt position of the participants' hand was related to activity in the right frontal insula, the right frontal operculum and the left frontal gyrus (Tsakiris et al. 2006). Compatible signals from different sensory systems and changes in activity in different brain regions show how bodily self-consciousness can change with conflicting sensory manipulations and prove sub-dimensions that constitute bodily self-consciousness.

Taken together, the rubber hand illusion revealed that the feeling of ownership can be induced and can be manipulated by integration of multisensory signals. In the following section, studies that used the whole-body illusion are summarized.

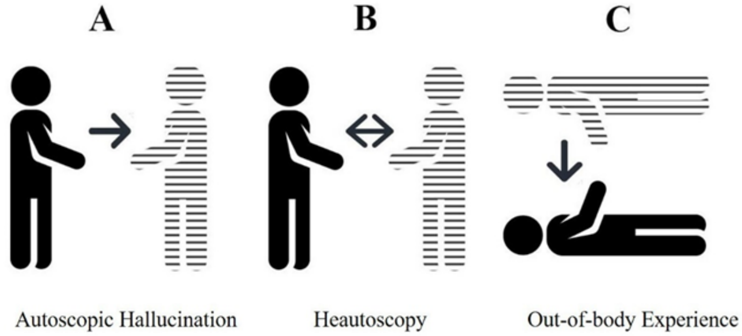

Figure 2. Visual illustration of autoscopic phenomena.
Black line drawings represent the physical body, dashed line drawings represent the illusory body. (A) In autoscopic hallucination, self-location and visuospatial perspective are at the location of the physical body. (B) In heautoscopy, self-location and visuospatial perspective might be in the location of the physical the illusory body or be in the both locations. (C) In out-of-body experiences, both self-location and visual perspective are at the location of the illusory body.

Representation of whole body and full body illusions

In research related to bodily self-consciousness that has been mentioned so far, the focus have only been on cases in which people feel changes in ownership over a body part. However, recent theories in the field of philosophy and neuropsychology put emphasis on three important components of bodily self-consciousness; body-ownership (This is my body), self-location (I am in my body), first-person perspective (I see the world with a given location of my body) (Blanke and Metzinger, 2009, Serino et al. 2013). That is to say, bodily self-consciousness means distinct mental states, such as owning one's own body and experiencing the external world from the point of view which is located in the body owned. In normal circumstances, posture and location of the body, and accordingly the first-person perspective, is determined by continuous multisensory signals such as visual, proprioceptive and vestibular cues. Thus, Metzinger (2003) defined bodily self-consciousness as a representation of multisensory bodily signals. Although the rubber hand illusion is interpreted as an altered sense of body ownership and self-location, people experiencing this maintain a coherent sense of ownership. However, as mentioned in the previous section, researchers are in agreement that people experience their bodies as a single and coherent physical structure, not as a combination of multiple body-parts (Mandrigin and Thompson, 2015). In order to support this claim, new experimental methods have been developed to dissociate sub-components of bodily self-consciousness (Blanke and Metzinger 2009, Blanke 2012).

In this context, recent studies have focused on bodily self-consciousness of the whole body (Blanke and Metzinger, 2009) and have shown that full-body illusions can be induced using multisensory conflicts, as in the case with the rubber hand illusion (Ehrsson 2007, Lenggenhager et al. 2007, Petkova and Ehrsson 2008). In addition, rare neurological disorders characterized by abnormalities in whole body perception were exemplified to support the global aspect of body representation (Blanke and Mohr, 2005). The following section describes pathological conditions and full-body illusions that affect whole-body representations.

Pathological body representations

Previous research has shown that there are disruptions in body ownership, self-location, and first-person perspective in the case of a subjective awareness disorder so-called autoscopic phenomena (Blanke et al. 2004). In general, this phenomenon is defined as people seeing their imaginary second body outside of their own body, and is described in three distinct forms: autoscopic hallucination, heautoscopy and out-of-body experience (Brugger et al. 1997) (see Figure 2). In autoscopic hallucinations, one sees an imaginary copy of one's own body from a normal point of view (first-person perspective). In this case, there is no disruption in the sub-components constituting bodily self-consciousness since the perception of ownership, first-person's perspective and self-location overlaps with one's physical body (Blanke et al. 2004). In heautoscopy, people's first-person perspective and self-location are experienced at the position of physical or reduplicated. Therefore, the insight of the person into their body is disrupted and often causes person to feel as being divided into two (Blanke et al. 2004). Finally, in out-of-body experiences, people experience themselves as being outside of their body for a period of time, and see the world and their physical body from a location in space outside of their actual body. Out-of-body experiences generally occur when people are lying down or about to fall asleep although the experiences can occur after an accident or during a surgical operation (Blanke et al. 2004). Out-of-body experience challenges the perception of the body and the self, which are always integrated and inseparable during daily life (Blanke and Arzy 2005). These findings suggest that, contrary to autoscopic hallucinations, during out-of-body and heautoscopic experiences, the sense of bodily ownership changes and this change depends on the dissociations between the sub-components of bodily self-consciousness. This suggest that out-of-body experiences are suitable for examining bodily self-consciousness since all the main components of bodily self-consciousness break down in these experiences.

Neurological basis of out-of-body experiences

It has been proposed that autoscopic experiences are related with the multisensory mechanisms including visual, proprioceptive and vestibular signals (Anzellotti et al. 2011). It has been found that each of the autoscopic phenomena results from breakdown of different multisensory mechanisms (Blanke et al. 2004). It has been claimed that all three forms of autoscopic phenomena are primarily caused by disintegration of multisensory information between peri-personal and extra-personal space, whereas variations in forms of the phenomena are due to vestibular disturbances.

Findings from brain imaging studies have demonstrated the critical role of the region between the temporal and parietal lobes, known as the temporoparietal junction, in out-of-body experiences (Blanke et al. 2004) (see Figure 3). For example, in the evaluation of an epileptic patient, electrical stimulation of the right temporoparietal junction caused an out-of-body experience (Blanke et al. 2002). The patient felt as if he was falling from the height after the first electrical stimulation, then reported the feeling being outside the body as the degree of electrical stimulation increased. Other studies, in which participants were asked to imagine themselves at different location or looking at an object outside of their body, revealed an increased activity in this brain region (Arzy et al. 2006, Blanke and Arz, 2005). Studies with patients suggest an association between the out-of-body experiences and damage to the temporoparietal junction (Blanke et al. 2004). These findings supported the critical role of the right temporoparietal junction, which is known to play an important role in combining information from different senses, and especially, processing vestibular signals (Blanke and Arzy 2005). In addition, people report the feeling of elevation and floating, suggesting that the out-of-body experiences are associated with the disruption in the vestibular system (Blanke et al. 2004).

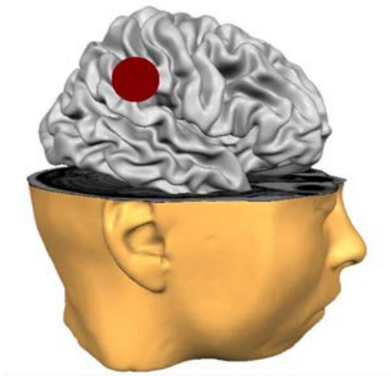

Figure 3. Temporoparietal junction related to out-of-body experiences (red dotted circle).

Full-body illusions

New experimental paradigms inspired by the autoscopic experiences mentioned above have been developed to investigate unitary aspect of bodily self-consciousness (Ehrsson 2007, Lenggenhager et al. 2007). The protocol for full-body illusions is very similar to that used in rubber hand illusion, with small differences. In the setup of the pioneering full-body illusions, a tactile stimulus was applied to the participants' physical body while they were watching a visual stimulus on their virtual body or video image of their body through a head-mounted display. The visual stimulus was presented either synchronous or asynchronous with the tactile stimulus. The general idea of these studies is to dissociate components of bodily self-consciousness, namely the self-location, self-identification and first-person perspective, by using multisensory conflicts (Ehrsson 2007, Lenggenhager et al. 2009, Petkova and Ehrsson 2009).

In the first study on bodily self-consciousness, Lenggenhager and colleagues (2007) developed a systematic paradigm to induce repeatable out-of-body experiences in an experimental environment with healthy individuals. First, participants were presented with the video image of their back, mannequin back or a rectangular object through head-mounted display connected to camera placed behind them (see Figure 4). A tactile stroking was applied on the participants' back while they viewed a visual stroking on the body presented. The visuo-tactile stimuli were applied to participants' own body, and the virtually seen body/object each condition which is synchronous or asynchronous. At the end of the experiment, participants completed a questionnaire about their experiences in the virtual environment and their self-identification with the body/object they saw. In addition, similar to the proprioceptive drift method used in rubber hand illusion, the participants were asked to return to their initial position after displacing them with eyes closed, as an objective measure of their awareness of body position. The results shown that the participants self-identify with the virtual or mannequin body, and felt the touch that they saw only following synchronous condition. However, the participants did not self-identify themselves with the rectangular object, regardless of whether visuo-tactile stimulus was synchronous or not. In addition, participants located themselves towards the virtual or mannequin body only in the synchronous condition, but did not locate themselves towards to the rectangular object in either condition. These results revealed that conflicting visual and tactile stimuli manipulate both bodily self-consciousness and the association between the sense of self and the place where the visual representation of their body-location.

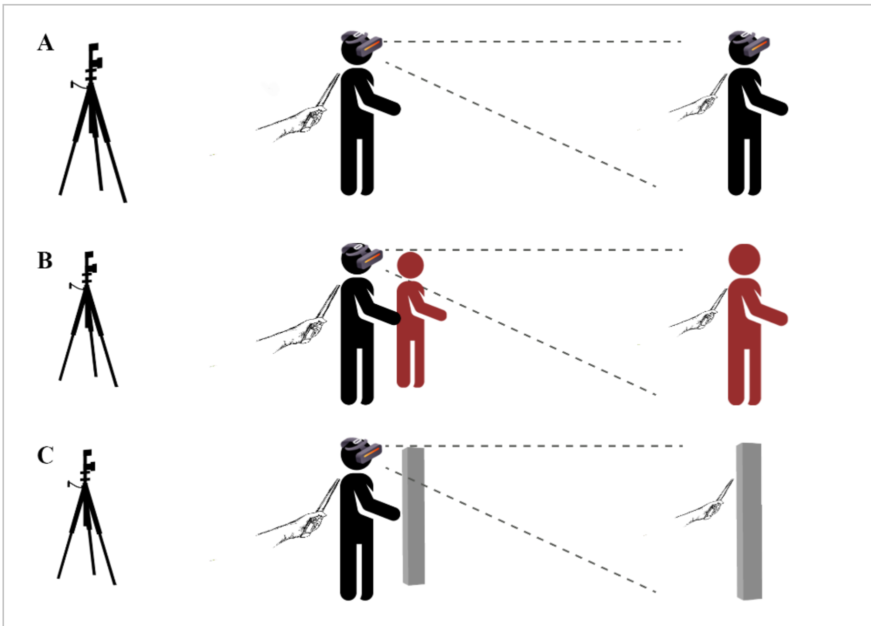

Figure 4. Illustration of the experimental design by Lenggenhager et al. (2007).
In experimental setup, visual stimulus presented to the participants via head-mounted display connected to camera behind. (A) Subjects watched the video image of their own body (black) (B) Subjects were presented with a mannequin body (red) located at their right side. (C) Participants were presented with an image of rectangular object located at their right side

Ehrsson et al. (2007) used a similar experimental procedure that dissociates the unity between the body and the self in healthy individuals by out-of-body illusion. Participants sitting in the chair were shown their own backs via head-mounted display connected to the video camera placed behind them. Tactile stimulation (touch) was applied to the participants' chest which was out of view, while a rod approached the location just below the camera (see Figure 5). It was found that participants felt the touch of the approaching rod on their chest, and mislocalized themselves to the location of the camera after synchronous condition. It is worth noting, however, that they reported feeling as if looking at someone else's body while watching the video of their own body.

These full-body illusions showed that individuals experience illusory self-location towards the seen body location and illusory self-identification with that body after synchronous visuo-tactile stimuli (Blanke and Metzinger 2009). In the below section, the interactions between the full-body illusions and sub-components of bodily self-consciousness are discussed.

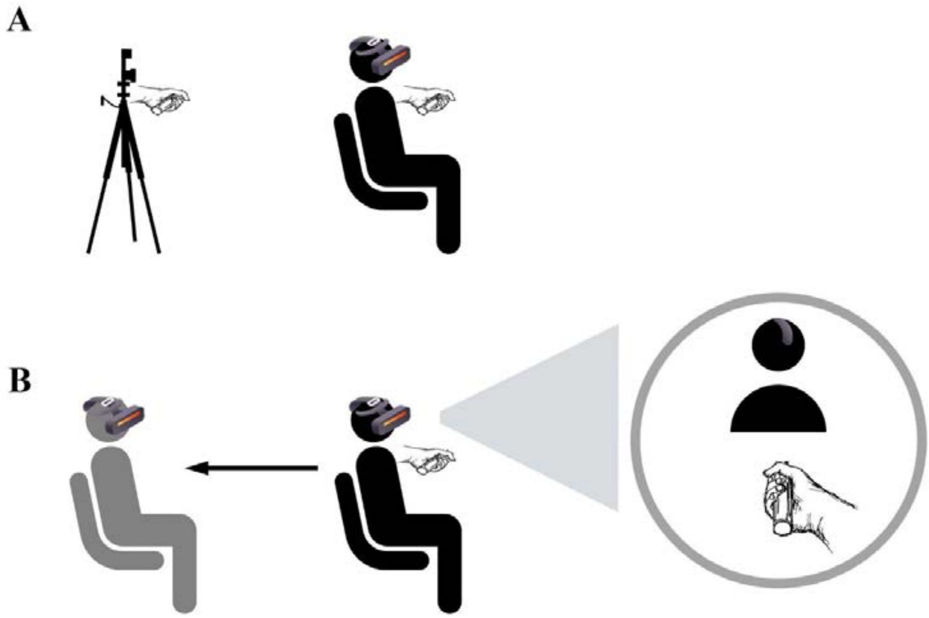

Figure 5. Illustration the experiment by Ehrsson (2007).
(A) Experimental setup. (B) Subjects locate themselves behind their own body (black) corresponding to the location of the camera (grey) and look at back of the physical body after synchronous stroking condition.

Self-identification

Self-identification can be considered as a conscious mental state of one’s feeling of ownership over own body. As shown by previous studies, this sub-component of bodily self-consciousness can be disrupted in various ways by different experimental setups. In the study by Lenggenhager et al. (2007), subjects experienced illusory self-identification with the seen body, whereas subjects reported a sensation of looking at someone else rather than identification with the seen body in the study by Ehrsson (2007). Differences between the two studies in body position, questionnaires and behavioural measures, however, prevent to direct comparison. Considering these limitations and the fact that out-of-body experiences occur frequently in a prone position, a comparative study was carried out with the participants lying on their back by Lenggenhager et al. (2009). The participants received a tactile stimulation to their back and chest either synchronously or asynchronously, while watching the virtual image of their bodies through a head-mounted display linked to the camera placed behind them. When the participants received synchronous back stroking, they experienced the virtual body as if it were their own, unlike with synchronous chest stroking. The illusion of self-identification was ascribed to spatial coincidence of the visual stroking with the tactile stroking. In the synchronous chest stroking condition, the participants experienced sensation of being at the location of their first-person perspective, resulting in decreased self-identification with the seen body (Lenggenhager et al. 2009).

Self-identification and perspective

In a daily life, we see the body, which we define as our own body, from the first-person perspective, and see other people and objects from a third-person perspective. As seen from the above example, visual perspective of individuals as well as visuo-tactile stimulation, plays a crucial role for the body ownership. The out-of-body illusions showed that change in the origin of the visual perspective resulted in different bodily experiences (Lenggenhager et al. 2007, Ehrsson 2007). Subjects self-identified themselves with a virtual body when the origin of their first-person perspective and physical body correspond (Lenggenhager et al. 2007). It has been argued that this is because the subjects perceive the touch as originating from the virtual body after synchronous visuo-tactile stimulation. In contrast, another study found decreased self-identification over a virtual body seen from a third-person perspective (Ehrsson 2007). Dislocation the visual perspective from the location of physical body did not affect perception of the touch on the virtual body but resulted in a sense of seeing someone else's body. These studies have shown that origin of visual perspective is responsible for change in self-location, accompanied by change in self-identification. It has therefore been argued that these two subcomponents (self-location and first-person perspective), which constitute bodily self-consciousness are interrelated (Lenggenhager et al. 2009, Ionta et al. 2011, Pffeir et al. 2013).

In addition to these, objective methods were used to measure physiological changes associated with self-identification with another body. For example, participants showed an increase in their skin conductance response when a hammer, as a threatening stimulus, was directed to below the camera, corresponding to illusory body after synchronous visuo-tactile stroking (Ehrsson 2007). These findings provided evidence that individuals self-identify with the illusory body from the location of their visual perspective. In another study by Petkova et al. (2008), participants saw a mannequin body instead of their own body through a head-mounted display. After synchronous visuo-tactile stroking to subjects' physical body and mannequin body, an increase in skin conductance responses was found when a knife, as threatening stimulus, approached the mannequin body. All these results showed the importance of the multisensory signals (visual and tactile) for the own body perception and it has been concluded that the multisensory integration leads to alterations in the way people process stimuli from their bodies (Blanke 2012).

Self-location and perspective

The full-body illusions in which the sense of subjects' self-location does not always coincide with their first-person perspective have shown that these two sub-components of bodily self-consciousness can be dissociated (Lenggenhager et al. 2009). Despite the self-identification, it has been proposed that the most important factor for perceived self-location is where the visual stimulus is seen. (Aspell et al. 2009). Drift in subjects' self-location towards a virtual body (Lenggenhager et al. 2007) and subjective reports of experienced self-location (Ehrsson 2007) underlie the approach emphasizing the importance of location of tactile stimulus.

It has been further suggested that self-location and first-person perspective are not only determined by processing of visuo-tactile integration, but also influenced by their integration with vestibular signals (Lenggenhager et al. 2009). In an fMRI study by Ionta et al. (2011), participants were placed in a supine position while viewing an image of virtual body in prone posture via head-mounted display. The participants received a tactile stroking on their back, and saw a visual stroking on the back of the virtual body, generating either synchronous or asynchronous visuo-tactile stimulation. Also, the participants' perceived self-location was assessed by "mental ball dropping" task. In the task, participants were asked to press and hold the button depressed to indicate the time an imaginary ball they were holding look to reach the floor from its release. It has been assumed that the duration of the button press will be longer depending on participants' self-location above the floor. Participants' self-identification with the virtual body was also measured by the questionnaire. Different from other studies, the direction of participants' first-person perspective was investigated. Thus, the participants were asked about their experienced direction of first-person perspective (up/down). Interestingly, although all participants received the same visuo-tactile stimulation, half stated that they looked upwards to the virtual body, whereas the other half looked downwards. More importantly, the study revealed that the participants' direction of the first-person perspective and self-location are interrelated (Ionta et al. 2011). For instance, participants indicating looking upwards at the virtual body located themselves towards the virtual body they saw above in the synchronous condition, whereas participants looking downwards at the virtual body located themselves toward the virtual body they saw below. According to these results, self-location is modulated by both visuo-tactile stimuli and the direction of first-person perspective (Ionta et al. 2011). However, it is shown that self-identification depends on only visuo-tactile stimuli, the direction of first-person perspective does not have an effect on self-identification. The findings from the fMRG analysis showed that the self-identification with the virtual body is associated with the activity in the right middle-inferior temporal cortex activity, while the self-location and first-person perspective is associated with the activity in the temporoparietal junction (Ionta et al. 2011). Based on these findings, it has been suggested that the subcomponents of bodily self-consciousness, such as self-identification and self-location, are modulated by different neural mechanisms (Ionta et al. 2011). Despite identical visuo-tactile stimulation, there are differences in the visual perspective and the participants looking at the virtual body from above variously reported that they were floating, flying or localized outside their body. These variations are considered as a result of individual differences in processing visual and vestibular signals (Ionta et al. 2011). The differences in the direction of the first-person perspective is ascribed to the relative weighting of visual or vestibular information.

The first study investigating the effects of visual-tactile and visual-vestibular signals on bodily self-consciousness by Pfeiffer and colleagues (2013), participants were presented with conflicting visuo-vestibular stimuli in which the direction of gravity was manipulated. The impression of the virtual body is in prone posture or standing was created by manipulating the direction of gravity on clothes and hair. The participants viewed the back of virtual body being stroked synchronously or asynchronously with respect to the tactile stroking on their physical back. As in the study by Ionta et al. (2011), participants were asked whether they were looking downward or upward to the virtual body and they were divided into two groups based on the experienced direction of their first-person perspective. The differences in the direction of first-person perspective were measured by questionnaires, and the self-location was measured by the mental ball dropping task. It is revealed that the self-identification depends on the degree of visuo-vestibular conflict. Independent of the direction of first-person perspective, the participants identify themselves with the image of standing virtual body when they received synchronous visuo-tactile stimulus with their physical body. It was revealed that the participants looking upwards at the virtual body gave longer response times for the ball falling to the floor when considered the self-localization. Longer response times in synchronous condition is considered as an indicator of self-location towards the virtual body seen above. However, no effect of visuo-vestibular conflict was found for self-location or the direction of first-person perspective. These findings supported the previous conclusions that tactile stimulus and direction of first-person perspective played an important role in determining self-location.

In the second experiment of the same study by Pfeiffer et al. (2013), the strategies used to solve visuo-vestibular conflicts were tested. It was suggested that there are individual differences for solving conflicting visuo-vestibular signals, and these differences were tested with the rod and frame test, which requires visual verticality judgements. In the rod and frame test, people are asked to orient a rod embedded in a tilted frame into the vertical position (Witkin and Asch 1948). Participants were classified into two groups as visual field dependent and visual field independent, based on the deviations in performance from the rod and frame task. These results suggest that the direction of the viewpoint for the visual field dependent participants changed according to the position of the virtual body and these participants reported that looking downward at the virtual body. In contrast, visual field independent participants reported looking upward at the virtual body, and taking into consideration the location of their physical body. To put it another way, the study showed a direct relationship between the direction of the first-person perspective and visual field dependency/independency. These findings point out the importance of visual perception style for bodily self-consciousness.

Individual differences in body illusions

In the literature, there is a limited amount of research regarding how individual differences and personality predispositions affect bodily self-consciousness. Since then most of the data in the literature comes from the measurements of the intensity of the rubber hand illusion (Haans et al. 2012, Kállai et al. 2015, Walsh et al. 2015). As an example, it has been found that dopamine transmission is associated with increased ownership over the rubber hand (Albrecht et al. 2011), and it was suggested that the people with novelty seeking personality a basic temperament factor, is closely associated with their dopamine levels and acceptance of the rubber hand (Cloninger et al. 1993). Related to those studies, previous findings showed that, participants in the synchronous visual-tactile stimulation condition experience greater proprioceptive drift, and found that their acceptance during the illusion predicts higher scores for novelty-seekers, whereas lower scores predicts higher harm avoidance (Kállai et al. 2015). Additionally, Kállai et al. (2015) found that during synchronous visual-tactile condition, elevated scores in paranoid ideation is associated with psychoticism scales. These findings can be interpreted as indicating people who experience the rubber hand illusion more easily accept inaccurate information, and thus change their body schema more readily. In this context, it is thought that some are more sensitive to rubber hand illusion because they give more weight to visual information (rubber hand) than their body's internal information (real hand). Supportive studies show that those interested in yoga and meditation can change their sensory systems at will, and thus experience different physical experiences (Kerr et al. 2011). It was observed that yoga practitioners were more successful in evaluations the verticality of visually presented stimuli because they rely more on bodily signals (eg vestibular, proprioceptive) rather than visual signals (Fiori et al. 2014). In another study by Xu and colleagues (2018), the rubber hand illusion was induced to mindfulness meditation practitioners and non-practitioners, and individual differences were investigated. In another study conducted by Xu et al. (2018), rubber hand illusion was applied to individuals who did and did not perform mindfulness meditation, and differences between individuals were examined. The results of this study showed that mindfulness meditation was associated with decreased ownership for the rubber hand. However, there was no difference in proprioceptive drift between meditating and non-meditating individuals. These findings are interpreted as showing that individuals who perform different bodily practices are able to change the weight of these signals, and might experience different self-consciousness experiences (Xu et al. 2018).

Psychiatric disorders and bodily illusions

The fact that individuals perceive their body as an integrity and distinguish them from the surrounding objects is the main criteria for distinguishing psychopathological syndromes. (Sass ve Parnas 2003). Considering that the body boundaries are manipulated by the rubber hand illusion, it helps to determine pathologies or some pathological predispositions. Studies show that the degree of rubber possession is indicative of a person's potential psychopathological features. A significant relationship was found between the intensity of rubber hand illusion, and healthy and sick people with delusional experiences, especially sensitive to psychopathological disorders, such as schizophrenia. (Peled et al. 2000, Germine et al. 2013). For example, healthy participants with high scores on interpersonal reactivity scales, such as positive schizotypes and in particular empathy, were found to have a stronger illusion of their real hands' position and ownership. (Asai et al. 2011). Another research has shown that, compared to healthy participants, patients with schizophrenia experience a stronger and more rapid illusion than healthy controls (Peled et al. 2000, 2003). Studies conducted with groups with eating disorders revealed a relationship between the intensity of the experiences of rubber hand illusion and the behaviours of bingeing and vomiting (purging) (Mussap and Salton 2006). Furthermore, stronger feelings of ownership and higher proprioceptive drift scores were observed in individuals with high scores on body dissatisfaction and emotional dysregulation scales (Eshkevari et al. 2011). This condition has been suggested to be due to the patient's ever-changing body image, and is explained by the variability in the plasticity of the brain's somatosensory system (Mussap and Salton 2006; Eshkevari et al. 2011).

Application of bodily illusions in rehabilitation

Both the rubber hand and full body illusions are novel tools for rehabilitation and therapeutic interventions (Christ and Reiner, 2014, Bolognini, Russo and Vallar 2015). More recently, both types of illusions have started being used in neuro-rehabilitation of various clinical populations including patients with acquired focal brain lesions (da Silva et al. 2013) and amputees with phantom limb pain (Alphonso et al. 2012).

The first clinical rehabilitation application using body illusions without virtual reality technology is called mirror box therapy. Mirror box therapy for the treatment of Phantom Limb Pain (PLP) was first conducted by Ramachandran and his colleagues (1995) for people with upper limp amputations. In this framework, it was showed that increasing the visual input for the missing limb causes relief from PLP by reducing the incongruence between motor output (intention) and sensory (proprioceptive) feedback (Ehrsson et al. 2008, Schmalzl et al. 2011). As a consequence of these procedures, missing sensory motor map is re-activated (Ramachandran and Altschuler 2009, Moseley and Flor 2012). Similar to the mirror box therapy, self-observation in a video replay also increases motor awareness in patients with anosognosia and hastens recovery (Fotopoulou et al. 2009). A recent functional magnetic resonance imaging study showed that synchronous visuotactile stimulation in people with an artificial hand (upper limb amputees) demonstrates increase multi-sensory integration in the brain regions (Bolognini, Russo and Vallar 2015). More recently, the mirror box therapy was also used for patients with somatoparaphrenia (a somatic delusion usually following right-hemisphere lesions) (Fotopoulou et al. 2011, Jenkinson et al. 2013, Schmalzl et al. 2013). In addition to visual feedback, cutaneous feedback was also showed to increase the integration of this process into the body schema (Marasco et al. 2011). Finally, for patients who use prosthesis, it takes a minimum of 14 days to adapt the artificial limb to body schema (Mayer et al. 2008) and it was showed that synchronous visual tactile stimulation enhances this adaption process (Wojtusch et al. 2012, Beckerle et al. 2013).

Virtual reality and bodily self-consciousness

The research dicussed above shows that perception of body ownership can change by applying synchronous multisensory stimulus. Virtual reality studies based on the bodily illusions have shown that body illusions can be generated by using virtual bodies, and these perceptual illusions are called as "body ownership illusion" (Petkova and Ehrsson 2008, Slater et al. 2009, Maselli and Slater 2013). Previous research show that people exposed to synchronous visuo-tactile stimulus identify themselves with the virtual body, and they see and feel less ownership over their own physical bodies (Lenggenhager et al. 2007, Petkova and Ehrsson 2008, Slater et al. 2008, Slater et al. 2009). The initial experiments showed that the rubber hand illusion could be reproduced in virtual reality by synchronous multisensory signals (Slater et al. 2008). Slater and colleagues (2010), showed that people can own an entirely virtual body by using an experimental setup separating their perspective from visuo-tactile stimulations. In the study, heart rate deceleration was detected in response to the virtual body being slapped as a threatening stimulus, in both participants seeing the slap from first-person and third person perspective. Even though subjective and physiological findings from the previous studies show the importance of first-person perspective for body ownership, individuals can still self-identify with the virtual body from third-person perspective. However, in another study, Petkova and colleagues (2011) revealed no feelings of ownership over the mannequin body seen from a third person perspective even in the synchronous visuo-tactile conditions. Different findings in these two studies can be explained by differences in experimental designs or involvement of different illusory perceptions (Maselli and Slater 2013). In summary, body ownership illusions from the first-person perspective is defined as transition of perceptual senses or centre of awareness into the virtual body which is owned by the real body (Petkova and Ehrsson 2008, Slater et al. 2010). The out-of-body or full-body illusions focus on where the participants locate themselves and from which body tactile stimulations originates (Ehrsson 2007, Lenggenhager et al. 2007, 2009, Ionta et al. 2011). There are also important differences between the illusion of body-ownership and the rubber hand illusion in which limb ownership is investigated. For example, Tsakiris and Haggard (2005) have shown that the physical properties of the artificial hand, and the similarity of the real hand are insignificant in the virtual reality environment, even when the wooden hand / object is used instead or the rubber hand is anatomically incompatible. Similarly, experiments with virtual reality and video display have been revealed that resemblance of the virtual body or mannequin body with the real body is not crucial (Petkova and Ehrsson 2008). In fact, a virtual body with a different gender or race does not prevent illusory ownership over the virtual body (Slater et al. 2010).

Conclusion

Bodily self-consciousness has attracted the attention of fields such as philosophy, psychology and neurology, since it is seen as the key element of the self. Experimental designs inspired by out-of-body experiences allow the differentiation of three main components of bodily self-consciousness, which are self-identification, self-location and first-person perspective. In this review, effects of the components on bodily self-consciousness and supporting evidence of subjective and physiological findings were summarized. Considering the studies mentioned in the current article, self-identification with a body is especially related with visual and tactile stimulations, whereas perspective and self-location are associated with integrated processing of the visuo-tactile stimulations that also includes vestibular system. Integrated processes of multisensory signals provide a fundamental explanation regarding bodily self-consciousness without the need for higher level of cognitive functions. However, there is still limited amount of research on bodily self-consciousness. Moreover, subjective nature of the consciousness often leads to very variable responses among the participants. Therefore, it is very important to develop innovative and efficient methods, meticulous approaches, and objective measurements in future studies.

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