

## THE ASSEMBLY OF THE SELF FROM SENSORY AND MOTOR FOUNDATIONS

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The problem of the self has captivated philosophers and psychologists for centuries. While the self is clearly a central facet of the human psyche, to date we have a limited understanding of the cognitive and neural mechanisms underlying this construct. The fundamental, pre-reflexive level of self-representation, often termed the minimal self has been the focus of recent work in psychology and neuroscience. This article will review recent advances in the study of the minimal self and its grounding in sensory and motor processing. I will suggest that the minimal self arises from unconscious integration of sensorimotor signals in specific brain systems, and that these same mechanisms may be of relevance to understanding disorders of the self such as schizophrenia. Finally, some influences of the minimal self on social cognition and future challenges will be discussed.

### THE SELF AND THE BODY

“Everywhere in the world, self starts with body.”

—Baumeister (1999, p. 2)

The self is a central and fundamental psychological construct underlying our ability to act as a coherent agent in the world. While the concept of the self is intuitively evident, its multidimensional character has given rise to numerous definitions and models. Philosophical and psychological models of the self have proposed that this concept includes several different levels of self-representation (Damasio, 2000; James, 1950; Neisser, 1993; Strawson, 1999; Zahavi, 2003), clearly evident in the developmental trajectory of the self (Amsterdam, 1972; Anderson, 1984; Ber-

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tenthal & Fischer, 1978; Butterworth, 1995; Gallagher & Meltzoff, 1996; Gallup, 1982; Rochat & Hespos, 1997) and its neural basis (Damasio et al., 2000; Gusnard, Akbudak, Shulman, & Raichle, 2001; Ionta, Martuzzi, Salomon, & Blanke, 2014; Kircher et al., 2000; Northoff et al., 2006; Peer, Salomon, Goldberg, Blanke, & Arzy, 2015; Salomon, Levy, & Malach, 2013). Recently, there has been a surge of interest in a fundamental level of the self-concept relating to the pre-reflective bodily foundations of selfhood. This level of self-representation often termed the minimal *self* relates to the “consciousness of oneself as an immediate subject of experience, unextended in time” (Gallagher, 2000, p. 15) and is grounded in our embodied experience of being a self in a body (Blanke & Metzinger, 2009; Damasio, 2000; for similar conceptualizations see Neisser, 1988, 1993). Thus the minimal self relates to the pre-reflexive and embodied sensation of being an “I” who is the subject of experience, which is independent of higher or second order semantic and cognitive self-representation (Blanke & Metzinger, 2009; Gallagher & Meltzoff, 1996; Legrand, 2006; Metzinger, 2004).

It has been argued that this fundamental level of self-representation, often termed bodily self-consciousness (BSC), is required for higher and more elaborate models of self, such as the narrative self and social self (Arzy, Molnar-Szakacs, & Blanke, 2008; Bermúdez, Marcel, & Eilan, 1998; Blanke & Metzinger, 2009; Csordas, 1994; Gallagher & Meltzoff, 1996; Metzinger, 2004). Three central features of the minimal self have been previously suggested: (1) self-identification with the body (also termed body ownership); (2) self-location (i.e., the experience of where I am in space), and (3) the first person perspective (“1PP”—the experience from where I perceive the world; Blanke, 2012; Blanke & Metzinger, 2009). Indeed, these aspects of our BSC are so strongly embedded in our experience that they are often taken for granted. However, several neurological and psychiatric conditions as well as experimental manipulations in healthy populations show perturbations of these features, allowing elucidation of some of the neural and cognitive underpinnings of the minimal self. Here I will review recent findings relating to the cognitive and neural mechanisms underlying the minimal self. First, I will discuss the role of the integration of sensory signals, from both exteroceptive and interoceptive modalities in establishing the sense of self. Second, I will relate the contributions of self-generated motor signals which provide important indications for the segregation of the self from others and when impaired may cause disturbances of the self such as those found in schizophrenia. Finally, links between the sensorimotor mechanisms of the minimal self and social cognition will be discussed, showing future directions of exploration.

## THE ROLE OF BODILY SENSORY SIGNALS IN SHAPING THE SELF

Current work on the minimal self has been guided by findings from neurological patients in whom brain damage has produced alterations of body ownership and BSC (e.g., Arzy, Overney, Landis, & Blanke, 2006; Berlucchi & Aglioti, 1997, 2010; Blanke, 2012; Heydrich & Blanke, 2013; Spinazzola, Pia, Folegatti, Marchetti, &

Berti, 2008; Vallar & Ronchi, 2009). For example, in somatoparaphrenia, typically following damage to the right brain hemisphere, patients misattribute their hand to another person (Feinberg, Venneri, Simone, Fan, & Northoff, 2010; Vallar & Ronchi, 2009). Interestingly, experimental work in healthy participants has shown that changes in body ownership can also be induced through multisensory conflicts. In the Rubber Hand Illusion (RHI) a visuo-tactile conflict is induced by stroking a seen rubber hand and the participant's real hand which is hidden from view. When the stroking of the viewed rubber hand and the real hand are spatially and temporally synchronous a multisensory conflict arises as the visual and tactile signals correspond, but not at the right location. This discrepancy between multisensory signals causes a bodily illusion which leads to subjective illusory ownership over the rubber hand as well as proprioceptive shift in which the real hand is felt to be closer to the rubber hand (Aimola Davies, White, & Davies, 2013; Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Hara et al., 2015; Tsakiris & Haggard, 2005). The RHI, and its many variants (Armel & Ramachandran, 2003; Costantini & Haggard, 2007; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Pavani, Spence, & Driver, 2000; Rohde, Di Luca, & Ernst, 2011; Tsakiris & Haggard, 2005), have allowed important insight into the mechanisms by which body ownership is achieved. Two fundamental, and somewhat non-intuitive, understandings have arisen from this line of work: First, our sense of ownership over our body is a dynamic process based on multisensory correspondences in which correlated signals from different sensory modalities are fused together to form a sense of being an embodied agent (Blanke, 2012; Ehrsson, 2012; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Second, these experiments indicated that body ownership is malleable and can be modified by multisensory conflicts (Blanke, Slater, & Serino, 2015; Tsakiris & Haggard, 2005). Thus, the minimal, bodily representation of the self is continuously assembled from correlated multisensory inputs.

At the neural level, brain imaging of the RHI has shown that frontal and parietal regions such as the intraparietal sulcus (IPS) premotor cortex (PMC), sensorimotor cortex and insula are involved in the illusory ownership of the hand (reviewed in Blanke, 2012; for experimental evidence see Ehrsson, Spence, & Passingham, 2004; Makin, Holmes, & Ehrsson, 2008; Makin, Holmes, & Zohary, 2007; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007). It has been suggested that such illusion arise from an enlargement of the visual receptive fields of bimodal or trimodal neurons, demonstrated in homologous regions in nonhuman primates, which respond to visual, tactile, and proprioceptive signals (Bremmer et al., 2001; Graziano, Yap, & Gross, 1994; Graziano, Hu, & Gross, 1997; Graziano, 1999). Such neurons may form the basis of multisensory representations of the bodily self (Blanke et al., 2015).

Yet, while such alterations of ownership for limbs provide important evidence of the role of multisensory integration and polymodal brain mechanisms in limb ownership they do not represent global changes of BSC associated with changes in the minimal self (i.e., changes to the full body representation rather than a limb; Blanke, 2012; Blanke & Metzinger, 2009). Indeed, our limbs represent dynamic and peripheral aspects of our body, while the trunk and head are more closely associated with the self (Alsmith & Longo, 2014; Bertossa, Besa, Ferrari, & Ferri, 2008).

Several striking neurological disturbances termed autoscopic phenomena produce such global changes in self-representation accompanied by strong sensations of dissociation with the real body (Blanke & Metzinger, 2009; Blanke & Mohr, 2005; Blanke, Ortigue, Landis, & Seeck, 2002a; Devinsky, Feldmann, Burrowes, & Bromfield, 1989; Heydrich & Blanke, 2013; Heydrich, Dieguez, Grunwald, Seeck, & Blanke, 2010; Lukianowicz, 1958). For example, in Out of Body Experiences (OBE) patients experience a change in self-location and the first person perspective in which they feel that they are outside their body and typically perceive their own body as viewed from an elevated position looking down (Blanke, Landis, Spinelli, & Seeck, 2004; Blanke & Mohr, 2005; De Ridder, Van Laere, Dupont, Menovsky, & Van de Heyning, 2007). These findings have led to interesting experimental work employing novel robotic and virtual reality paradigms to induce such phenomena in healthy individuals. Following previous findings from the RHI paradigm, these paradigms induce Full Body Illusions (FBI), by applying temporally synchronous visuo-tactile stimulation on the back of the participants while they see the touch on the body of an avatar or mannequin from a first or third person point of view. During synchronous, but not asynchronous, visuo-tactile stimulation changes in full body ownership (participants report the seen body to be felt as their own) as well as self-location (participants judge themselves to be closer to the seen body) occur (Ehrsson, 2007; Ionta et al., 2011; Lenggenhager et al., 2007; Petkova, Björnsdotter, et al., 2011; Petkova & Ehrsson, 2008; Petkova, Khoshnevis, & Ehrsson, 2011; Salomon, Lim, Pfeiffer, Gassert, & Blanke 2013). Experimental paradigms of FBI have also uncovered physiological changes during the illusion such as global body temperature changes (Salomon, Lim, Pfeiffer, et al., 2013) and skin conductance changes to threat (Ehrsson, 2007; Petkova & Ehrsson, 2008) showing objective changes in bodily processing during the illusion.

Brain imaging, stimulation, and neuropsychological investigations of these full body illusions have implicated the premotor cortex (PMC), and the extrastriate body area (EBA) in changes of body ownership (Arzy, Thut, Mohr, Michel, & Blanke, 2006; for detailed review see Blanke, 2012; Blanke et al., 2005; Blanke, Ortigue, Landis, & Seeck, 2002b; Heydrich & Blanke, 2013; Ionta et al., 2011; Ionta, Martuzzi, Salomon, & Blanke, 2014; Petkova, Björnsdotter et al., 2011). For example, using fMRI compatible robotic devices to stroke participants' backs along with virtual reality have allowed replication of the FBI within the fMRI scanner. This experiment found that changes in the first person perspective and self-location are linked to activity in the temporo-parietal junction (TPJ) which was modulated by the subjective perspective of the participants and with higher blood-oxygen-level dependent (BOLD) activations during the synchronous stroking for those who felt themselves to be looking down at the body (Ionta et al., 2011). Functional connectivity analysis revealed a cortical network including the TPJ, insular cortex, and SMA related to the experience of 1PP and self-location, which also showed a right hemisphere bias mirroring evidence from neurological cases of body ownership disorders (Heydrich et al., 2010; Ionta, Martuzzi, Salomon, & Blanke, 2014). Thus, changes in the minimal self can be experimentally induced by multisensory

conflicts and are related to processing in multisensory integration systems in the brain.

## INTEROCEPTIVE SIGNALS IN THE MINIMAL SELF

Based on theoretical accounts emphasizing a central role for interoceptive information in self-consciousness (Craig, 2003; Craig, 2002; Damasio, 2000; Seth, 2013; Seth, Suzuki, & Critchley, 2011), recent studies have highlighted contributions of interoceptive signals such as cardiac, breathing, and visceral inputs to the minimal self (Adler, Herbelin, Similowski, & Blanke, 2014; Ainley, Tajadura Jiménez, Fotopoulou, & Tsakiris, 2012; Aspell et al., 2013; Ronchi et al., 2015; Suzuki, Garfinkel, Critchley, & Seth, 2013; Tsakiris, Tajadura-Jiménez, & Costantini, 2011). For example, variants of the RHI and FBI using visuo-cardiac stimulations (in which cardiac signals are presented visually) have produced changes in subjective feelings of embodiment. In these studies, a virtual hand/body were presented and cardiac signals in the form of color or contrast changes, which were linked either to one's current heartbeat or an asynchronous heartbeat were presented on or near the body/hand. When the viewed visualization of the cardiac activity was synchronous to the participants' heartbeat, a modulation of self-location and body/limb ownership was induced (Aspell et al., 2013; Suzuki et al., 2013), thus providing evidence for an integration of intero- and exteroceptive signals for body ownership. Other studies have linked the ability to monitor interoceptive states with changes in body ownership (Ainley, Brass, & Tsakiris, 2014; Ainley et al., 2012; Tajadura-Jiménez & Tsakiris, 2014). For example, Tsakiris and colleagues have shown that participants with higher interoceptive sensitivity are less susceptible to the RHI (Tsakiris et al., 2011). The authors hypothesize that the enhanced monitoring of internal states in people with increased interoceptive awareness may reduce the effects of the RHI due to a stronger representation of the self, stemming from the interoceptive signals (but see Suzuki et al., 2013 for an alternative account). These interoceptive contributions to the sense of self indicate an important role for internal bodily signals, of which we are typically unaware, which through multisensory integration with exteroceptive signals form a primary model of the bodily self.

## UNCONSCIOUS INTEGRATION OF MULTISENSORY SIGNALS

The studies reviewed above point toward an important role for the integration of multisensory bodily signals from both exteroceptive and interoceptive senses in the formation of the minimal self. However, one would expect such a pre-reflexive and fundamental representation of the self to take place without any conscious attention or monitoring. This is especially true as most of the proprioceptive, tactile, vestibular, and interoceptive signals underlying BSC do not reach conscious awareness (e.g., the sensation of your clothes against your skin or vestibular sensations from moving your head). Early theories regarding multisensory integration have suggested that binding together information from different senses requires

conscious awareness of the stimuli (Baars, 2002) in line with theories supporting modularity in cognitive and neural processing (Fodor, 1983; Zeki & Bartels, 1998). However, recent studies have shown that multisensory stimuli can be integrated in the absence of conscious awareness (Arzi et al., 2012; Faivre, Mudrik, Schwartz, & Koch, 2014; Lunghi, Binda, & Morrone, 2010; Zhou, Jiang, He, & Chen, 2010). Recently, studies have shown that bodily signals responsible for the formation of the minimal self, such as proprioception, vestibular, cardiac, and tactile sensations are integrated with vision in the absence of consciousness (Lunghi & Alais, 2013; Salomon, Galli et al., 2015; Salomon, Kaliuzhna, Herbelin, & Blanke, 2015; Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013; Salomon, Ronchi et al., 2016). These studies have shown that congruent multisensory information has faster access to awareness suggesting preferential processing of visual stimuli which converge with concurrent bodily states. Moreover, in a recent study using the full body illusion setup, it has been shown that access to visual awareness is modulated by visuo-tactile synchrony, and the presence of a visual body form similarly to the FBI suggesting that they may rely on similar mechanisms (Salomon, Galli et al., 2015). Taken together, these studies show that multisensory signals are rapidly integrated in the absence of awareness providing a viable basis for pre-reflexive sensory basis of the minimal self (reviewed in Faivre, Salomon, & Blanke, 2015). Further research is required to elucidate the neural systems which link this unconscious multisensory integration with body ownership (e.g., Salomon, Noel et al., 2015).

## THE ROLE OF ACTION IN BUILDING THE SENSE OF SELF

While a large volume has focused on the multisensory sources shaping the minimal self, it is clear that these are intimately linked with motor signals arising from volitional action. A prominent model for integration of motor action in self-representation is the comparator model (Wolpert & Kawato, 1998; Wolpert, Ghahramani, & Jordan, 1995). In this model, based on early observations by Helmholtz (Von Helmholtz, 1867), for each self-generated action an efference copy is created which in turn provides forward models which predict the sensory consequences of the action. These predicted sensory signals are in turn compared with reafferent signals from sensory inputs. If the two signals are congruent the sensory consequences are attributed to the self and a sense of agency is ascribed to the action (Bays, Wolpert, & Flanagan, 2005; Blakemore, Wolpert, & Frith, 2000; Blakemore, Goodbody, & Wolpert, 1998; David, Newen, & Vogeley, 2008; Gallagher, 2007; Haggard & Chambon, 2012; Marcel, 2003; Wolpert & Kawato, 1998; Wolpert et al., 1995). However, if the predicted and reafferent sensory signals are divergent this denotes that the signals are not self-generated and their source is attributed to an external source. This model has received widespread experimental support and provides a behavioral and neurobiological model for self-representation based on motor signals (Farrer, Franck, Georgieff et al., 2003; Farrer & Frith, 2002; Jeannerod & Pacherie, 2004; Kannape, Schwabe, Tadi, & Blanke, 2010; Salomon, Lim, Kan-

nape, Llobera, & Blanke, 2013; Salomon, Szpiro-Grinberg, & Lamy, 2011; Sato & Yasuda, 2005; Sperduti, Delaveau, Fossati, & Nadel, 2011; Synofzik, Vosgerau, & Newen, 2008a). For example this model has been used to explain the phenomenon that one cannot tickle oneself (Blakemore, Wolpert, & Frith, 1998; Blakemore et al., 2000) and can account for sensory attenuation found for self-generated actions in several modalities (Baess, Widmann, Roye, Schröger, & Jacobsen, 2009; Bays, Flanagan, & Wolpert, 2006; Hesse, Nishitani, Fink, Jousmäki, & Hari, 2010; Shergill et al., 2012; van Elk, Salomon, Kannape, & Blanke, 2014). Thus, this model allows an internal representation of the self by discriminating sensory consequences of one's action from those arising from external sources. The sensation of control over our actions, the sense of agency, has been suggested to have a prominent role in the formation and maintenance of the sense of self across the dynamic situations encountered in daily life (David et al., 2008; De Vignemont & Fournieret, 2004; Gallagher, 2007; Jeannerod, 2003; Jeannerod & Pacherie, 2004; Knoblich, 2002; Knoblich, Elsner, Aschersleben, & Metzinger, 2003; Marcel, 2003; Synofzik, Vosgerau, & Newen, 2008b; Tsakiris, Schütz-Bosbach, & Gallagher, 2007). Several studies have addressed the effects of agency on the sense of self, typically by investigating the effects of providing deviated sensory feedback to one's actions (Farrer, Franck, Paillard, & Jeannerod, 2003; Fournieret & Jeannerod, 1998; Inzlicht, Gutsell, & Legault, 2012; Jeannerod, 2004; Salomon, Lim, Kannape, et al., 2013; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; van den Bos & Jeannerod, 2002). Interestingly, it has been found that for small deviations the sense of agency for the actions is retained, yet the motor system compensates for the perturbation without any subjective awareness of these corrections (Fournieret & Jeannerod, 1998; Franck et al., 2001; Kannape et al., 2010; Knoblich & Kircher, 2004; Nielsen, 1963). Thus, while the motor system is highly sensitive to incongruences between action and sensory consequences, explicit awareness of these errors is restricted to larger discrepancies, supporting a model of unconscious integration of sensorimotor information for self-representation (Faivre et al., 2015; Kelso, 2016).

Recently, several studies have investigated the direct contributions of motor signals to body ownership (Banakou, Groten, & Slater, 2013; Hara et al., 2015; Kalckert & Ehrsson, 2012; Rognini et al., 2013; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Sato & Yasuda, 2005; Serino et al., 2015; Tsakiris, Longo, & Haggard, 2010). For example it has been shown that visuo-motor correlations between one's actions and a virtual hand or body cause a sense of ownership over the limb or body (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012, 2014; Longo & Haggard, 2009; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris et al., 2010). Furthermore, such agency driven embodiment has been found to induce changes in perception and social cognition (Banakou et al., 2013; Peck, Seinfeld, Aglioti, & Slater, 2013). In another line of work, the effects of self-touch on the construal of body representation has been pursued (Aimola Davies et al., 2013; Blanke et al., 2014; Ehrsson, Holmes, & Passingham, 2005; Hara et al., 2015; Hara et al., 2014; Pozeg, Rognini, Salomon, & Blanke, 2014; White, Davies, & Davies, 2011). Self-touch has been suggested to have an influential role in the development of self-awareness (Gallagher & Meltzoff, 1996; Rochat, 1998, 2003)

through the integration of efferent and afferent signals linking agency and sensory body representations. In a recent experiment we have found that modulating sensorimotor feedback of self-touch can create an alteration of one's body representation such that a feeling of a nearby presence of another person (*Feeling of Presence*) is induced. In this experiment we used a novel master slave robotic system (Hara et al., 2011) in which the participants' hand movements are translated into temporally synchronous or asynchronous touch on their back. When the tactile feedback was asynchronous a bodily illusion of a *Feeling of Presence*, found in neurological (Brugger, Regard, & Landis, 1996) and psychiatric conditions (Blanke, Arzy, & Landis, 2008; Jaspers, 1963) was induced (Blanke et al., 2014). Thus, inducing sensorimotor incongruences by using spatiotemporal conflicts between action and its sensory consequences may modulate body representations, similarly to those induced by multisensory conflicts.

Taken together, these studies show that voluntary action contributes to self-recognition through the addition of predictive signals which allow a "testing ground" for afferent sensory signals. Thus, while these motor signals are perhaps not a *necessary condition* for the establishment of the minimal self (as evident from the fact that patients with paralysis or when we are immobile we do not lose our sense of self) it is clearly a central mechanism for delineating the self in dynamic environments.

## **DISTURBANCES OF THE MINIMAL SELF: A FAILURE OF ACTION PREDICTION?**

The previous sections have presented evidence of the role of sensorimotor signals in the formation of the sense of self. In this context it would be interesting to test this model of the minimal self in light of disturbances of the self-representation as found in clinical cases. While such disturbances of the self are present in several neurological disorders (Biran & Chatterjee, 2004; Blanke & Mohr, 2005; Dewhurst & Pearson, 1955; Feinberg, 1997; Feinberg & Keenan, 2005; Feinberg et al., 2010; Turk et al., 2002; Vallar & Ronchi, 2009), the most common breakdown of self-representation is found in schizophrenia. Schizophrenia is a devastating psychiatric disorder affecting about 1% of the population worldwide (Bhugra, 2005). It has been proposed that schizophrenia constitutes an *ipseity* disturbance characterized by a diminished self-model leading to inclusion of external objects in the self-model and conversely to externalization of some parts of the self (Parnas, 2003; Parnas & Sass, 2001; Sass & Parnas, 2001). Thus, one would expect that such abnormal modulation of the self would be related to changes in the sensorimotor foundations of the minimal self-model. Several studies have now addressed this intriguing issue employing paradigms linking body ownership and especially agency to schizophrenia. It has been suggested that deficient sensorimotor prediction may underlie the symptoms found in schizophrenia (Blakemore, Wolpert, & Frith, 2002; Feinberg, 1978; Fletcher & Frith, 2008; Frith, 2005; Frith, Blakemore, & Wolpert, 2000a, 2000b; Frith & Done, 2009). This theory, termed the central moni-



toring theory, posits a breakdown of agency in schizophrenia which could explain many symptoms such as auditory verbal hallucinations (misattribution of internal speech) or passivity symptoms (attribution of voluntary action to another agent) (Fletcher & Frith, 2008; Frith, 2005; Frith & Done, 2009). This theory is now supported by many studies which have found deficits in agency and sensorimotor prediction (Daprati et al., 1997; Fournieret, Franck, Slachevsky, & Jeannerod, 2001; Franck et al., 2001; Kircher & Leube, 2003; Lindner, Thier, Kircher, Haarmeier, & Leube, 2005; Malenka, Angel, Hampton, & Berger, 1982; Shergill, Samson, Bays, Frith, & Wolpert, 2005; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010) as well as reduced sensory attenuation for self-generated actions in schizophrenia (Ford et al., 2001; Ford, Palzes, Roach, & Mathalon, 2013; Perez et al., 2011; Shergill et al., 2005). The induction of a schizophrenia-like state of a *feeling of a presence* by sensorimotor conflict discussed previously (Blanke et al., 2014) offers an interesting approach to study the relation between sensorimotor error and schizophrenia symptoms. At the neurobiological level this deficit in sensorimotor prediction is in line with numerous findings of reduced functional connectivity in schizophrenia (Bleich-Cohen et al., 2011; Camchong, MacDonald, Bell, Mueller, & Lim, 2009; Greicius, 2008; Honey et al., 2005; Liang et al., 2006; Pawel et al., 2010; Salomon, Bleich-Cohen et al., 2011; Whalley et al., 2005) which may inhibit the dissemination of efferent copy signals in the brain. Further studies linking cortical disconnectivity and deficits in sensorimotor prediction are required to fully understand this relation.

Other studies investigating changes in body ownership in schizophrenia have found somewhat variable results (Lev-Ari, Hirschmann, Dyskin, Goldman, & Hirschmann, 2015; Peled, Pressman, Geva, & Modai, 2003; Thakkar, Nichols, McIntosh, & Park, 2011) possibly due to the difficulty of subjective assessment of illusions in this population. Indeed, somatic disturbances, such as hand misattribution, in schizophrenia are usually secondary and less common symptoms compared with hallucinations and delusions (Andreasen, Arndt, Alliger, Miller, & Flaum, 1995; Bleuler, 1951; Mellor, 1970).

## THE SOCIAL-COGNITIVE ASPECTS OF THE MINIMAL SELF

The previous sections have outlined the role of the integration of multisensory bodily signals and action in the formation of the fundamental sense of self. However, beyond the basic segregation of the organism from its environment, these mechanisms defining the bodily representation of the self also modulate our interactions with conspecifics in the social domain (Baumeister, 1999; Christoff, Cosmelli, Legrand, & Thompson, 2011; Northoff & Panksepp, 2008; Uddin, Iacoboni, Lange, & Keenan, 2007). Here I will briefly outline two examples of how the sensorimotor mechanisms of the minimal self also extend to social-cognitive processing.

Several recent studies have focused on changing social interaction through modulations of the minimal self. For example, using immersive virtual reality, Peck and colleagues allowed participants to control the movements of an avatar from

a different racial group and found that this experience reduced racial bias (Peck et al., 2013) but only when they had active control over the avatar's movements. Similar results have been shown for ownership over a rubber hand (of a different race) induced by visuo-tactile synchrony, which reduced racial biases (Maister, Sebanz, Knoblich, & Tsakiris, 2013). Such findings, linking social processing to the sensorimotor mechanisms involved in the formation of the minimal self (Avenanti, Sirigu, & Aglioti, 2010; Fini, Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013; Serino, Giovagnoli, & Làdavas, 2009; Tajadura-Jiménez & Tsakiris, 2014; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013; Tsakiris, 2016), indicate the close relations between how we determine who we are and how we determine how to deal with others. These approaches show promise in their ability to reduce racial bias and could be extended to other social conflict situations.

Another novel line of research has extended the investigation of the role of efferent, action generated signals to the social domain. As mentioned previously, sensorimotor signals (in the context of the comparator model) underlie our sense of agency linking our actions with their consequences in the world. At the fundamental level this model allows us to conceive the self through our volition and segregate the organism from its environment, however it also shapes our sense of casualty and responsibility for these actions (Gallagher, 2000; Haggard & Tsakiris, 2009; Jeannerod, 2006). Our moral judgments are determined not only by the outcomes of one's actions but on the agency or intentionality behind them (Young, Cushman, Hauser, & Saxe, 2007). Thus, our sense of moral responsibility may depend on underlying sensorimotor processes. Indeed, recent studies have shown that people show less agency for actions with negative outcomes (Yoshie & Haggard, 2013) and that the sense of agency and brain activity is reduced for coerced actions (Caspar, Christensen, Cleeremans, & Haggard, 2016) which are more similar to passive, unwilling actions. Furthermore, there is an overlap between several of the regions relating to the sense of agency and empathy (Corradi-Dell'Acqua, Civai, Rumiat, & Fink, 2013; Koban, Corradi-Dell'Acqua, & Vuilleumier, 2013). Taken together, these studies point to the strong link between sensorimotor processing underlying the sense of agency and social processing of empathy and moral judgment. This link is especially pertinent today, when novel technologies allow us to act in distal locations. For example, how is the sense of responsibility or morality modified when one is operating an attack drone in a distant location? Further studies on disembodied actions are needed to more fully understand the ramifications of such novel sensorimotor situations.

## CONCLUSION

The sense of self is one of the most mysterious and controversial issues in psychology, and to date there is no consensual cognitive or neurobiological model which can account for the many levels of self-representation found in humans. However, recent advances in the study of the minimal self have led to important understandings regarding the roles of sensory and motor process in construing this basic

self-representation. The reviewed studies point to the unconscious integration of multisensory signals, supported by predictive models from motor action as the basis of the minimal self. The correspondences between these exteroceptive and interoceptive sensory signals allow a fundamental representation of the organism as a discrete agent, allowing a functional segregation from the environment and conspecifics. Failures in these sensorimotor systems may have dire consequences to the self-model propagating from basic motor prediction errors to more complex symptoms including hallucinations and delusions.

The minimal self is often viewed as the core, pre-reflexive, representation of the self in the world upon which more complex models such as the autobiographical, semantic, and social self are established. Yet despite these intriguing findings our understanding of the sense of self is pronouncedly limited. The neural and developmental processes giving rise to the minimal self from sensory and motor signals are not well understood. Furthermore, the interactions between the sensorimotor representations of the self and other more complex levels are still obscure. The last decades have witnessed a renewed interest in the scientific study of the self and it is possible that the next decades will bring around a deeper understanding of this so fundamental psychological concept.

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