BRAIN MECHANISMS OF BODILY SELF-CONSCIOUSNESS AND SUBJECTIVITY: REVIEW AND OUTLOOK

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Abstract

Recent data that have linked self-consciousness to the processing of multisensory bodily signals in human temporo-parietal and premotor cortex. Studies in which subjects receive ambiguous multisensory information about the location and appearance of their own body have shown that activity in these brain areas reflects the conscious experience of identifying with the body (self-identification), the experience of where «I» am in space (self-location), and the experience of the perspective from where «I» perceive the world (first-person perspective). These findings may form the basis for a neurobiological model of self-consciousness. In the conclusion I highlight other domains of cognitive neuroscience that are of relevance for understanding higher-order forms of self-consciousness and the relevance of these findings for cognitive neuroprosthetics.

Introduction

Human adults experience a «real me» that «resides in my body» and is the subject or «I» of experience and thought. This is self-consciousness, the feeling that conscious experiences are bound to the self and belong to «somebody». It is this unitary entity, the «I», that is often considered to be one of the most astonishing features of the human mind. Recent approaches to investigate self-consciousness have targeted brain mechanisms that process bodily signals (i.e. bodily self-consciousness)[1-6,54]. The study of such bodily signals is complex as they are continuously present and updated and are conveyed by different senses as well as motor and visceral signals. Recent developments, however, using video, virtual reality and robotics technologies have allowed us to investigate the central mechanisms of bodily self-consciousness by providing subjects with ambiguous multisensory information about the location and appearance of their own body. In the present article I review three important aspects of bodily self-consciousness, how they relate to the processing of bodily signals, and which functional and neural mechanisms they may share: self-identification with the body (that is the experience of owning a body), self-location (that is the experience of where I am in space), and the first-person perspective (that is the experience from where I perceive the world).

Altered states of bodily self-consciousness

If you ever – while lying in bed and about to fall asleep – suddenly had the distinct impression of floating up near the ceiling and looking back down at your body on the bed, then it is likely that you had an out-of-body experience (OBE). Here is a description of an OBE by Sylvan Muldoon, one of the first authors to describe his own OBEs (and those of others) in great detail: «I was floating in the very air, rigidly horizontal, a few feet above the bed […] I was moving toward the ceiling, horizontal and powerless […] I managed to turn around and there […] was another «me» lying quietly upon the bed» (from Muldoon & Carrington «The projection of the astral body» 1929).

OBEs are not bizarre departures from normal human experience and more than a mere curiosity. They are, instead, selective disturbances of bodily self-consciousness and their study (and of related phenomena) has lead to insights into the bodily foundations of self-consciousness. Moreover, they have impacted experimental research in cognitive neuroscience. OBEs are striking phenomena because they challenge our everyday experience of the spatial unity of self and body: they challenge our experience of a «real me» that «resides» in my body and is the subject or «I» of experience and thought[8].

OBEs are not rare, have been reported since time immemorial, and have been estimated to occur in about 5% of the general population[8]. During an OBE, the subject has the subjective feeling of being awake and experiences the «self,» or center of awareness, as being located outside the physical body, at a somewhat elevated level (i.e. abnormal self-location). It is from this elevated extrapersonal location that the patient's body and the world are perceived (i.e. abnormal first-person perspective)[7-9]. During an OBE most subjects experience to see their own body as lying on the ground or in bed, and the experience tends to be described as vivid and realistic. Thus, self-identification with a body, that is the sensation of owning a body, is experienced at the elevated, disembodied location and not at the location of the physical body (i.e. abnormal self-identification). What causes this disunity between self and body and the changes in self-identification, self-location, and our everyday body-centered first-person perspective?

Neurology of out-of-body experiences

OBEs of neurological origin have been reported in patients suffering from many different etiologies[7-9], such as migraine [10], epilepsy[7,8,11], but also after focal electrical cortical stimulation[12,13], general anesthesia[14], typhoid fever[15], and spinal cord damage[16]. OBEs due to focal brain damage have allowed further insights and have linked OBEs with the right and left temporo-parietal junction (TPJ)[8,17,18], the precuneus[13], and fronto-temporal cortex. A recent lesion analysis in the to date largest sample of patients with OBEs due to focal brain damage, however, revealed a well-localized origin at the junction of the right angular gyrus with the posterior superior temporal gyrus[19] (Figure 1).

Figure 1: Brain mechanisms of self-location and first-person perspective
Location of brain damage associated with changes in self-location and the experienced direction of the first-person perspective in patients suffering from out-of-body experiences (reproduced with permission from Ionta et al., 2011).

Based on the frequent association of OBEs with visuo-somatosensory illusions, abnormal vestibular sensations[20,21], and the role of the TPJ in multisensory integration[22,23], it has been suggested that OBEs (and abnormal self-identification, self-location, and first-person perspective) occur due to disturbed multisensory integration of bodily signals in (peri) personal space (somatosensory, visual and proprioceptive signals) and extrapersonal space (visual and vestibular signals)[8,19].

Experimentally-induced altered states of self-consciousness: Video Ergo Sum

Recently these clinical insights have been combined with methods from cognitive neuroscience to study bodily self-consciousness. This line of research used video, virtual reality and/or robotic devices in combinations with neuroimaging. Several experimental procedures have been developed that employ various visuo-tactile and visuo-vestibular conflicts to induce changes in self-location, self-identification and first-person perspective in healthy subjects[24-26]. In most such research paradigms, a tactile stroking stimulus is repeatedly applied to the back or chest of a participant who is being filmed and simultaneously views (through a head-mounted display [HMD]) the stroking of a human body in a real-time film or virtual-reality animation. The video camera was placed 2 m behind the person, filming the participant's back from behind (Figure 2). Thus, participants viewed a video image of their body (the «virtual body») from an «outside», third-person perspective[26] while an experimenter stroked their back with a stick. The stroking was thus felt by the participants on their back and also seen on the back of the virtual body. The HMD displayed the stroking of the virtual body either in real time or not (using an online video-delay or offline pre-recorded data), generating synchronous and asynchronous visuo-tactile stimulation, respectively.

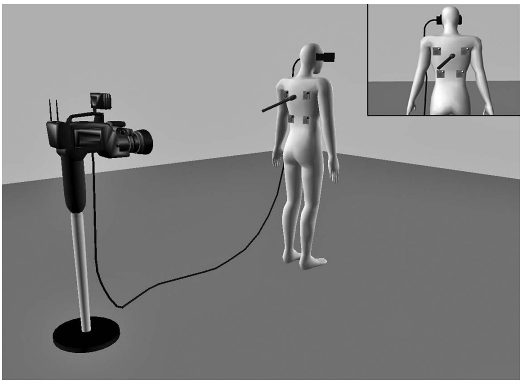

Figure 2: Video Ergo Sum
Depiction of the experimental setup using video and visuo-tactile mismatch to induce changes in self-identification, self-location and first-person perspective.

Under these conditions subjects self-identified with the seen virtual body (hence: Video ergo sum) and such illusory self-identification with the virtual body was stronger during synchronous than during asynchronous stroking conditions[26] (for a similar approach see[24]). Self-location was measured by passively displacing the body of the blindfolded subject after the stroking period and then asking her to walk back to the original position. As predicted, self-location was experienced at a position that was closer to the virtual body, as if subjects were located «in front» of the position where they had been standing during the experiment (or as if they were located «out-of-the-body»)[26]. Later work confirmed that self-location towards and self-identification with the virtual body are strongly and systematically influenced by different visuo-tactile conflicts and can also be achieved these changes in the supine position[25,27]. Moreover, self-identification and self-location are also associated with physiological (i.e. skin conductance response to a threat directed towards the virtual body[24]) and nociceptive changes (i.e. pain thresholds are elevated during the full body illusion[28]).

Multisensory brain mechanisms

Concerning self-identification, a comprehensive fMRI study[27] of a full-body illusion reported that self-identification with a virtual body is associated with activity in bilateral ventral premotor cortex, left posterior parietal cortex, and the left putamen (Figure 3A). The activity in these three regions was enhanced by visuo-tactile stimulation. Another fMRI study[25] found that self-identification with a virtual body is associated with activation in the right middle-inferior temporal cortex (partially overlapping with the extrastriate body area [EBA]) (Figure 3A), a region that is like premotor and posterior parietal cortex involved in the multisensory processing of human bodies[29-32].

These former experimental procedures were able to induce changes in self-identification, but did not report changes in self-location and the first-person perspective that are a crucial aspect of bodily self-consciousness and prominently altered in an out-of-body experience. Using fMRI and robotics (while participants were in a supine position and viewed a virtual body that was filmed from an elevated position) a recent fMRI study[25] was able to experimentally manipulate also these two aspects. Thus, despite identical visuo-tactile stimulation, half of the participants experienced looking upward towards the virtual body (Up-group), and half experienced looking down on the virtual body (Down-group) and these perspectival changes were associated with consistent changes in self-lo-

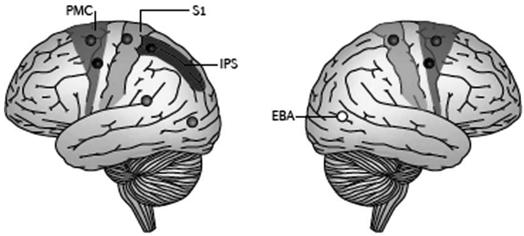

Figure 3A: Brain mechanisms of self-identification
Location of brain activity during experimentally- and neurologically-induced changes in self-identification. Note the involvement of premotor cortex (PMC, brown), primary somatosensory cortex (S1), posterior parietal cortex (IPS, purple), the temporo-parietal and the occipito-temporal cortex of both hemispheres. The location of the small circles indicates location of brain activation in different brain imaging studies (reproduced with permission from Blanke, 2012).

cation in both groups[25]. These data show that self-location depends on visuo-tactile stimulation and on the experienced direction of the first-person perspective and that different multisensory mechanisms underlie self-location versus self-identification (the latter was independent on the first-person perspective). Changes in self-location and the first-person perspective were reflected in activity at the TPJ bilaterally[25], peaking in the posterior superior temporal gyri (Figure 3B).

Based on these findings it has been argued that self-location and the first-person perspective may be caused by visuo-vestibular mechanisms, because in the study by Ionta et al.[25] participants viewed a visual image on the HMD that contained a conflict between the visual gravitational cues of the virtual body and the vestibular gravitational cues of the participant's physical body. Blanke (2012) argued that this probably caused the observed differences in the experienced direction of the first-person perspective, with participants from the Up-group relying more strongly on vestibular cues from the physical body (indicating downward gravity directed towards the physical body) than on visual gravitational cues from the virtual body (indicating downward gravity directed away from the physical body), whereas participants from the Down-group show the opposite pattern. This is compatible with interindividual differences

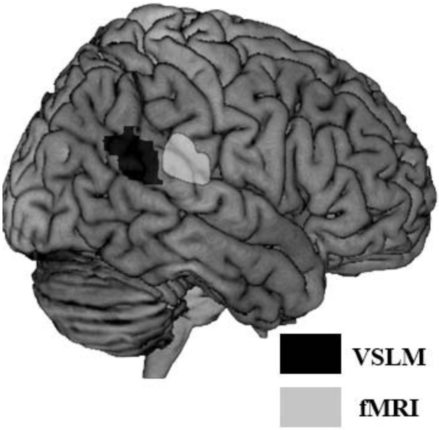

Figure 3B: Brain mechanisms of self-location and first-person perspective
Location of brain activity during experimentally-induced changes in self-location and the experienced direction of the first-person perspective (grey area) and location of brain damage associated with neurologically-induced changes in self-location and the experienced direction of the first-person perspective in patients suffering from out-of-body experiences (black area). Note the anatomical proximity of these clinically and experimentally defined brain mechanisms of bodily self-consciousness at the right temporo-parietal junction (reproduced with permission from Ionta et al., 2011).

in visuo-vestibular integration[33-36], subjects with OBEs and so-called inversion illusions. More work on visuo-vestibular integration and its relevance for bodily self-consciousness is ongoing.

Conclusions

The «I» of conscious experience is one of the most astonishing features of the human mind. The reviewed neuroscientific investigations of self-identification, self-location and first-person perspective have described some of the multisensory brain processes that may give rise to bodily self-consciousness. As argued elsewhere[1], these three aspects are the necessary constituents of the simplest form of self-consciousness that arises when the brain encodes the origin of the first-person perspective from within a spatial frame of reference (i.e. self-location) associated with self-identification. The present data highlight the primary role of the temporo-parietal cortex in bodily self-consciousness as informed by multisensory and vestibular signals. Self-identification depends on somatosensory and visual signals and involves bimodal visuo-tactile neurons, whereas self-location and the first-person perspective depend on the integration of these bodily signals with vestibular cues, in trimodal visuo-tactile-vestibular neurons. These differences between self-identification versus self-location and first-person perspective are corroborated by neuroimaging and neurological data, showing that self-identification recruits primarily bilateral premotor and parietal regions, whereas self-location and the first-person perspective recruit posterior parietal-TPJ regions with a right hemispheric predominance.

These recent data extend other prominent proposals concerning the neural basis of bodily self-consciousness that have highlighted brain processes related to internal states of the body, such as interoceptive and homeostatic systems (e.g. the heartbeat) as important signals, and that have highlighted the contribution of either the insula[37] or the posterior medial parietal cortex[38,39]. Ongoing research explores the interactions between exteroceptive bodily signals (which the present review focused on) and interoceptive and sensorimotor signals[5,40]. Recent results confirm that both types of bodily signals (extero- and interoceptive signals) are of relevance for self-consciousness and should despite their neuroanatomical differences be considered as a single system. These more recent findings also highlight the role of emotional mechanisms related to self-identification[41].

Cognitive psychologists and neuroscientists have studied many different aspects of the self-related for example to language and memory (i.e.[2,4,5,42-51]). Along this line, mechanisms of bodily self-consciousness overlap with self-related processes such as perceptual and imagined viewpoint changes[51], theory-of-mind, mentalizing[52], empathy, and egocentric perspective taking. It will also be an exciting endeavour to better understand how the reviewed brain mechanisms on bodily self-consciousness are linked to language (i.e.[53,54]) and to memory and future prediction[39] (see also[55,56]), as the latter functions have been prominently linked to so-called higher-order forms of self-consciousness, such as «narrative» and «extended» self-consciousness and personhood.

Recent advances in virtual reality and robotics are also opening novel avenues for treatment and human enhancement of sensorimotor and cognitive functions. Virtual reality has already played an important role in augmenting cognition, assisting motor rehabilitation, and as an effective treatment in anxiety and specific phobias[57,58]. These treatments may be complemented and improved by including automatized manipulations of illusory hand ownership, self-location and self-identification. Diagnosis and treatments of other medical conditions such as pain syndromes[28,59] and inflammation[60] may also benefit from artificially induced changes in hand ownership, self-location and self-identification. Finally, the manipulation of bodily self-consciousness may generate and enhance bodily feelings for de-afferented body parts in patients with tetra- and paraplegia following spinal cord injury. Recent work in amputee patients – initiated by Ramachandran and colleagues[61] – has already explored these possibilities for the design of future artificial limbs[62,63]. Patients with medical conditions such as para- and tetraplegia as well as limb amputation may profit in the future from automatized procedures to enhance or augment artificial bodies allowing them not only to move, but also to feel the «digital body» as their own body[64-67].

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