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Neuroscience of self-consciousness and subjectivity

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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). I argue that these findings may form the basis for a neurobiological model of self-consciousness, grounding higher-order notions of self- consciousness and personhood in multisensory brain mechanisms.

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. Thus, experiences are felt as belonging to "somebody" and it is this unitary entity, the "I", that is often considered to be one of the most astonishing features of the human mind.

A powerful approach to investigate self-consciousness has been to target 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, in 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

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their own body. The detailed study of abnormal states of bodily self-consciousness in neurological patients has also provided important additional data. Here I discuss 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 (i.e. the experience of owning a body), self-location (i.e. the experience of where I am in space), and the first-person perspective (i.e. the experience from where I perceive the world).

I start with the breakdown of bodily self-consciousness and will describe the results of detailed observations in neurological patients with abnormal self-identification, self-location, and first-person perspective. Next, the major experimental paradigms, behavioural results, and neuroimaging findings will be described with the goal to develop a data-driven neurobiological model of self-consciousness and subjectivity.

When the self leaves the body: the out-of-body experience

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 may be considered a bizarre departure from normal human experience. Yet, they are more than a mere curiosity and of relevance for science and the humanities. They are a distortion of bodily self-consciousness and the study of this phenomenon has lead to insights into the bodily foundations of self-consciousness, and has 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]

Yet, 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] 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?

The neurology of self-consciousness: the right temporo-parietal junction

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] in particular the posterior superior temporal gyrus,[8] angular gyrus,[12,18] and the supramarginal gyrus.[13,17] Outside the TPJ, damage has been found in the precuneus[13] and fronto-temporal cortex (Devinsky *et al.*, 1989). A recent lesion analysis study using voxel-based lesion symptom mapping 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].

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] Translating these clinical data into the research laboratory, it has been investigated shown that multisensory conflicts of bodily signals can alter bodily self-consciousness by inducing altered states of self-identification, self-location, and the first-person perspective.

Video Ergo Sum: The induction of illusory self-location through visuo-tactile conflict

Extending paradigms from cognitive neuroscience and multisensory perception of the upper limb to paradigms targeting full-body representations recent research using video, virtual reality and/or robotic devices in combinations with neuroimaging has allowed to study self- consciousness. Here, I will describe experimental procedures that have been developed to induce changes in self-location, self-identification and first-person perspective in healthy subjects.[24-26] These experiments induce full-body-illusions or out-of-body-illusions and exploit visuo–tactile and visuo–vestibular conflicts. 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. 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.

Under these conditions subjects self-identified with the seen virtual body (*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]

These changes in bodily self-consciousness are also associated with an alteration how co-applied visual stimuli interfere with the perception of tactile stimuli.[28,29] Such visuo-tactile interference is a behavioural index of whether visual and tactile stimuli are functionally perceived to be in the same spatial location.[28,30-33] Applied during the abovementioned paradigms and during states of illusory self-identification and self-location, it was found that visual stimuli seen at a position that is 2 meters in front of the subject's back and tactile stimuli (that were applied on the subject's back) were functionally perceived to be in the same spatial location (see also[28,30-35]). These data provide robust perceptual evidence (based on reaction times and accuracy rates) that self-identification and self-location with a virtual body alters how the brain perceives stimuli applied to the subject's own physical body. 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 during the full body illusion)[36].

Multisensory brain mechanisms of self-identification and self-location

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. The activity in these three regions was enhanced by visuo-tactile stimulation. An EEG study[37] linked self-identification and self-location with a virtual body to activity in bilateral medial sensorimotor cortices and medial PMC. In this EEG study, self-identification and self-location with a virtual body induced by synchronous versus asynchronous visual-tactile stimulation of the real and the virtual body was associated with differential suppression of alpha band power (8–13 Hz) oscillations in bilateral medial sensorimotor regions and medial premotor cortex. Alpha band oscillations over central areas (that is, the mu rhythm) has been linked to sensorimotor processing[38] and mu rhythm suppression is thought to reflect increased cortical activation in sensorimotor and/or premotor cortices.[39] 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)), a region that is like the premotor cortex involved in the multisensory processing of human bodies.[40-43]

The first-person perspective and visuo-vestibular processing

These former experimental procedures were able to induce changes in self-identification and self-location, but did not report changes in the first-person perspective that are a crucial aspect of bodily self-consciousness and prominently altered in an out-of-body experience. Recently changes in first-person perspective have also been achieved using fMRI and robotics, while participants were in a supine position and viewed a virtual body that was filmed from an elevated position.[25] 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-location in both groups. In addition, subjective reports of elevated self-location and sensations of flying, floating, rising, lightness, (that are common in out-of-body experiences) were frequent in the Down-group and rare in the Up-group.[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 not found to depend on the first-person perspective). These changes in self-location and the first-person perspective were reflected in activity at the TPJ bilaterally.[25] TPJ activity peaked in the posterior superior temporal gyri, differed between synchronous and asynchronous stroking conditions, and depended on the experienced direction of the first-person perspective.

Based on these findings it has been argued that the dependence of self-location on the first- person perspective may be caused by visuo-vestibular mechanisms (Blanke, 2012). Thus, 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 experienced by the participant's physical body: the body that was shown in these experiments was presented in a direction that was incongruent with the direction of veridical gravity. 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. Indeed, past vestibular research has revealed prominent inter-individual differences in visuo-vestibular integration with some subjects relying more strongly on visual signals and others more on vestibular signals.[44-47] This is further corroborated by findings in subjects with OBEs and subjects with the so-called inversion illusion. Accordingly, these neurologically and experimentally-induced changes in the experienced direction of the first-person perspective are due to abnormal signal integration of otolithic vestibular cues and visual cues (Blanke, 2012).

Self-consciousness in humans and non-human primates?

Based on the involvement of human posterior parietal and premotor cortex in self- identification[27] and the known properties of bimodal visuo-tactile neurons in these regions in non-human primates, the observed changes in self-identification may be due to stroking-induced changes in the size and position of trunk-centred bimodal visuo-tactile neurons with respect to the virtual body that is seen on the HMD (Blanke, 2012). In brief, the visual receptive fields of such bimodal neurons would be enlarged following visuo-tactile stroking, and would after stroking also encode the more distant position of the seen virtual body in peripersonal space.[48] Experimentally induced changes in illusory self-identification with a fake or virtual body via video-based virtual reality systems may therefore be associated with a stroking-induced enlargement or alteration of the brain's peripersonal space representation (visual receptive fields) of such bimodal parietal and/or premotor neurons. The described changes in self-identification may therefore be based on displaced or enlarged visual receptive fields of such bimodal neurons in premotor and posterior parietal cortex, so that they now also encode the more distant position of the seen virtual body. However, the reviewed neuroimaging and neurological data also suggest that there are differences between the brain mechanisms of self-location and the first-person perspective versus self-identification. Thus, self-location, but not self-identification, has been shown to depend on the first-person perspective, and relies on additional vestibular graviceptive (otolithic) signals and their integration with visual graviceptive signals. These distinct processes may recruit distinct brain regions in the posterior parietal cortex and the TPJ[49-51] (the parieto-insular vestibular cortex (PIVC), VIP and the middle superior temporal region (MST).[52]

Conclusions

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[53] or the posterior medial parietal cortex.[54,55] Ongoing research explores the interactions between exteroceptive bodily signals (which the present review focused on) and interoceptive and sensorimotor signals5,56. 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.[57]

Bodily self-consciousness may also turn out to be an important component for consciousness generally.[55] As Gerald Edelman stated "it is not enough to say that the mind (and consciousness) is embodied. You also have to say how".[58] Bodily self-consciousness may provide this link. Cognitive psychologists and neuroscientists have studied many different aspects of the self-related for example to language and memory (i.e. [2,4,5,59-68]). Along this line, mechanisms of bodily self-consciousness overlap with self-related processes such as perceptual and imagined viewpoint changes,[68] theory-of-mind, mentalizing,[69] and empathy.

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. It will be an exciting endeavour to better understand how the reviewed brain mechanisms are linked to language (i.e. [70,71]) and to memory and future prediction[55] (see also [72,73]) to also study higher-order – "narrative" and "extended" – aspects of self-consciousness and personhood.

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