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Neuroscience of Bodily Self-Consciousness

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Abstract

We review recent research about human subjectivity and self-consciousness that has focused on cognitive psychology and neuroimaging of bodily self-consciousness. Multidisciplinary research on the fields of neurology, cognitive neuroscience and virtual reality opens new avenues to investigate brain mechanisms underlying a fundamental sense of the bodily self. Clinical evidence for the implication of right temporo-parietal junction for bodily self-consciousness has received support by studies in which virtual-reality based own body illusions are evoked in healthy participants to study the underlying processes. A series of experiments will be reviewed in which it was shown that the experiences of self-location, self-identification and the first-person perspective can be manipulated experimentally and rely on the integration of multisensory stimuli (touch, vision, proprioception, vestibular information). Specific protocols are available to predictably influence the different aspects of bodily self-consciousness. We predict that the understanding of fundamental brain mechanisms of bodily self-consciousness will lead to unprecedented empirical insights that are of broad relevance for science, virtual reality, engineering, the humanities, as well as medicine and psychotherapy.

A Neuroscience Approach to Subjective Experience

«The body is always there» (James, 1891) has become a famous expression as it highlights the fact that the human brain continuously receives information from the body (as opposed to vision or sound) which is afferent to the brain. All human beings are confined to a biological container (i.e. their body) in which subjective experience originates. French philosopher René Descartes (1637) radically rejected the idea of unity between body and subjective experience when postulating his famous «Cogito ergo sum» (engl. «I think so I am»), which capitalized one of the major philosophical debates around the body-mind problem. Dualists, such as Descartes, claim that body and mind are very distinct substances of very distinct quality. Most present philosophers and neuroscientists reject such dualist models and study the brain mechanisms underlying the self and self-consciousness empirically or conceptually based on this data (for recent discussion see Metzinger, 2007).

Neuroscientists have always been fascinated by the scientific study of subjective experience and the related concepts of consciousness and awareness (e.g. Grüsser and Landis, 1991), but only recently a vast array of experimental procedures has become available to study the brain mechanisms of self-consciousness. Previous cognitive neuroscience research on the self has focused on high-level aspects such as language, conceptual knowledge or memory. In the present review we will highlight some recent discoveries related to low-level contributions to self-consciousness,

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such as the role of perception, multisensory and sensorimotor integration. Based on the reviewed findings Blanke and Metzinger (2009) proposed that a minimal phenomenal sense of self is based on the brain's integration of perceptual information from multiple senses, as for example from vision, touch and proprioception (i.e. information about the configuration of the body in space).

This was largely based on clinical data in patients that suffered from specific neurologic or psychiatric impairments which show common phenomenology of complex bodily hallucinations. One example is the out-of-body experience, for which Blanke and Mohr (2005) identified three major characteristics. First, a feeling of being located outside one's body in an elevated position a few meters above the physical body (disembodiment), secondly a feeling of identification with this elevated body and finally a feeling of seeing the environment including the physical body from this elevated location. Converging evidence suggests that out-of-body experiences are caused by interference with the right temporoparietal junction (Blanke et al., 2002, 2004; Ionta et al., 2011). These experiences of disembodiment differ from other autoscopic hallucinations, during which patients see a double in external space but locate the self and perceive the world from within bodily borders (Blanke and Mohr, 2005). Partly based on this clinical evidence Blanke and Metzinger (2009) hypothesized that bodily self-consciousness is fundamentally based on three aspects. First, experiencing the phenomenal self as being located in space – typically within bodily borders (self-location); secondly, attributing the self to the body as a whole – as opposed to body parts (self-identification); and finally, a spatial origin of subjective experience – which can be directed to the outside world (first-person perspective).

Experimentation with Self-Identification and Self-Location

A very fruitful approach for the scientific study of bodily self-consciousness and underlying mechanisms has been to elicit bodily illusions in healthy participants and to study the underlying factors that allow these illusions to be evoked, maintained or abolished. One of these illusions is the so-called full-body illusion (Ehrsson, 2007; Lenggenhager et al., 2007, 2009). In a typical full-body illusion experiment a participant is standing in the experimentation room and is filmed by a video camera located a few meters behind the participant. The camera recording is transmitted to a head-mounted display by means of which the participant sees a back view projection of his or her own body a few meters in front (virtual body). During the experiment

the researcher, unseen by the participant, touches the back of participant's body with a wooden stick. When the «felt stroking» on the back of the body is synchronous with the «seen stroking» on the virtual body most participants experience strong self-identification with the virtual body and report in questionnaires the sensation that the touch they felt was located where the touch was seen on the virtual body (illusory touch). After blindfolding participants, displacing them in the room and asking them to return to their initial position, most participants localized themselves about 25 cm closer to the virtual body (illusory self-location). Participants are also presented to a second period of stimulation in which a delay is introduced between the video projection they see (virtual body) and the touch they feel (physical body), such that visuo-tactile stimulation is asynchronous. In this condition, the subjective ratings and illusory self-location indicated by blind walking showed no bias towards the virtual body. These data show that synchrony of visual and tactile stimulation leads to an illusory self-identification with and errors in self-location towards the virtual body. In other words, this experiment demonstrates that two key aspects of bodily self-consciousness (i.e. self-location and self-identification) depend on visuo-tactile signal integration and that this integration can be predictably manipulated in participants that do not suffer of any neurological or psychiatric impairment. These data extend neurological data in providing further evidence for the idea that mechanisms of multisensory integration are important for bodily self-consciousness.

These findings were extended in other experiments by using the crossmodal congruency effect (CCE) during the full-body illusion paradigm (Aspell, Lenggenhager and Blanke, 2009). The CCE is a behavioral measure that indicates whether or not a visual and a touch stimulus are perceived to be at identical spatial locations (Spence, Pavani and Driver, 1998). In the experiment participants are asked to indicate where they perceived a single touch stimulus (i.e. short vibration) that could be applied just below the shoulder or at the lower back. Distracting visual stimuli (i.e. short light flashes) were also presented on the back and either presented at the same or at a different position. Under these conditions, participants are faster to detect a touch stimulus if the visual distractor was presented at the same location (i.e. congruent trial) compared to touches co-presented with a more distanced visual distractor (i.e. incongruent trial; the CCE is calculated as the difference between reaction times of incongruent versus congruent trials). In addition, the CCE is larger if the visual stimulus is closer in space to the

tactile stimulus. Importantly, if measured during the full-body illusion paradigm, it was found that the CCE magnitude reflects changes in bodily self-consciousness (self-identification and self-location) and may thus function as a behavioral proxy of such changes. Thus, the CCEs differed between periods of synchronous stroking (i.e. high CCE, more effect of visual distracters on tactile discrimination) and asynchronous stroking (i.e. low CCE, less effect of visual distracters on tactile discrimination) showing that the spatial perception of tactile cues applied to the human skin changes when self-identification and self-location are altered.

Up to now, the full-body illusion paradigm showed that in healthy humans there is the possibility to alter bodily self-consciousness by inducing states of illusory self-identification and self-location with a virtual body, and that this is associated with changes in touch perception. However, vision and touch are not the only senses that convey information about the position of the body to the brain. In a different study Palluel, Aspell and Blanke (2011) used the full-body illusion to demonstrate that bodily signals about the position of the limbs in space (often referred to as proprioceptive information) are relevant for bodily self-consciousness. The researchers applied constant vibration stimulation at the ankles of participants, which induced a perturbation of proprioceptive leg signals carrying information about the spatial location of the body. Under these conditions the full-body illusion was diminished with respect to the classical illusion-inducing conditions and synchronous visuo-tactile stimulation did not differ from asynchronous stimulation (this was reflected in CCE measures and subjective ratings, see figure 1). However, if the vibration was applied to a different body part (at the wrists) that was not relevant for spatial location of the body when standing, illusory changes in self-identification were successfully evoked. This experiment shows that – as predicted based on own body illusions of neurological origin – visual, tactile, and proprioceptive cues and their integration are relevant for bodily self-consciousness (Blanke et al., 2002, 2004).

These and other results suggest that vision, touch and proprioception are sensory signals that are highly relevant for the brain in order to rapidly update an online representation of the body in space (see also Maurer, Mergner and Peterka, 2006). Another important sensory signal from the body is pain, also because it is notoriously more than merely perceptual and pain is characterized by a high inter- and intra-individual variability. Can subjective changes of pain experience be modulated by subjective chang-

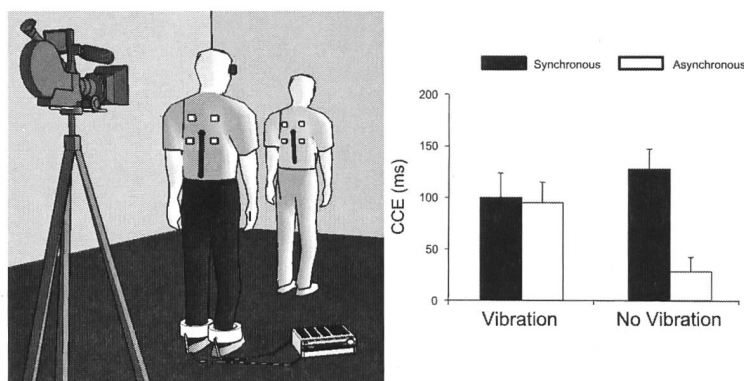


Figure 1 Ankle vibration experiment. Left panel shows experimental setup. A participant (black trousers) is filmed from a few meters behind and sees a video projection of this recording on a head-mounted display, resulting in seeing a virtual body (grey trousers) a few meters in front. Vibrators for continuous stimulation are attached to the ankles of the participant (white cuffs). Four light-attached vibrators for the crossmodal congruency task are attached to the back of the participant (white squares). Tactile stroking at the participant's back is manually applied by means of a wooden stick (black rod). Right panel shows experimental results. Crossmodal-congruency effect (CCE in ms) is plotted as a function of experimental condition. Note that there was no difference between synchronous and asynchronous back stroking conditions if continuous ankle vibration was applied. However, if no vibration was present, the typical illusion-related CCE-difference was found (see also Aspell et al., 2009).

es related to bodily self-consciousness? Combining experimentation using full-body illusions with subjective pain reports we found that changes in self-identification and self-location are associated with an elevation of pain thresholds. Hänsel and coworkers (2011) investigated whether pain thresholds for tactile pressure at the index finger are modulated during the full-body illusion. During synchronous or asynchronous backstroking participants received repeated touch pressure stimuli at the index fingers (with slowly increasing pressure levels) and were asked to report at which moment the stimulus felt painful. It was found that participants support more pain (increase in pain thresholds) during synchronous stroking as compared to the asynchronous condition. The perception of pain was therefore decreased when participants self-identified with the virtual body. These data show that subjective experience of pain is associated with bodily self-consciousness and is in line with reports of analgesic effects during anecdotal reports out-of-body experiences (Thonnard, 2008).

How can the third hypothesized aspect of bodily self-consciousness, the experienced direction of the first-person perspective, be studied experimentally (for a related but distinct approach see Vogeley and Fink, 2003)? This was achieved in a recent study by Ionta and coworkers (2011) suggesting the relevance of vestibular (balance) signals. These authors involved participants in a full-body illusion experiment while lying on their backs (methods similar to Lenggenhag-

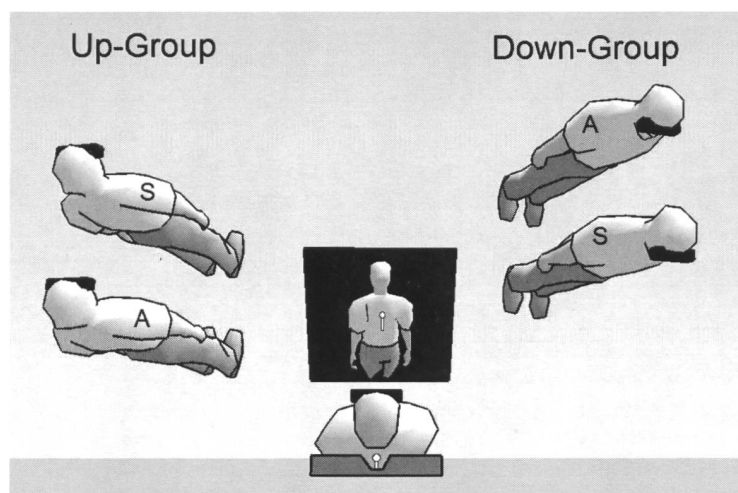


Figure 2 First-person perspective experiment. The central column shows the experimental setup. A participant is lying on a robotic device for tactile stroking on the back (grey rectangle). A pre-recorded video is presented on a head-mounted display showing visual stroking on a body from a few meters distance (within black square). Visuo-tactile stroking was presented in synchronous or asynchronous fashion. Left and right column represent results for experienced self-location of participants (Up-Group, Down-Group) for the different stroking conditions (S for synchronous, A for asynchronous), reflecting an upward drift for Up-Group participants and a downward drift for Down-Group participants. See main text and Ionta et al. (2011) for more information.

er, 2009). About half of the participants experienced a direction of the first-person perspective that was congruent with their physical up-looking perspective (Up-group), whereas the remaining half of the participants had the impression to be looking down in line with the visual perspective on the virtual body that was used to induce the full-body illusion (Down-group; thus the direction of gravity of the virtual body was different than the direction of gravity conveyed by vestibular information; visuo-vestibular conflict). Both groups showed higher self-identification towards the virtual body under conditions of visuo-tactile synchrony. An adapted self-location measure showed results that were compatible with these group differences in the experienced direction of the first-person perspective. Specifically, the direction of the drift in self-location was congruent with the experienced direction of the first-person perspective, but, in addition, participants in the Down-group had a generally higher level of self-location than the participants of the Up-group (see figure 2). Finally, both groups showed higher self-identification towards the virtual body under conditions of visuo-tactile synchrony, as compared to the asynchronous condition. This data showed that participants may experience self-location either predominantly based on signals from their own physical body (Up- group; based on vestibular and/or somatosensory cues) or based on visual signals from the seen virtual body (Down- group). Concurrent neuroimaging during the experiment revealed right and left temporo-pari-

etal junction (TPJ), that showed specific modulation of activity in line with the behavioral dissociation between Up- and Down-group and the specific direction of drift. This is the first study to show that activity in bilateral TPJ in healthy human beings reflects changes in experienced self-location and direction of the first-person perspective. It is also in line with earlier clinical research associating damage in right TPJ to such changes during out-of-body experiences (Blanke et al., 2002, 2004).

Conclusions and Beyond

In the present review we argue that the clinical findings of a causal link between damage to right temporo-parietal cortex and complex body illusions with their characteristic changes in self-identification, self-location and the first-person perspective, can be extended to the research laboratory. We reviewed empirical studies that systematically investigated similar mechanisms in healthy participants, and we suggest that this approach will allow the study of fundamental properties of bodily self-consciousness in a more fine-grained scientific manner. In utilizing variations of the full-body illusion paradigm in healthy participants, it is now clear that specific multisensory integration in the brain - relying on visual, tactile, proprioceptive, and vestibular cues - encodes key aspects of bodily self-consciousness. Predictable experimental control over bodily self-consciousness will enable scientists and engineers to extend their investigations to other aspects of consciousness (e.g. to the question: What are the consequences for visual consciousness if bodily self-consciousness is manipulated?) as well as to linguistic, conceptual, and mnemonic aspects of the self and consciousness. Importantly, such research can now be combined with all major brain imaging techniques (for example Ionta et al., 2011; Lenggenhager et al., 2011; Petkova et al., 2011) generating a new field within the cognitive neurosciences dedicated to study the neurobiology of self-consciousness. As there is a growing interest in virtual reality for education (i.e. of surgeons, firemen, pilots) or psychotherapy (i.e. for treating phobia, post-traumatic-stress-disorder) these findings on self-identification and embodiment of avatars is likely to be useful to further refine such applications for virtual education and treatments and may help improving the representation of the user in virtual-reality systems to increase efficacy of virtual reality use for its dedicated demand. The merger of these approaches may also lead to specific sensory treatment protocols that may help to diminish the suffering of chronic pain patients. ■

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