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Notes on the neurobiological
origins of bodily self-awareness

Text: Fabian Richter

Fabian Richter is a psychologist (MSc) and PhD candidate in Neuroscience. He has published articles on interoception in various international journals (e.g. Human Brain Mapping, Biological Psychology, Cortex) and has practical experience as a clinical neuropsychologist.

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After the amputation of a limb, patients often experience sensation in the detached body part. A wounded soldier during the American Civil War who had lost both his arms and legs recalled: »Often, at night, I would try with one lost hand to grope for the other« (Kean 2014). Such phantom sensations may include positioning, movements, feelings of warmth or cold, tingling, pain, itching and other paraesthesias (cf. Ko-oijman et al. 2000). In some cases, these phantom sensations are so vividly and realistically experienced that patients try to walk on an amputated leg. However, perceiving phantom sensations and illusory embodiment does not require amputation. During an experimental paradigm known as the *rubber hand illusion* (RHI), a fake limb is perceived as belonging to one's own body. The RHI creates a visuotactile multisensory conflict when a hand is stroked while being out of sight, but a visible rubber hand is stroked in sync (cf. Botvinick & Cohen 1998). Here, the dominance of the visual system causes the transfer of the tactile input sensed in the real left hand to the visible rubber hand.

These phenomena raise the question of how an organism creates self-awareness of its bodily structures and which areas of the brain are associated with the corresponding processes. For such *bodily self-awareness*, two different types of input seem to play a crucial role: exteroceptive and interoceptive information. *Exteroception* describes any perception of stimuli located outside the body. *Interoception*, in contrast, means the perception of signals stemming from within our own body. To determine where in the brain interoceptive and exteroceptive signals may converge in order to build the sense of *bodily self-awareness*, Gerardo Salvato and I (2020) performed two separate meta-analyses on neuroimaging (functional magnetic resonance imaging & positron emission tomography) studies. The dimensions were treated separately in each meta-analysis. A meta-analysis is useful for synthesising data from different studies and establishing consistency with respect to their variability. Our meta-analysis on *body ownership* included 16 studies investigating the sense of *body ownership* and its modulation by exteroceptive visuotactile stimulation. The meta-analysis on *interoception* comprised 40 studies dealing with sensitivity to bodily signals. In order to reveal areas of the brain that support integrating information coming from inside and outside the body to create subjective awareness of one's own body, areas were identified that showed similar significant activation in both meta-analyses. This conjunction analysis revealed the *supramarginal gyrus*, a portion of the parietal lobe, as a key area for the integration of interoceptive and exteroceptive information in order to build *bodily self-awareness* (see Figure 1). Thus, our findings indicate that the *supramarginal gyrus* may be considered a higher-order brain area involved in integrating

multi-sensory signals. Traditionally, this region is considered to be a language-relevant region, as lesions of this cortical area cause aphasic symptoms like difficulties understanding written and spoken language (cf. Karnath & Thier 2012). However, the *supramarginal gyrus* has also been discussed as a proprioceptive region (cf. Ben-Shabat et al. 2015). *Proprioception* is to be distinguished from *interoception* and describes the ability to sense bodily movement and position in space. It is created through continuous feedback from sensory receptors in the skin, joints and muscles during movements. These proprioceptive signals contribute to the sense of *body ownership*. However, our findings go further by linking *body ownership* with *interoception*. Thereby, the sense of *bodily self-awareness* emerges. *Bodily self-awareness* is defined as the feeling that conscious experiences are bound to the self and are experiences of a unitary entity (cf. Blanke 2012). For this purpose, feeling the body in space is necessary (*proprioception*), but beyond that we must have the experience of owning a body and have agency over our actions (*body ownership*) and we further need to sense the visceral signals coming from our own body (*interoception*).

Apart from the examples presented at the beginning, *bodily self-awareness* is clinically relevant in cases of eating disorders, for instance. Particularly in anorexia nervosa, a dysfunctional bodily perception constitutes a central aspect of this condition. Remarkably, and in line with our findings, this disorder is also associated with impaired interoceptive abilities (cf. Kaye, Fudge & Paulus 2009). Given that the etiology and neurobiology of anorexia nervosa is still poorly understood, an understanding that brings a disturbance of the interoceptive system and therefore an impairment of the *bodily self-awareness* into focus seems promising for novel therapeutic approaches.

Another interesting clinical connection regarding *bodily self-awareness* arises in conditions of schizophrenia. From a constructivist viewpoint, psychosis can be explained as the result of reality constructions that deviate from those of the social context in an incomprehensible way. Depending on whether the deviation is related to the description or the explanation of phenomena, symptoms arise that can be classified either as hallucinations or paranoia (cf. Simon 2000). Following this theory, observations imply a distinction between a relevant object and its environment. Deviant, psychotic constructions of reality would then occur when distinctions are drawn that are not socially accepted. In relation to *bodily self-awareness*, this would apply if the bodily boundaries are defined to not coincide with the boundaries of the skin. In doing so, one is unable to distinguish whether the voices being heard come from inside or outside the body, or whether something is seen in front of the inner eye or in the outer world.

In summary, *bodily self-awareness* – the awareness of one's own body – is not just an epiphenomenon of the conscious mind. It is rather a property of highly developed primates to successfully adapt to exteroceptive as well as interoceptive events. Our study highlights this by identifying the *supramarginal gyrus* as a cortical convergence region for interoceptive and exteroceptive information in order to build the sense of *bodily self-awareness*. Thereby, we showed that the »I« of conscious bodily experience (*bodily self-awareness*) most likely requires the sensation of owning a body and having agency over our actions (*body ownership*) and moreover needs sensing of our own bodily signals (*interoception*).

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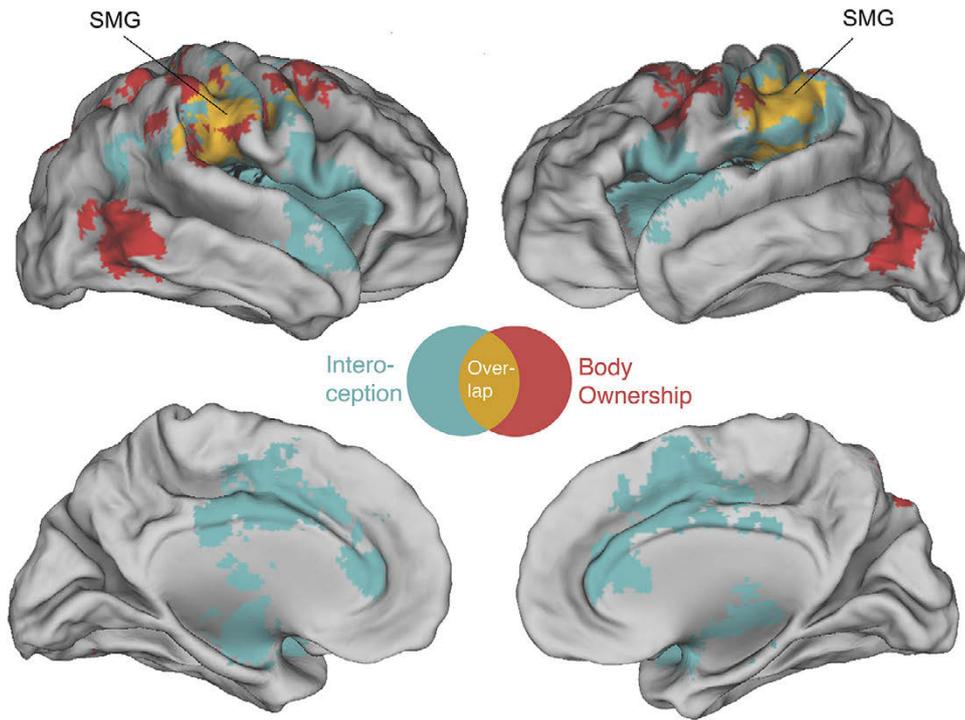


Figure 1. Results of the meta-analyses on interoception and body ownership (Salvato et al., 2020). Areas significantly activated (family-wise error rate corrected at $p < .05$) by body ownership (red) and interoception (light blue) tasks are displayed on a brain template. The overlapping voxels are shown in yellow. SMG = supramarginal gyrus.

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