

Relationship between rubber hand illusion and interoceptive awareness



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When an artificial hand is placed in a position compatible with the participant's own posture, i. e. a position that is plausible anatomically with regard to the participant's body, then the combination of visual input from the rubber hand and tactile stimulation to the participant's hidden hand produces the feeling that the rubber hand is part of the body in around half of participants. The incidence of the illusion as well as its intensity is substantially reduced when the visual and tactile stimuli are applied asynchronously, so that the feeling on the hand is not matched by what the participant sees on the rubber hand. This reduction also occurs when the rubber hand is put in a posture that is anatomically implausible (e. g. Tsakiris & Haggard, 2005).

The term 'interoception' was coined by Charles Sherrington (1907) in the same paper that he introduces the terms proprioception and exteroception. In the original definition, the term referred solely to visceral sensations. However, now it has come to encompass the physiological state of the body as a whole, and the mechanism by which afferent information reaches conscious awareness and affects behaviour, which can occur both indirectly and directly. Interoception relates to the way in which people perceive feelings from their bodies that affect mood, the sense of well-being and even emotions (Cameron, 2002). The field of interoception has been aided greatly by the advent of functional imaging. Thus far, research has been limited in its scope to contribute to the understanding of self-awareness and, by extension, consciousness.

The rubber hand illusion has important implications for interoception because it implies that information from proprioceptors- the

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mechanoreceptors in the hand and arm- can be overridden fairly easily by visual information. However, it is important to remember that it is not visual information alone that the participant is subject to; they are also receiving proprioceptive input to their unseen hand. Ramachandran (2005) suggests that rather than the more cognitive Helmholtzian ‘unconscious inference’ explanation posited by others (e. g. Lackner, 1988), the rubber hand illusion can be explained from a Bayesian perspective. Several (e. g. Alais & Burr, 2004; Ernst & Banks, 2002) have shown that adults are able to integrate information both within and between senses in what appears to be a statistically optimal (Bayes-optimal) fashion. The fact that Bayesian models fit human behavioural results so well fits with the evidence that synchronous stimulation in two modalities can bring about changes in interoception. In a more natural environment, the probability of seeing something in the outside world being stimulated and feeling identical stimulation on a consistent body part is vanishingly unlikely and so it seems unsurprising that the neural machinery that fuses information between the senses is subject to this illusion.

A more recent experiment has shown that both the afferent and efferent elements of the body in motion are able to influence the feeling of ownership (Tsakiris, Prabhu & Haggard, 2006). The authors found that the rubber hand illusion could be elicited solely on the basis of hand movements. In a variation on the methodology, participants had a virtual hand projected to the front of them while their own hand was hidden. Both the participant’s index finger and the same finger of the virtual hand underwent up and down motions, which could be done either actively or passively. When movements

were in synchrony, participants reported that they felt as if their own hand was nearer the virtual hand than when motion was asynchronous as in the classic illusion. Under the passive condition, as in the classic condition, the illusion is a result of integration of visual and proprioceptive information. Conversely, there is also efferent information signalling that the finger is moving in the active condition. One difference between the conditions was that the proprioceptive drift only affected the index finger in the passive condition. The rest of the fingers were not perceived as being closer to the virtual hand. However, in the active condition, proprioceptive drift affected the whole hand. Therefore, the effect was more local when afferent information alone was available, but more global when there was efferent information as well. Tsakiris et al came to the conclusion that efferent information can influence interoception and the sense of bodily ownership by unifying the body into a coherent whole.

One possible argument against the view that the rubber hand illusion shows that visual information can override proprioceptive information is that the participant may simply be speaking metaphorically when they say that they feel as if the rubber hand is part of their body. This problem arises from the fact that measures of the extent of the illusion are based on self report.

Galvanic Skin Response (GSR) studies have examined whether the rubber hand is truly incorporated into the participant's body image. Evolutionarily, it is necessary to protect the body from physical harm, and so threat to the body elicits feelings of anxiety, the withdrawal tendency, and increased autonomic arousal (e. g. Cooke & Graziano, 2003; Kalisch et al, 2005).

Therefore, it seems fair to say that for something to qualify as being part of

the body, the brain's homeostatic mechanisms should react as if it is when it is under threat. This hypothesis has received support from the fact that hitting the table near the false hand with a hammer leads to increased GSR during the rubber hand illusion (Armel & Ramachandran, 2003). There was no change in GSR during the control condition in which the rubber and real hands were stimulated asynchronously.

Ehrsson et al (2007) have gone even further than this and shown using functional Magnetic Resonance Imaging that areas of the brain associated with interoception, i. e. the anterior cingulate cortex and insula are active during the rubber hand illusion. The convexity cortex of the anterior cingulate and cingulate cortex have been shown to become active during both the experience of pain and anticipation of it (e. g. Craig et al, 1996; Wager et al, 2004). The anterior insular cortex has also been shown to become active during pain anticipation, the experience of pain and also pain empathy (e. g. Singer et al, 2004). Furthermore, coactivation of these regions during experiments has been linked to interoceptive awareness and emotional processing (Farrell, Laird & Egan, 2005; Craig, 2003). The authors suggested that the activity they found in response to threat to the rubber hand most likely reflected participants' anxiety as they were elevated more when the participant felt ownership of the rubber hand than when they did not. Significantly, this activity was specific to threats to the body and was not seen in response to empathy for pain or looking at the syringe (which was used to threaten the rubber hand). This is strong evidence that the rubber hand illusion leads to changes in the participant's interoception.

Tsakaris (2010) describes the rubber hand illusion as a model example of how the normal sense of 'embodiment' works, and argues that it can be used to examine how the experience of the body as belonging to the individual comes about, is maintained, and perhaps even how it can be disturbed. He puts forward a neurocognitive model in which body ownership is the result of interactions between current information from all of the senses and internal models regarding the body. This model begins with pre-existing models of the body that are stored in the right temporo-parietal junction. These allow distinction between objects that may be embodied and those that may not. Subsequently, on-line postural and anatomical representations of the body (in the secondary somatosensory cortex) allow modulation of this multisensory information. This in turn allows the visual and haptic co-ordinate systems to be recalibrated in order to respond to current demands of the environment. This is done by the ventral premotor and posterior parietal cortices, which contain neurons that code for recalibration of the hand-centred co-ordinate system. This results in referral of haptic sensation that leads to subjective experiences of body ownership, which arises in the right posterior insula.

Some similar ideas are expressed by de Vignemont. She argues that bodily sensations are experienced through a multimodal spatial representation of one's body. This view leads directly to the prediction that the sense of ownership of the body should be influenced by information in the visual modality, as in the rubber hand illusion. She also points out that proprioceptive information decays very quickly while the hand is stationary, and that it is often vision that dominates the other sensory modalities (e. g.

Welch and Warren, 1986). This provides further support for the idea that the spatial content of haptic sensations should rely more on the visual modality than proprioception. This can account for the fact that when Botvinick and Cohen asked their participants to reach towards the hand that had been stimulated (using their other hand), this motion was displaced toward the rubber hand rather than their unseen hand. This distortion of proprioception and the sense of the location of the body comes from the emphasis on information in the visual modality, which can also account for the subjective feeling of ownership of the hand. This results from the localisation of the haptic information within a representation of the body that has been constructed from the information available to the participant. In the illusion, the descriptive aspect of the haptic sensation is accurate, however, the spatial aspect has been shifted.

Craig (2009) examines the role of the insula in interoceptive awareness in areas as diverse as gastric distension, heartbeat and pain. He identifies awareness of bodily movements (rather than the sense of agency regarding movements) as a possible role for the insular cortex, as well as speech, self recognition and various emotions, describing an 'emotional salience network' in which insular cortical areas feature. He also suggests that the anterior insular cortex plays a role in performance maintenance in which it is put at the heart of the switch to self reflective networks from central executive functioning. The insula is argued to contain representations of the self at every moment in time and to provide comparison between representations at different points in time. The predictive role that this implies may explain the role of the insula in emotions such as anxiety. He also examines the role

of the anterior cingulate cortex in interoception and self awareness, noting its numerous connections with the insular cortex. He also posits an evolutionary theory, wherein the anterior cingulate and anterior insular cortex developed independently, but subsequently came to have more integrated functioning that performed the role of interoception, specifically managing autonomic activity. He argues that this explains the close relationship of the two areas in various neuroimaging studies.

In conclusion, the rubber hand illusion has provided much insight into human interoception. It has revealed the different kinds of information involved in this process by showing how it can be tricked, as well as the flexibility inherent in the system. Neuroimaging studies using the illusion have revealed the mediating brain areas, which in turn leads to tantalising hints about how the conscious sense of the body arises. The experience of ownership of the body may be a significant aspect of self-specificity. This is illustrated by the different ways that multisensory integration and internal models of the body are able to manipulate important psychological and even physical elements of the self, the prime example being the rubber hand illusion. Interoception has important implications for some groups of patients, in particular amputees. The rubber hand illusion has shown how ‘outside objects’ can fairly easily be integrated into the body image. The withdrawal reactions that are elicited from participants are the same in kind to those that arise when replacement limbs are under threat.