CORTEX 104 (2018) 180–192

Available online at www.sciencedirect.com

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Journal homepage: www.elsevier.com/locate/cortex

Special issue: Research report

Interoceptive ingredients of body ownership: Affective touch and cardiac awareness in the rubber hand illusion

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ARTICLE INFO

Article history:
Received 16 November 2016
Reviewed 13 December 2016
Revised 31 January 2017
Accepted 21 April 2017
Published online 1 May 2017

Keywords:
Body ownership
Affective touch
Cardiac awareness
Interoception
Multisensory integration

ABSTRACT

The sense of body ownership represents a fundamental aspect of bodily self-consciousness. Using multisensory integration paradigms, recent studies have shown that both exteroceptive and interoceptive information contribute to our sense of body ownership. Interoception refers to the physiological sense of the condition of the body, including afferent signals that originate inside the body and outside the body. However, it remains unclear whether individual sensitivity to interoceptive modalities is unitary or differs between modalities. It is also unclear whether the effect of interoceptive information on body ownership is caused by exteroceptive 'visual capture' of these modalities, or by bottom-up processing of interoceptive information. This study aimed to test these questions in two separate samples. In the first experiment ($N = 76$), we examined the relationship between two different interoceptive modalities, namely cardiac awareness based on a heartbeat counting task, and affective touch perception based on stimulation of a specialized C tactile (CT) afferent system. This is an interoceptive modality of affective and social significance. In a second experiment ($N = 63$), we explored whether 'off-line' trait interoceptive sensitivity based on a heartbeat counting task would modulate the extent to which CT affective touch influences the multisensory process during the rubber hand illusion (RHI).

We found that affective touch enhanced the subjective experience of body ownership during the RHI. Nevertheless, interoceptive sensitivity, as measured by a heartbeat counting task, did not modulate this effect, nor did it relate to the perception of ownership or of CT-optimal affective touch more generally. By contrast, this trait measure of interoceptive sensitivity appeared most relevant when the multisensory context of interoception was ambiguous, suggesting that the perception of interoceptive signals and their effects on

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http://dx.doi.org/10.1016/j.cortex.2017.04.018

body ownership may depend on individual abilities to regulate the balance of interoception and exteroception in given contexts.

1. Introduction

The sense of body ownership represents a fundamental aspect of the psychological self (Gallagher, 2000). We usually take the ability to identify our body as our own for granted, but empirical research in the past few decades has shown that the sense of body ownership relies on our cognitive ability to combine information about the body originating from different sensory modalities (Tsakiris & Haggard, 2005). More specifically, the integration of different sensory modalities (i.e., multisensory integration) can be defined as the combination or synergy of information originating from two or more sensory channels, leading to unitary, yet not necessarily more accurate percepts than unisensory information (Guest & Spence, 2003; see Maravita, Spence, & Driver, 2003; Stein & Stanford, 2008, for reviews).

One of the most widely used multisensory integration paradigms is the Rubber Hand Illusion (RHI, Botvinick & Cohen, 1998). In its classic version, the illusion relies on synchronous tactile stimulation of a visible rubber hand and of the participant's hidden hand, after which participants typically experience subjective feelings of ownership for the rubber hand ("it feels like the rubber hand is my own hand") and they may perceive the position of their own hand as shifted towards that of the rubber hand (Botvinick & Cohen, 1998). These effects do not occur when the touch is asynchronous and hence are typically explained by a three-way weighted interaction between vision, touch, and proprioception: vision of tactile stimulation on the rubber hand 'captures' the tactile sensation on the participant's own hand, and this visual capture results in a mislocalisation of the felt location of one's own hand towards the spatial location of the visual percept, and corresponding changes in subjective ownership ratings. These bottom-up multisensory integration effects are subject to a number of top-down influences (Tsakiris et al., 2011, for review; see also Ferri, Ardizzi, Ambrosecchia, & Gallese, 2013). Recently, the relation between the two has been modelled according to Bayesian predictive coding schemes, emphasising that perception as a whole is not stimulus-driven, but rather an active process of instantiating neural contexts that allow for the enhanced or attenuated processing of forthcoming sensory events based on preexisting expectations (Friston, 2010). Specifically, the RHI is explained as the attenuation of the weighting of ascending, proprioceptive signals about the actual position of the participant's own arm in order to accept the more plausible (even if illusory) perceptual hypothesis that it is one's own body that receives synchronous tactile and visual information, rather than the alternative hypothesis that another body evokes tactile sensations (Apps & Tsakiris, 2013; Zeller, Litvak, Friston, & Joseph Classen, 2014). Moreover, the experience of owning a rubber hand during the RHI can cause a drop in temperature of the participant's own hand (Moseley et al., 2008), suggesting a down regulation not only of proprioception, but possibly also of the physiological state of one's own arm (see also Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). However, as subsequent studies have failed to replicate this temperature and other related findings regarding the downregulation of sensations from the participants' arm (Guterstam, Petkova, & Ehrsson, 2011; Rohde, Wold, Karnath, & Ernst, 2013; Schütz-Bosbach, Tausche, & Weiss, 2009), further investigations of this measure and the physiological condition of participant's own arm are needed.

However, it is only in the last five years that a handful of studies have explored the role of interoception in multisensory integration and body ownership. This is especially relevant as according to a recent re-classification of the senses, interoception refers to information about the physiological condition of the body, involving sensations from within the body (e.g., relating to cardiac and respiratory functions or digestion) but also from the outside (e.g., temperature, itch, pain, and pleasure from sensual touch) conveyed by a specialised afferent pathway (Craig, 2002). Moreover, interoception is uniquely related to the generation of bodily feelings, informing the organism about its bodily needs (Craig, 2009; Seth, 2013). As such, the impact of interoception is thought to extend beyond homeostatic regulation, and to relate to self-awareness (Craig, 2009; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Damasio, 1994).

Interoceptive sensitivity refers to paradigms that quantify individual differences in behavioural performance, such as the Heartbeat Counting Task (Schandry, 1981), which entails participants silently counting their own heartbeat in specified time windows without taking their pulse or feeling their chest (see Garfinkel, Seth, Barrett, Suzuky, & Chritcley, 2015, for a broader discussion on such tasks and their relation to other subjective or metacognitive measures of interoceptive awareness). Tsakiris, Tajadura-Jiménez, and Costantini (2011) showed that individual differences in cardiac interoceptive sensitivity can affect the RHI. In particular, participants with low interoceptive sensitivity, as measured by an 'off-line' (i.e., administered prior to and independently of the RHI task) heartbeat counting task, reported a greater subjective experience of ownership for the rubber hand compared to people with high interoceptive sensitivity. Moreover, 'off-line' interoceptive sensitivity seems to predict behavioural and autonomic measures of temporary change in body ownership, namely increased proprioceptive drift and a drop in skin temperature of the real hand (Tsakiris et al., 2011). These studies suggest that individuals who can perceive their own interceptive signals with greater accuracy are less susceptible to the down-regulating effects of multisensory integration on