Interoceptive Ingredients of Body Ownership: Affective Touch and Cardiac Awareness in the Rubber Hand Illusion

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

Keywords: body ownership; affective touch; cardiac awareness; interoception; multisensory integration

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, 2011, for review; see also Ferri et al., 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, 2014; Zeller et al., 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, Olthof, Venema, Don, Wijers 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 et al., 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 (Damasio, 1994; Critchley, Wiens, Rotshtein, Öhman & Dolan, 2004; Craig, 2009).

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, Suzuki & Chritcley, 2015, for a broader discussion on such tasks and their relation to other subjective or metacognitive measures of interoceptive awareness). Tsakiris and colleagues (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, Tajadura-Jiménez & Costantini, 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 both proprioception and the physiological state of one's own body.

However, the relationship between interoception and body representation has been investigated also in the context of the virtual body illusion (Aspell et al., 2013) and virtual RHI (Suzuki, Garfinkel, Critchley & Seth, 2013). In both studies, visual feedback of participants' own heartbeat was provided 'on-line' (i.e. during the virtual reality tasks) by means of a flashing virtual body or hand in synchrony or out-of-synchrony with the participants' own heartbeats, with the synchronous condition increasing self-identification with the virtual body (Aspell et al., 2013) and embodiment of the rubber hand (Suzuki et al., 2013), respectively. Thus, somewhat contrary to the findings of Tsakiris and colleagues, when interoceptive signals are artificially provided also in the visual domain, vision seems capable of 'capturing' interoception, leading to enhanced down regulation of proprioception as in the classic RHI paradigm. Nevertheless, it remains unclear whether individuals with greater 'off-line' interoceptive sensitivity would be less susceptible to these visual effects, given their greater ability to perceive cardiac signals 'from within', or on the contrary, whether they would be more susceptible to these effects, given their ability to better regulate how much attention they attribute to interoception based on context (see Fotopoulou, 2013; Decety & Fotopoulou, 2015; Ainley, Apps, Fotopoulou & Tsakiris, 2016, for the wider theoretical context of this hypothesis). To our knowledge, no study has assessed the relationship between 'on-line' and 'off-line' interoception during the RHI across different interoceptive modalities.

Importantly, the above studies on the role of interoception in body ownership have almost exclusively examined cardiac awareness. As there are currently only a handful of studies on whether sensitivity to cardiac signals predicts interoceptive sensitivity across other modalities (e.g. Herbert, Muth, Pollatos & Herbert, 2012; Weiss, Sack, Henningsen & Pollatos, 2014; but see Werner, Duschek, Mattern & Schandry, 2009; Garfinkel, Manassei, Hamilton-Fletcher, In den Bosch, Critchley & Engels, 2016), the results of such studies cannot easily be generalised to all interoceptive modalities. Moreover, the ecological validity of providing 'on-line' visual or auditory feedback of interoceptive modalities that are not habitually experienced via such exteroceptive modalities (e.g. heartbeat related flashing of virtual bodies or hands) may be low, particularly in the context of multisensory integration tasks. By contrast, interoceptive modalities such as cutaneous pain or affective touch, whose stimuli are habitually located outside the body, can be manipulated 'on-line' with greater ecological validity.

In particular, a type of sensory pleasure on the skin is thought to be coded by specialised, unmyelinated C tactile (CT) afferents, which maximally respond to low-pressure, slow, caress-like tactile stimulation delivered at velocities between 1 and 10 cm/s (Löken, Wessberg, Morrison, McGlone & Olausson, 2009). These fibres are present only in the hairy skin of the body, and their activation linearly correlates with subjective reports of pleasantness (Löken et al., 2009). The discovery of a phylogenetically new primate lamina I spinothalamocortical pathway that conveys signals from small-diameter primary afferents from most tissues of the body, has led to some neuroscientists proposing a reclassification of the senses and an expansion of the term interoception. Specifically, CT afferents might take a distinct ascending pathway from the periphery to the posterior insular cortex (Olausson, Lamarre, Backlund, Morin, Wallin et al., 2002; Morrison, Björnsdotter & Olausson, 2011; but see Gazzola, Spezio, Etzel, Castelli, Adolphs et al., 2012 for evidence about concurrent activations of primary somatosensory cortices). Thus, key sensations from the body as such pain, itch, temperature and *affective touch* have been re-classified as interoceptive feelings and clearly separated from other discriminatory, exteroceptive sensations, such as non-affective touch. While several researchers continue to use the term interoception in its classic meaning, in this manuscript we define interoception according to this new reclassification which we think offers an important new perspective on homeostatic and affective regulation (Craig, 2002; Gentsch et al., 2016; Fotopoulou & Tsakiris, 2017).

Slow, caress-like touch activates both the CT system and other tactile modalities; in contrast, fast touch does not activate the CT afferents system to the same degree. Hence, comparing these two velocities is a way to make inferences about the involvement of the CT system in the perception of touch and the body more generally. In addition to this specialised, bottom-up interoceptive pathway, humans appear to be able to perceive slow, gentle touch as more pleasant than faster touch by vision alone and presumably due to top-down, learned processes (Morrison et al., 2011; Gentsch, Panagiotopolou & Fotopoulou, 2015). Thus, manipulating the affective properties of touch in both felt and seen modalities in paradigms such as the RHI is both easier and more ecologically valid than using virtual cardiac signals, and may be better suited to characterise the relationship between multisensory integration, interoceptive sensitivity and the physiological regulation of body parts during the RHI.

Indeed, recent studies have found that affective touch can modulate the sense of body ownership in the RHI. In particular, slow, caress-like touch that activates CT afferents optimally can enhance the experience of owning a rubber hand more than fast, emotionally neutral touch that does not cause optimal CT activation (Crucianelli, Metcalf, Fotopoulou & Jenkinson, 2013; Lloyd, Gillis, Lewis, Farrell & Morrison, 2013; van Stralen, van Zandvoort, Hoppenbrouwers, Vissers, Kappelle et al., 2014). Additionally, Lloyd and colleagues (2013) showed that slow/CT-optimal touch enhanced the subjective embodiment of the rubber hand also in the condition when touch was applied to glabrous (non-hairy) skin, known to lack CT afferents (Vallbo, Olausson & Wessberg, 1999). This finding suggests that the observed enhancing effect of affective touch in the RHI could be driven, at least partly, by top-down, learned expectations of sensory pleasure conveyed by the 'seen' slow touch on the rubber hand (Morrison et al., 2011; Gentsch, Panagiotopolou & Fotopoulou, 2015), in the same manner as the virtual cardiac signals led to increased illusory ownership.

Moreover, in this setting, one could test whether individuals with higher versus lower interoceptive sensitivity, as measured by 'off-line' heartbeat perception accuracy, would either be less susceptible to the effects of affective touch on the RHI (as they would be more aware of the CT-related felt pleasure on their own hand, which should reduce the visual capture of touch in the RHI), or on the contrary, would be more susceptible to the illusion, given their greater capacity to regulate the perceptual (attentional) weighting they allocate to interoception depending on contextual factors (see Fotopoulou, 2013; Krahé, Springer, Weinman, & Fotopoulou, 2013; Decety & Fotopoulou, 2015; Ainley et al., 2016). The first hypothesis in turn assumes that cardiac awareness and CT-optimal affective touch perception will be related, so that individuals with greater cardiac awareness will also be more sensitive to perceiving the difference between CT-optimal and CT-suboptimal touch.

This study aimed to test these two hypotheses, and their relation, in two separate experiments. In addition, we aimed to test in an exploratory manner the relation between synchronicity and tactile pleasantness. Synchronous touch in the context of the RHI should be perceived as more pleasant, given its predictability (Joffily & Coricelli, 2013), but to our knowledge no study has examined the relation between the combined effects of synchronicity, CT-optimality and cardiac sensitivity on tactile pleasure.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Seventy-six women, aged 18 and over (*M* = 22.07, *SD* = 2.75), were recruited via the University of Hertfordshire research participation system. Participants received course credit or £5 for participating. Exclusion criteria included: being left handed or having a personal history of neurological or psychiatric disorders. The study was approved by an institutional ethics committee and conducted in accordance with the Declaration of Helsinki.

2.1.2. Design and statistical analysis

This experiment aimed to explore the role of individual differences in interoceptive sensitivity, operationalised as the degree of accuracy on a heartbeat counting task (Schandry, 1981), on subjective ratings of sensory, tactile pleasantness elicited by slow (CT-optimal, 3 cm/s) versus fast (CT sub-optimal, 18 cm/s) tactile stimulation (the touch task).

All statistical analyses were conducted in Stata 13 (StataCorp, 2013). As repeated measures (stroking velocity) were nested within individuals, we specified a multilevel model with pleasantness rating as the outcome variable, stroking velocity condition (slow vs. fast) as a categorical predictor and interoceptive sensitivity (mean-centred) as a continuous predictor, and included the interaction term. In addition, we computed a pleasantness rating difference score (slow minus fast) and conducted a regression analysis to examine whether interoceptive sensitivity predicted the difference in perceived pleasantness of slow vs. fast touch. We controlled for age, BMI and baseline heart rate in both analyses.

2.2.Materials and Procedures

Heartbeat Counting Task: Participants sat at a table in front of a 40 cm x 40 cm white screen with a fixation cross at the centre of the screen and about 60 cm distance from the participant. A heart rate baseline reading was obtained over a three minute period before the beginning of the counting task. The participant's heart rate (HR) was recorded using a Biopac MP150 Heart Rate oximeter, attached to the participant's non-dominant index finger and connected to an Apple Mac laptop with AcqKnowledge software (version 3.9.2), which recorded the number of heartbeats after pre-set time intervals using the 'count peaks' function. To reduce the possibility that participants would perceive the pulsations in fingers due to the pulse oximeter, attention was paid to ensuring a comfortable but not over-tight fit of the finger cuff. The well-established heartbeat counting task (Schandry, 1981) was employed as follows: upon hearing an audio start cue participants were instructed to begin counting their heartbeat until they heard an audio stop cue. They were instructed not to take their pulse and/or feel their chest; they were only allowed to "feel" the sensation of their heart beating. They did not receive any feedback regarding their performance. Following the audio stop cue, participants verbally reported the number of heartbeats counted and a rest period of 30 seconds was given before the next interval began. Participants received no information about the interval lengths (25, 45 and 65 seconds), and these were presented in a random order.

Touch Task: Participants were first familiarised with the pleasantness rating scale and the touch stimuli. Two rectangles were drawn on the hairy skin of the participants' left forearm, each measuring 4 cm x 9 cm. To avoid visual feedback of the tactile stimuli, participants placed their left arm with the palm facing down inside a white plastic box (25 x 40 x 25 cm), open on two opposite sides to allow the experimenter to deliver the touch. Tactile stimulation (i.e. stroking) was administered for three seconds using a soft cosmetic make-up brush (Natural hair Blush Brush, N◦7, The Boots Company) at two different velocities: one CT-optimal (3 cm/s) and one not CT-optimal (18 cm/s). Tactile stimulation, of four trials of each velocity in a random order, was alternated between the rectangles drawn on the skin, to minimise habituation (Crucianelli et al., 2013). After each brush stroke, participants verbally rated the pleasantness of the touch using a scale from 0 (not at all pleasant) to 100 (extremely pleasant), which was presented visually.

The order of the heartbeat counting task and the touch task was counterbalanced across participants.

2.3.Results

Interoceptive sensitivity

Interoceptive Sensitivity (IS) was calculated using the following formula (Schandry, 1981; Pollatos, Kurz, Albrecht, Schreder, Kleemann et al., 2008):

$$1/3 \sum (1 - (\lvert \text{recorded heartbeats} - \text{counted heartbeats} \rvert) / \text{recorded heartbeats})$$

The Interoceptive Sensitivity scores obtained following this transformation vary between 0 and 1, with higher scores indicating a better estimation of the heartbeats (i.e. smaller differences between estimated and actual heartbeats). The mean Interoceptive Sensitivity score was 0.67 (SD = 0.19) in the present sample.

Pleasant touch

As expected, stroking velocity significantly predicted pleasantness ratings, $b = 14.68$, $SE = 2.03$, $p < .001$, with slow velocity stroking being rated as more pleasant ($M = 62.64$, $SE = 2.35$) than fast velocity stroking ($M = 47.96$, $SE = 2.35$). However, interoceptive sensitivity did not predict pleasantness ratings, $b = 20.02$, $SE = 12.73$, $p = .116$ and the interaction between stroking velocity and interoceptive sensitivity was also non-significant, $b = -1.09$, $SE = 10.90$,

p = .920. Furthermore, interoceptive sensitivity did not predict the difference in perceived pleasantness to slow vs. fast touch, b = -3.78, SE = 11.03, p = .733.

2.4. Experiment 1 Discussion

Experiment 1 tested the hypothesis that cardiac awareness and CT-optimal, affective touch perception would be related, such that higher sensitivity to one's heartbeat would be associated with greater sensitivity to perceiving the difference between CT-optimal and CT suboptimal touch. Our results did not confirm this hypothesis, as cardiac sensitivity did not predict pleasantness sensitivity to CT-optimal tactile stimulation. This finding goes against the assumption that interoceptive sensitivity is a unitary trait (Herbert et al., 2012; Weiss, Sack, Henningsen & Pollatos, 2014; but see Werner, Duschek, Mattern & Schandry, 2009). Instead, one interpretation of our results may be that as individuals may have differences in their sensitivity to exteroceptive modalities (e.g. visual acuity may not predict auditory acuity), they may also have differences in their sensitivity to interoceptive modalities. Future studies would need to establish if such differences relate to peripheral receptor sensitivity, spinal cord mechanisms, or central processes.

Alternatively, our findings may suggest that cardiac sensitivity as measured by a heartbeat counting task and pleasantness sensitivity to CT-optimal tactile stimulation as measured by a rating task may be subject to different demand characteristics. Previous studies have indeed found that individuals differ in their cardiac awareness, depending on whether this is measured by heartbeat counting tasks, questionnaires or metacognitive measures derived by examining the relation between heartbeat counting accuracy and confidence ratings (Garfinkel et al., 2015). Similarly, the particular speeds, body sites and word labels used to assess sensitivity to CT-optimal stimulation have been known to lead to differences within subjects (Guest, Dessirier, Mehrabyan, McGlone, Essik et al., 2011; Gentsch et al., 2015), and it remains unclear to what extent the pleasantness ratings following CT-optimal stroking are explained by bottom-up CT-sensitivity and to what degree top-down mechanisms contribute to such ratings. Indeed, in recent work on interoceptive modalities such as cardiac awareness and pain, we have argued that interoceptive sensitivity can be best conceived as the attention or salience (precision in the terminology of an influential neurocomputational model; Friston, 2010) that individuals are able to allocate to interoceptive as opposed to exteroceptive modalities depending on context (see Fotopoulou, 2013; Krahé et al., 2013; Decety & Fotopoulou, 2015; Ainley et al., 2016). In the following experiment, to disentangle some of these possibilities, as well as to address our hypotheses regarding the role of cardiac awareness and affective touch to multisensory integration and body ownership (see Introduction), we tested the perception of a third tactile velocity, namely 9 cm/s. This velocity is within the CT-optimal range, but nevertheless is not typically perceived as maximally pleasant and it is used less spontaneously in intimate social interactions (Croy, Luong, Triscoli, Hofmann, Olausson et al., 2016). Although Löken et al. (2009) did not investigate 18cm/s stroking velocity, their data shows that at about 9 cms/s pleasantness ratings are starting to be lower than the optimal velocities of about 3cm/s (see supplementary materials in Löken et al., 2009). Moreover, in Crucianelli et al. (2013; 2016) and even more comprehensively in Gentsch et al. (2015), we presented data to show that participants rated touch at a velocity of 18cm/s as significantly less pleasant than touch at CT-optimal velocities of 3 cm/s and 9 cm/s. A velocity which is between 3 cm/s and 18 cm/s is thus considered to activate the CT system to an intermediate degree and is thus assumed to be affectively more 'ambiguous'.

We thus expected that sensitivity to such a 'borderline' velocity may be better related to interoceptive sensitivity as measured by a heartbeat counting task that requires attention to bodily signals (heartbeats) that are not habitually focused upon (Ainley et al., 2016).

3. <u>Experiment 2</u>

3.1. Methods

3.1.1. Participants

Sixty-nine right-handed women participated in the experiment in exchange for University credit or a £6 financial compensation. Six participants were later excluded from the analysis because we could not verify that they followed the experimental instruction correctly (i.e. they seemed to use the rating scale in an inverse manner). Thus, the final sample comprised 63 participants with a mean age of 24.03 years (*SD* = 6.48). Institutional ethical approval was obtained and the experiment was conducted in accordance with the Declaration of Helsinki.

3.1.2. Design and Statistical analysis

This experiment tested the hypothesis that individuals with higher interoceptive sensitivity, as measured by cardiac awareness, would be less susceptible to the effects of affective touch on a Rubber Hand Illusion (RHI) task. We first administered the baseline heartbeat counting task, followed by a RHI task. The latter had a within-subjects design, with repeated measures of stroking velocities to the participant's arm and a visible rubber arm in synchrony at three levels: 'Slow' = the most CT-optimal velocity of 3 cm/s vs. 'Borderline' = a velocity falling just within the CT-optimal range 9 cm/s vs. 'Fast' = a faster, CT-sub-optimal velocity of 18 cm/s (Löken et al., 2009; Ackerkey, Backlund Wasling, Liljencrantz, Olausson, Johnson et al., 2014). An asynchronous control condition was also included using only the borderline velocity in order to assess the role of synchronicity in multisensory integration and the RHI. The order of conditions was randomised across participants.

Dependent variables comprised: (1) An embodiment questionnaire (Longo, Schüür, Kammers, Tsakiris & Haggard, 2008) used to capture the subjective experience of rubber hand ownership (13 statements rated on a 7-point Likert-type scale; -3 = strongly disagree, +3 = strongly agree) by means of vision alone (*visual capture of ownership* measure); (2) The same embodiment questionnaire (Longo et al., 2008) was administered pre-stroking and post-stroking, and the difference was calculated to obtain a measure of subjective *'embodiment change'* due to visuo-tactile integration. This questionnaire is composed of 4 sub-components: ownership, location, agency and affect. We also recorded (3) the proprioceptive drift, defined as the degree to which the hand was perceived to be closer to the rubber hand after the stroking. In each condition, the value corresponding to the actual position of the participant's index finger was subtracted from the value corresponding to *the felt* position (see Materials and Procedures below and Figure 1c). This procedure was repeated before ('pre' value) and after ('post' value) vision of the hand and subsequent stroking, and the difference was calculated to obtain a measure of '*proprioceptive drift'* due to multisensory integration. In addition, (4) *temperature change* was measured, defined as the difference in skin temperature of the actual left hand before and after multisensory integration. Following the procedure of Moseley et al. (2008), we checked the temperature in three different locations on the hand (Figure 1b). An average of these three measurements was considered as the final hand skin temperature and used for the calculation of temperature change. (5) Lastly, a subjective *pleasantness rating* (101-point rating scale; 0 = not at all pleasant, 100 = extremely pleasant) of stroking per condition was used to assess the tactile pleasantness of each condition.

We first examined whether interoceptive sensitivity was associated with visual capture of ownership, which is the extent to which participants acquired ownership over the rubber hand only by means of visual feedback. As in Experiment 1, repeated measures (stroking conditions) were nested within individuals. Thus, for outcome variables embodiment change, pleasantness rating, proprioceptive drift and temperature change separately, we again specified multilevel models with (dependent on analysis) synchronous stroking (slow vs. borderline vs.

fast) or stroking mode (borderline synchronous vs. borderline asynchronous) as a categorical predictor. In each model, interoceptive sensitivity (mean-centred) was entered as a continuous predictor, and we also included the interaction term. For analyses including synchronous stroking (three levels) as the categorical predictor, Wald tests were conducted to test simple and composite linear hypotheses about the parameters of the model. Significant interactions were followed up to examine differences between stroking conditions at low (minus 1SD), moderate (mean) and high (plus 1SD) continuous interoceptive sensitivity scores.

3.2.Materials and Procedures

Heartbeat Counting Task: The same materials and procedures as in Experiment 1 were used, with the exception that this task was always administered before the RHI task.

Rubber Hand Illusion Task: The RHI was performed using a black, wooden box measuring 34 cm x 65 cm x 44 cm to control visual feedback of the participants' arm and the rubber hand during the experiment (see Figure 1d). Participants sat at a table and the box was placed approximately 15 cm in front of the participant's torso, with the centre of the box in alignment with the participant's left shoulder. The box was divided into two equal parts by a perpendicularly placed piece of opaque glass. Two circular holes (14 cm in diameter) on either side of the box allowed the participant and experimenter to place their arms inside; the left half of the box accommodated the participant's left forearm and hand, and the right half the rubber hand/arm. A wooden lid prevented visual feedback of the participant's own arm. The top side of the box on the right was uncovered, allowing direct vision of the rubber forearm and hand. The participant also wore a black cape to occlude vision of the proximal end of the rubber arm and participant's left arm.

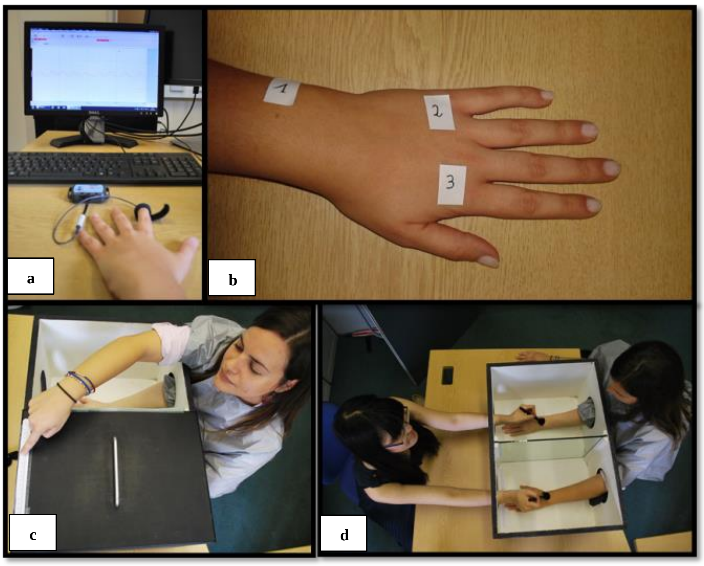


Figure 1. Materials and experimental procedure. **(a)** The Biopac pulse oximeter was attached to the participant's non-dominant index finger. **(b)** Sites at which the skin temperature was recorded on the participant's left hand before and after the stroking. **(c)** Procedure to record the proprioceptive drift. Participants were asked to close their eyes and indicate with their right hand using the ruler the position where they felt the location of their left index finger to be inside the box. This procedure was repeated before and after each condition of the RHI. **(d)** To induce the RHI, the participant's left hand (usually hidden inside the box) was synchronously brushed with a rubber hand placed in front of the participant's view.

Prior to the RHI, participants were familiarised with the general procedures and all rating scales (see section Design and Statistical Analysis above). Two adjacent stroking areas, each measuring 9 cm long x 4 cm wide were identified and marked with a washable marker on the hairy skin of the participants' left forearm (wrist crease to elbow, McGlone, Olausson, Boyle, Jones-Gotman, Dancer et al., 2012). Tactile stimulation was alternated between these two areas to minimise habituation (Crucianelli et al., 2013) because CT fibers are easily fatigued (Vallbo et al., 1999). The corresponding stroking area was touched on the rubber hand in all instances.

In each condition, the experimenter asked the participant to place her left hand (palm facing down; fingers pointing forwards) at a fixed point inside the wooden box. Skin temperature was measured at the three sites on the participant's left hand (Moseley et al. 2008) using an infrared thermometer with dual laser targeting (Precision Gold, N85FR) before obtaining a pre-stroking estimate of finger position (see section Design and Statistical Analysis above regarding the measurement of proprioceptive drift) using a tailor's tape-measure placed on top of the box lid. Participants were asked to close their eyes and to indicate on the ruler with their right hand the position they felt their own left index finger to be inside the box (Figure 1c). The experimenter then measured and recorded the actual position of the participant's left index finger. Subsequently, the rubber arm was positioned in front of the participant's body midline in a congruent position. The participant's left arm and the visible arm (on the sagittal plane) were placed at a distance of approximately 25 cm. The participant was then instructed to look at the rubber arm for 15 seconds, before completing the pre-stroking embodiment questionnaire.

The experimenter then sat opposite the participant and stroked the previously identified stroking areas (McGlone et al., 2012) for three minutes using two identical cosmetic make-up brushes (Natural hair Blush Brush, N°7, The Boots Company) at a velocity of either 3 cm/s (slow/pleasant); 9 cm/s (borderline) or 18 cm/s (fast/neutral). In the synchronous conditions, the participant's left forearm and the rubber arm were stroked such that visual and tactile feedback were congruent, whereas in the asynchronous conditions, there was a temporal mismatch between visual and tactile stimulation.

After the stimulation period, temperature and the felt and actual location of the participant's left index finger was again measured following the pre-induction procedure. Participants then completed the post-stroking embodiment questionnaire. Prior to commencing the next condition, they were given a 60s rest period, during which they were instructed to freely move their left hand.

3.3.Results

Interoceptive Sensitivity and Subjective Embodiment of the Rubber Hand

Interoceptive sensitivity (M = 0.67, SD = 0.23) was not associated with *visual capture of ownership*, $r = .05$, $p > .05$. Therefore, interoceptive sensitivity was not related to the propensity to acquire ownership of the rubber hand by vision alone.

Stroking mode (synchronous vs. asynchronous) significantly predicted embodiment change scores, $b = 1.41$, $SE = .21$, $p < .001$. Embodiment change scores were higher for synchronous stroking ($M = 1.30$, $SE = .15$) compared to asynchronous stroking ($M = -0.12$, $SE = .15$), confirming that the procedure was able to elicit the classic RHI. Interoceptive sensitivity did not predict embodiment change scores, $b = -.20$, $SE = .67$, $p = .766$, and the stroking mode by interoceptive sensitivity interaction was non-significant, $b = .37$, $SE = .94$, $p = .697$. Thus, interoceptive sensitivity did not have an effect on embodiment change scores overall, nor on the synchronous condition in particular.

Interoceptive Sensitivity, Affective Touch and Subjective Embodiment of the Rubber Hand

Next, we investigated whether the velocity of synchronous stroking influenced the embodiment change scores (see Figure 2). Velocity significantly predicted embodiment change scores (Wald test χ^2 (2) = 9.47, p = .009). Embodiment scores were highest for borderline (9 cm/s) stroking (M = 1.30, SE = .16), followed by slow (3 cm/s) stroking (M = 1.20, SE = .16) and were lowest in the fast (18 cm/s) stroking condition (M = .91, SE = .16). Bonferroni-corrected pairwise comparisons showed that borderline and fast stroking conditions differed significantly from each other (p = .009), while slow and fast stroking conditions showed trend differences (p = .077) and there were no significant differences (p = .999) between the two velocities within the range of CT optimal activation (slow, 3 cm/s and borderline 9 cm/s).

Interoceptive sensitivity did not predict embodiment change scores, b = .16, SE = .72, p = .822, and the stroking velocity by interoceptive sensitivity interaction was non-significant (Wald test χ^2 (2) = .01, p = .995). Thus, although stroking at CT-optimal versus sub-optimal velocities enhanced subjective embodiment during the RHI, individual differences in interoceptive sensitivity did not modulate the effects of synchronicity on embodiment change scores, nor the effect of velocity on embodiment change scores.

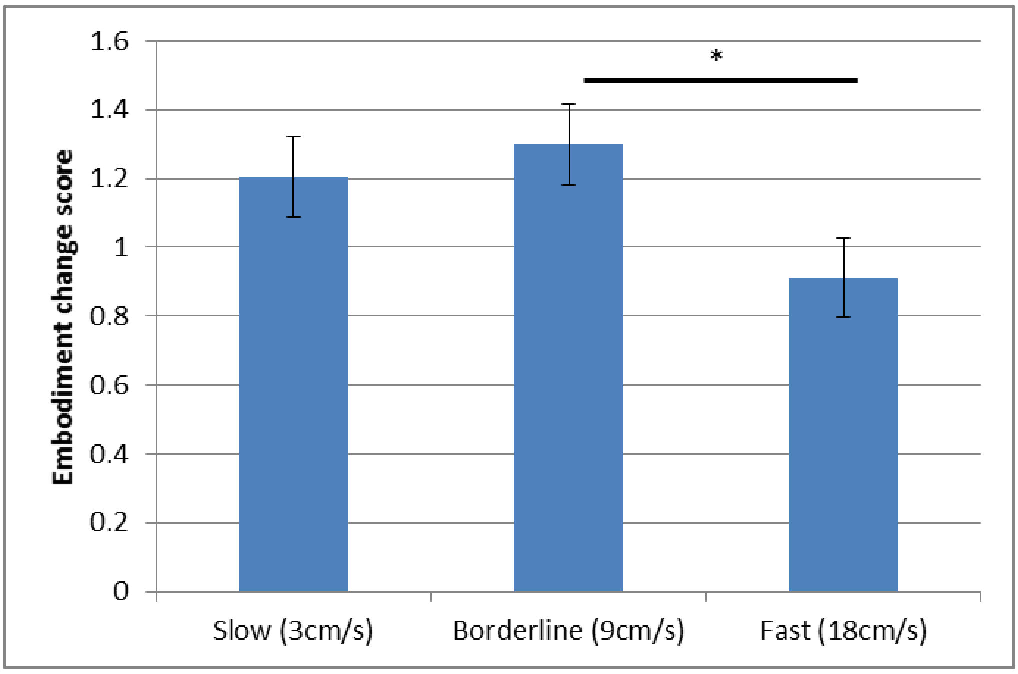
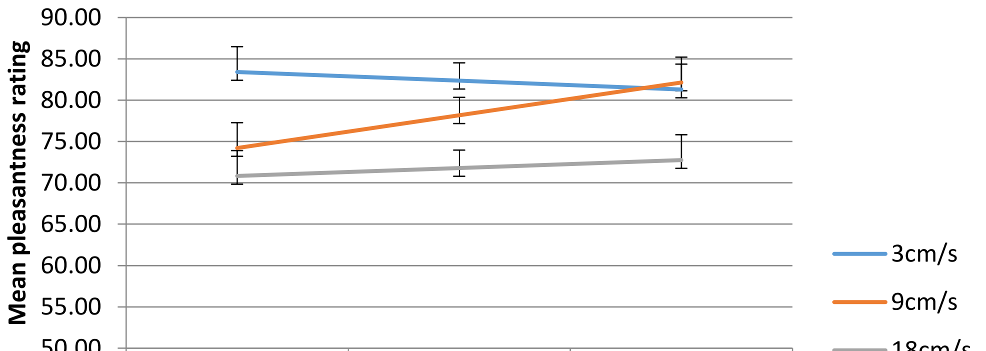


Figure 2. Mean embodiment change scores for the three synchronous stroking velocity conditions. Error bars denote +/- 1 standard error of the mean.

Pleasantness ratings

Stroking velocity significantly predicted pleasantness ratings (Wald test $\chi^2(2) = 45.62$, $p < .001$). As expected, pleasantness ratings were highest for slow (3 cm/s) stroking ($M = 82.35$, $SE = 2.17$), followed by borderline (9 cm/s) stroking ($M = 78.17$, $SE = 2.17$) and were lowest in the fast (18 cm/s) stroking condition ($M = 71.79$, $SE = 2.17$). Bonferroni-corrected pairwise comparisons revealed that all conditions differed significantly from each other (3 cm/s vs. 9 cm/s contrast: $p = .016$; 3 cm/s vs. 18 cm/s contrast: $p < .001$; 9 cm/s vs. 18 cm/s contrast: $p < .001$). Interoceptive sensitivity did not predict pleasantness ratings, $b = 4.22$, $SE = 9.58$, $p = .659$; however, the interaction between stroking velocity and interoceptive sensitivity was significant (Wald test χ^2 (2) = 10.13, $p = .006$; see Figure 3). Slow stroking was perceived as more pleasant than fast stroking across interoceptive sensitivity scores (i.e., at low, moderate and high interoceptive sensitivity scores, *p*s < .001). Slow and borderline stroking conditions differed at low ($p < .001$) and moderate ($p = .008$) but not high ($p = .706$) interoceptive sensitivity scores, and borderline and fast stroking conditions did not differ at low ($p = .132$) but did differ at moderate ($p < .001$) and high ($p < .001$) interoceptive sensitivity scores. Thus, velocity influenced the perceived pleasantness of the touch dependent on interoceptive sensitivity, with higher (vs. lower) interoceptive sensitivity scores predicting greater perceived pleasantness of touch delivered at borderline velocity.



	Low (-1SD)	Moderate (mean)	High (+1SD)
3cm/s	83.41	82.35	81.29
9cm/s	74.21	78.17	82.14
18cm/s	70.84	71.79	72.75

Interoceptive sensitivity

Figure 3. Stroking velocity by interoceptive sensitivity interaction on mean pleasantness rating. Error bars denote +/- 1 standard error of the mean.

Furthermore, stroking mode (synchronous vs. asynchronous) significantly predicted pleasantness ratings, $b = 8.15$, $SE = 1.99$, $p < .001$. Pleasantness ratings were higher for synchronous stroking ($M = 78.17$, $SE = 2.45$) compared to asynchronous stroking ($M = 69.78$, $SE = 2.45$). Interoceptive sensitivity did not predict pleasantness ratings, $b = -3.31$, $SE = 10.80$, $p = .759$, but the stroking mode by interoceptive sensitivity interaction was significant, $b = 20.77$, $SE = 8.76$, $p = .018$ (see Figure 4). There was no difference in perceived pleasantness between synchronous and asynchronous stroking at low levels of interoceptive sensitivity ($p = .191$). However, synchronous stroking was perceived as more pleasant than asynchronous stroking at moderate ($p < .001$) and high ($p < .001$) interoceptive sensitivity scores. Thus, stroking mode influenced the perceived pleasantness of the touch dependent on interoceptive sensitivity, with greater interoceptive sensitivity being associated with greater subjective pleasantness after synchronous compared with asynchronous stimulation.

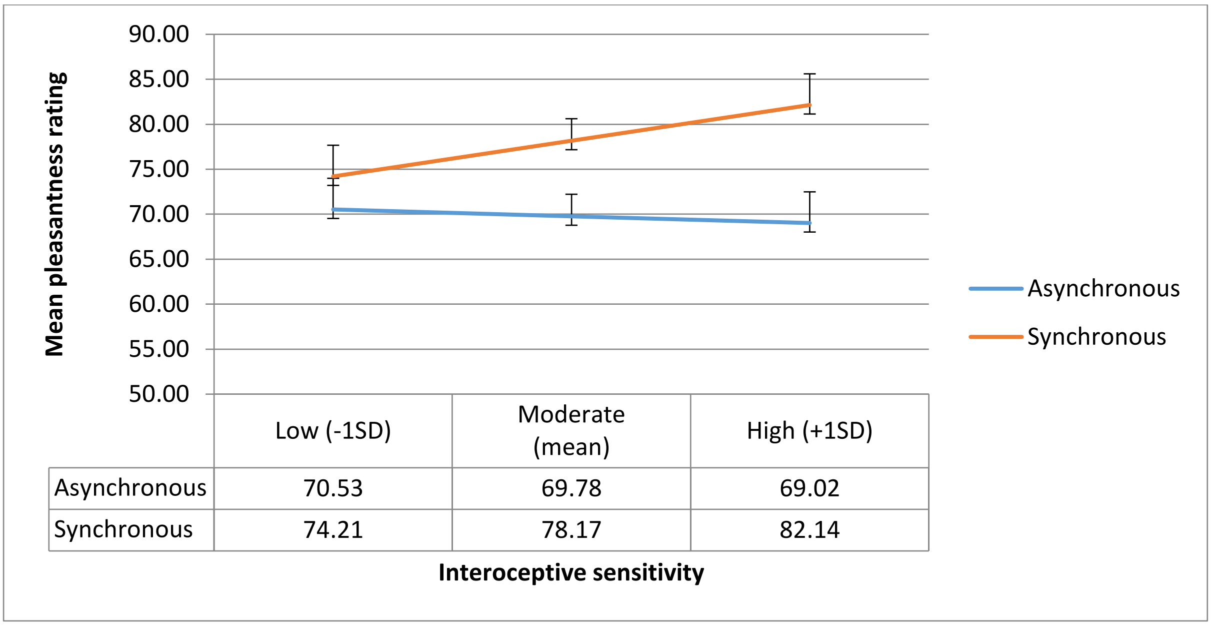


Figure 4. Stroking mode by interoceptive sensitivity interaction on mean pleasantness rating. Error bars denote +/- 1 standard error of the mean.

Proprioceptive Drift and Temperature Change

Neither stroking mode / stroking velocity nor interoceptive sensitivity nor their interaction predicted proprioceptive drift or temperature change (see Table 1).

Table 1. Multilevel modelling results for proprioceptive drift and temperature change

	Stroking mode				**Stroking velocity**			
Outcome	Effect	Unstandardized coefficient (b)	Standard error	p value	Effect	Unstandardized coefficient (b) / Wald test ($\chi 2$)	Standard error	p value
Proprioceptive drift	Stroking mode	-0.52	0.55	0.342	Stroking velocity	$\chi 2$ (2) = 1.09	--	0.578
	Interoceptive sensitivity	1.91	1.72	0.267	Interoceptive sensitivity	-1.52	1.72	0.375
	Stroking mode x interoceptive sensitivity	-2.25	2.44	0.356	Stroking velocity x interoceptive sensitivity	$\chi 2$ (2) = 2.42	--	0.299
Temperature change	Stroking mode	0.20	0.13	0.121	Stroking velocity	$\chi 2$ (2) = 3.88	--	0.144
	Interoceptive sensitivity	-0.07	0.40	0.856	Interoceptive sensitivity	-0.03	0.41	0.939
	Stroking mode x interoceptive sensitivity	-0.09	0.56	0.873	Stroking velocity x interoceptive sensitivity	$\chi 2$ (2) = .07	--	0.964

Note: Stroking mode = Synchronous vs. Asynchronous; Stroking Velocity = Fast vs. Borderline vs. Slow

4. Discussion of Experiment 2 and General Discussion

The aim of this second experiment was to investigate for the first time the interplay between different interoceptive modalities, namely cardiac awareness and affective touch, in body ownership. In particular, it sought to explore whether interoceptive sensitivity would modulate the extent to which affective touch influences the multisensory process taking place during the rubber hand illusion and leading to changes in various measures of ownership and sensory pleasure.

The results confirmed our hypothesis that the illusion would be enhanced by slow, affective touch in comparison to faster, neutral touch, although this was the case only for the subjective (i.e. embodiment questionnaire) measures and not the behavioural proprioceptive measure, consistent with recent studies on the independence of these measures (Rohde, Di Luca & Ernst, 2011; Abdulkarim & Ehrsson, 2016). In addition, in line with recent studies (e.g. Rohde et al., 2013), this study failed to replicate previous findings regarding temperature changes as a consequence of the illusion and other related findings regarding the downregulation of sensations from the participant’s arm (Moseley et al., 2008). This findings are still controversial, and further investigations of this measure and the physiological condition of participant’s own arm are needed. Taken together, these results confirmed previous findings on the facilitatory role of affective touch in subjective ownership (Crucianelli et al., 2013; Lloyd et al., 2013; but see van Stralen et al., 2014, for proprioceptive drift effects). However, as stated in the introduction (see also Lloyd et al., 2013), it remains to be specified whether these effects are caused by bottom-up signals relating to the CT-system or by top-down factors such as learned expectations of sensory pleasure relating to the seen slow touch.

To begin to address this question, we also assessed whether individual differences in interoceptive sensitivity, as measured by ‘off-line’ heartbeat perception accuracy, would moderate the effects of affective touch on the RHI. Contrary to our prediction, interoceptive sensitivity did not moderate the effects of affective touch on the experience of the illusion. Also, in contrast to previous studies we did not find an overall modulatory effect of interoceptive sensitivity on the subjective or behavioral/physiological outcome measures of the rubber hand illusion (Tsakiris et al., 2011; Aspell et al., 2013; Suzuki et al., 2013), or on ownership ratings related to the more simple integration of vision and proprioception (visual capture of ownership, see Martinau et al., 2016). These findings may be explained by methodological challenges relating to measuring interoception, as well as differences between the studies. For example, recent studies have challenged the validity of the heartbeat detection task, given its susceptibility to confounds such as beliefs (Ring & Brener, 1996), contingent feedback and physical exercise (Ring, Brener, Knapp & Mailloux, 2015). Moreover, there were differences in sampling (we tested only women) and the precise methods used to measure proprioceptive drift and temperature changes in the RHI (e.g. we measured the temperature change only on the hidden hand and not in both hands as other studies; Tsakiris et al., 2011; Rohde et al., 2013). However, beyond these differences, our results do not confirm the idea that individuals who can perceive their own interoceptive signals with greater accuracy are less susceptible to the down regulating effects of multisensory integration on proprioception or physiology.

The negative finding that cardiac interoceptive sensitivity did not moderate the effect of affective touch on the RHI may relate to the lack of a more general association between cardiac interoceptive sensitivity and sensitivity to CT-optimal stimulation, as found in Experiment 1. Nevertheless, it should be noted that in a separate analysis on the perception of sensory pleasure during the RHI in Experiment 2, interoceptive sensitivity modulated the effect of velocity on tactile pleasantness during the RHI, but only partly. In particular, while interoceptive sensitivity as measured by heartbeat perception accuracy did not influence pleasantness ratings overall, it did predict pleasantness ratings in a ‘borderline’ (9 cm/s) velocity. Sensitivity to this velocity, which falls within the CT-optimal range but nevertheless is not typically perceived as maximally pleasant, was modulated by heartbeat perception accuracy. Specifically, at low levels of interoceptive sensitivity, this borderline velocity did not differ from sub-optimal stroking, while at high levels of interoceptive sensitivity, stroking at this borderline velocity was perceived to be as pleasant as stroking at the most CT-optimal velocity. This finding suggests that interoceptive sensitivity as measured by heartbeat counting tasks is best related to affective touch perception when some degree of difficulty and disambiguation of interoceptive from exteroceptive signals is required. Furthermore, these findings are in line with evidence showing that individual differences in interoceptive ability (as measured by heartbeat detection) can affect the perceived intensity of emotional experience, but not its valence (Wiens, Mezzacappa & Katkin, 2000).

In addition, it should be highlighted that we did find that cardiac interoceptive sensitivity played a role in another aspect of perceived sensory pleasure. Namely, as we predicted, we found that visuo-tactile synchronicity was experienced as more pleasant than asynchronous stimulation, and interoceptive sensitivity as measured by heartbeat perception accuracy was found to modulate this effect. Specifically, higher and moderate but not lower interoceptive sensitivity scores were predictive of increased perceived pleasantness during visual-tactile synchrony versus asynchrony. Synchronous as opposed to asynchronous touch in the context of the RHI should be perceived as more pleasant, given its predictability (Joffily & Coricelli, 2013), but to our knowledge no study has examined the relation between this effect and cardiac sensitivity. It appears that the higher the cardiac accuracy, the more the confirmation of one's multisensory predictions (the correspondence of the touch they feel and the touch they see on the rubber hand) in an ambiguous context is perceived as pleasant. This finding adds further support for the above idea that interoceptive sensitivity is more relevant to the perception of situations that require some disambiguation. In this case, interoceptive sensitivity seemed to influence the affective perception of a situation in which one's body is receiving tactile stimuli that appear visually to be delivered on a different body. Future studies could thus investigate such 'ambiguous' sensory and multisensory stimuli and determine the role of interoceptive sensitivity as the disambiguating factor in relation to one's top-down predictions regarding body ownership. Taken together, our positive and negative findings regarding interoceptive sensitivity as measured by heartbeat counting tasks suggest that this trait should not be regarded as similar to the subjective perception of interoceptive signals, as classically measured by psychophysical tasks. Instead, interoceptive sensitivity can be best understood as the ability to regulate the (attentional) weighting (or precision in some neurocoputational frameworks, Friston, 2010) individuals allocate to interoception depending on multisensory and other contextual factors (see also Fotopoulou, 2013; Krahé**,** Springer, Weinman, & Fotopoulou, 2013; Decety & Fotopoulou, 2015; Ainley et al., 2016). The particular, multisensory conditions under which such a capacity can determine the sense of body ownership as previous studies suggest (Tsakiris et al., 2011), or only the pleasantness associated with synchronous multisensory stimulation as this study found, remains to be determined.

5. Conclusion

In conclusion, this study found that CT-optimal affective touch, an interoceptive modality of affective and social significance, 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 body ownership may depend on individual abilities to regulate the weight given to interoception versus exteroception in a given ambiguous context.

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