

Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations

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Body-awareness relies on the representation of both interoceptive and exteroceptive percepts coming from one's body. However, the exact relationship and possible interaction of interoceptive and exteroceptive systems for body-awareness remain unknown. We sought to understand for the first time, to our knowledge, the interaction between interoceptive and exteroceptive awareness of the body. First, we measured interoceptive awareness with an established heartbeat monitoring task. We, then, used a multi-sensory-induced manipulation of body-ownership (e.g. Rubber Hand Illusion (RHI)) and we quantified the extent to which participants experienced ownership over a foreign body-part using behavioural, physiological and introspective measures. The results suggest that interoceptive sensitivity predicts the malleability of body representations, that is, people with low interoceptive sensitivity experienced a stronger illusion of ownership in the RHI. Importantly, this effect was not simply owing to a poor proprioceptive representation or differences in autonomic states of one's body prior to the multi-sensory stimulation, suggesting that interoceptive awareness modulates the online integration of multi-sensory body-percepts.

Keywords: interoception; multi-sensory; body-awareness

1. INTRODUCTION

Awareness of one's body is intimately linked to self-identity, the sense of being 'me' [1]. A key question is how the brain integrates different sensory signals from the body to produce the experience of this body as *mine*, known as sense of body-ownership. Converging evidence suggests that the integration of exteroceptive signals related to the body, such as vision and touch, produces or even alters the sense of body-ownership [2]. For example, in the Rubber Hand Illusion (RHI), watching a rubber hand being stroked synchronously with one's own unseen hand causes the rubber hand to be attributed to one's own body, to 'feel like it's my hand' [3]. This feeling of body-ownership can be quantified behaviourally as a drift in the perceived location of one's own hand towards the rubber hand [4], as well as physiologically, as a drop in skin temperature of one's own hand [5].

However, multi-sensory integration conveys information about the body as perceived *from the outside*, and hence, represents only one channel of information available for self-awareness. Interoception, defined here as the sense of the physiological condition of the body, is a ubiquitous information channel used to represent one's body *from within* [6]. A renewed interest in the functional role of basic homeostatic processes [7] has emphasized the primary role of interoception for the representation of one's body from within [6], and for the more general awareness of the 'material me' [8].

While the effects of exteroception on the physiological regulation of the body have been recently documented [5], no study has directly investigated whether interoceptive awareness may influence exteroceptive representations of one's body. We, therefore, sought to understand for the first time, to our knowledge, the interaction between interoceptive and exteroceptive awareness of the body. We combined an interoceptive sensitivity task with a multi-sensory task that evokes a bodily illusion to test whether interoceptive awareness can predict the malleability of body-representations. First, we measured interoceptive awareness with an established heartbeat monitoring task [9]. We, then, used a multi-sensory-induced manipulation of body-ownership (RHI) and we quantified the extent to which participants experienced ownership over a fake hand using behavioural, autonomic and psychometric measures. Our focus was on the relationship between interoceptive awareness and the magnitude of the changes in body-image induced with the RHI.

2. METHODS

(a) *Participants*

Forty-six female neurologically healthy volunteers (mean age 21.5, s.d. 2.8) participated. The study was approved by the Department of Psychology Ethics Committee, Royal Holloway. After giving their informed consent, participants reported their age, height and weight. The reported height and weight were used to calculate the body mass index (BMI) for each participant. Participants were also asked to

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complete the body image questionnaire (BIQ) that assesses body-image dissatisfaction [10].

(b) *Experimental procedure and apparatus*

First, participants performed a heartbeat monitoring task. Heart rate was monitored with a piezo-electric pulse transducer attached to the participant's non-dominant index finger (PowerLab 26T, AD Instruments, UK). Heartbeat perception was measured using the Mental Tracking Method [9] that has been widely used to assess interoceptive awareness, has good test–retest reliability (e.g. 81%) and correlates highly with other heartbeat detection tasks [11]. Participants were instructed to start silently counting their own heartbeat on an audiovisual start cue, and until they received an audiovisual stop cue. After one brief training session (15 s), the actual experiment started. This consisted of four different time intervals of 100 s, 45 s, 35 s and 25 s, presented in a random order across participants. Participants were asked to type in the number of heartbeats counted at the end of each interval. Throughout, participants were not permitted to take their pulse, and no feedback on the length of the counting phases or the quality of their performance was given.

Participants were, then, exposed to the RHI phase. They sat at a table across from the experimenter, with their left hand placed inside a specially constructed box, measuring 36.5 cm in width, 19 cm in height and 29 cm in depth. One hole was cut in front, through which the participant placed their hand; another hole was cut on top, through which the participant could see a life-sized prosthetic left hand; and most of the back side of the box was removed, allowing the experimenter to brush both hands. A black cover (59.5 cm by 29 cm) was connected to the box by two hinges. When the cover was open, the rubber hand could be seen by the participant, but the experimenter was hidden from view; when it was closed, the opposite was true. Participants wore a cloth smock, such that their arms were out of view throughout the experiment.

The RHI phase consisted of two blocks, completed by all participants in a counterbalanced order. At the beginning of each block, the cover was lowered and participants were asked to place their left hand inside the box. A pre-induction proprioceptive location judgement was obtained by asking participants to indicate the felt location of their left index finger. Participants were asked, 'Where do you feel your left index finger is?' and in response, they verbally reported a number on the ruler. They were instructed to judge the position of their finger by projecting a parasagittal line from the centre of their fingertip to the ruler laid across the box top, parallel to their frontal plane. A random ruler offset varied from trial to trial to discourage participants from re-using values from prior trials. Following the pre-induction proprioceptive judgement, skin temperature at the knuckle of the participants' left index finger was measured with an Infrared Thermometer (Maplin, UK). Next, the cover was raised and a 120 s induction phase began in which the index fingers of the rubber hand and the participant's hand were brushed with two identical paintbrushes with a frequency of approximately 1 Hz. In the synchronous condition, the hands were brushed at the same time, while in the asynchronous condition they were brushed 180° out of phase. After 120 s, the cover was lowered and a post-induction temperature measurement was taken, followed by a post-induction proprioceptive location

judgement performed in the same manner as before, while ensuring a random ruler offset that varied from trial to trial was used to discourage participants from re-using remembered verbal labels from prior trials. Participants were then asked to remove their hand from the box and to complete an eight-item questionnaire that assessed their subjective experience during visuotactile stimulation (adapted from [12]). The eight items in the questionnaire were a subset of the questions used in Longo *et al.*'s [12] study. The first five questions were previously shown to form the component of ownership associated with the RHI, and the remaining questions formed the component of location associated with the RHI. The second block of the RHI took place shortly after the completion of the questionnaire, with the same measurements and order of events as described above for the first block. The presentation of the synchronous and asynchronous visuo-tactile blocks was counterbalanced across participants.

3. RESULTS

(a) *Interoceptive sensitivity measure*

Interoceptive sensitivity was calculated as the mean score of four heartbeat perception intervals according to the following transformation (see [9,13]):

$$1/4 \sum (1 - (|\text{recorded heartbeats} - \text{counted heartbeats}|) / \text{recorded heartbeats}).$$

According to this transformation, the interoceptive sensitivity score can vary between 0 and 1, with higher scores indicating small differences between recorded and counted heartbeats (i.e. higher interoceptive sensitivity). The median value of interoceptive sensitivity was 0.64 (s.d. 0.18). Using a median split method, the group of 46 participants were split into two groups of high interoceptive sensitivity (HIGH group, mean heartbeat perception 0.81, s.d. 0.1, $n = 23$) and low interoceptive sensitivity (LOW group, mean heartbeat perception 0.49, s.d. 0.01, $n = 23$).

(b) *BMI and BIQ*

The BMI and BIQ scores were recorded to ensure that there were not between-group differences in the weight (e.g. pathological underweight, see BMI) and perception (e.g. body-image dissatisfaction, see BIQ) of the real body that could potentially confound performance in the interoceptive sensitivity task (see [13]). The mean BMI for the HIGH group was 20.4 kg/m² (s.d. 1.9), and for the LOW group was 21.7 kg/m² (s.d. 2.7), with no significant differences observed between groups ($t_{44} = 1.7$, $p > 0.05$). The mean BIQ [10] score for the HIGH group was 1.80 (s.d. 0.33) and for the LOW group was 2.07 (s.d. 0.33), with no significant differences observed between groups ($t_{44} = -0.58$, $p > 0.05$).

(c) *RHI*

The mean proprioceptive mislocalization prior to the induction period was -1.24 cm (s.d. 3.16) for the HIGH group and -0.82 cm (s.d. 2.59) for the LOW group, and the between-groups difference was not significant ($t_{44} = -0.48$, $p > 0.05$). The absence of a significant difference suggests that both the HIGH and the LOW

groups had comparable proprioceptive representations prior to the induction period.

Proprioceptive drifts were calculated as the difference between the pre-induction proprioceptive judgments and the post-induction judgments. Positive values represent a mislocalization towards the rubber hand. The mean proprioceptive drifts were submitted in a mixed ANOVA, with the within-subjects factor of visuo-tactile stimulation, and the between-subjects factor of HIGH or LOW interoceptive sensitivity. The effect of visuo-tactile stimulation (i.e. synchronous versus asynchronous) on proprioception was significant ($F_{1,44} = 4.52$, $p < 0.05$), as well as the interaction of stimulation by interoceptive group ($F_{1,44} = 4.3$, $p < 0.05$). Independent samples *t*-test were used to compare the proprioceptive drift between the two groups for each visuo-tactile stimulation. Following synchronous visuo-tactile stimulation, the difference in proprioceptive drifts between the HIGH (mean 0.113 cm) and LOW (mean 1.978 cm) groups was significant ($t_{44} = -2.57$, $p < 0.05$, two-tailed). Following asynchronous visuo-tactile stimulation, the difference in proprioceptive drifts between the HIGH (mean 0.391 cm) and LOW (mean -0.108 cm) groups was not significant ($t_{44} = 0.77$, $p > 0.05$). Therefore, the interaction was owing to the two groups differing in the synchronous, but not in the asynchronous, condition.

In addition, to directly compare the two groups, we focused on the part of the proprioceptive drift owing to visual-tactile integration [4]. This integration component, called proprioceptive shift, can be defined as the increase in proprioceptive drift when visual and tactile stimulation are correlated (i.e. synchronous conditions), over and above the drift caused by the same stimuli when they are not correlated (i.e. asynchronous conditions). We calculated these shifts by subtracting the proprioceptive drifts obtained in the asynchronous conditions from the proprioceptive drifts obtained in the synchronous conditions [4]. Figure 1a (left panel) shows the mean proprioceptive shifts of the HIGH (mean -0.27 , s.d. 3.13) and LOW (mean 2.08, s.d. 3.55) groups. Differences between the two groups were significant ($t_{44} = 2.39$, $p < 0.05$, two-tailed). Furthermore, a linear regression analysis (figure 1b, right panel) revealed that lower interoceptive sensitivity predicted larger proprioceptive shifts towards the rubber hand ($r^2 = 0.12$, $b = -6.5$, $p < 0.05$, two-tailed).

The mean skin temperature prior to the induction was 30.95° (s.d. 2.99) for the HIGH group and 30.76° (s.d. 2.78) for the LOW group, and their difference was not significant ($t_{44} = 0.21$, $p > 0.05$). The temperature change was calculated as the difference between the pre-induction and post-induction measurements. The mean temperature changes were submitted in a mixed ANOVA, with the within-subjects factor of visuo-tactile stimulation, and the between-subjects factor of HIGH or LOW interoceptive sensitivity. The interaction of visuo-tactile stimulation by interoceptive group on skin-temperature changes was significant ($F_{1,44} = 4.83$, $p < 0.05$), while the main effects of type of stimulation and group failed to reach significance.

To directly compare the two groups, we focused on the part of the temperature change owing to visual-tactile integration, calculated by subtracting the change in skin temperature obtained in the asynchronous condition

from the change obtained in the synchronous condition. Figure 1b (left panel) shows the mean temperature shifts of the HIGH (mean 0.16° , s.d. 1.36) and the LOW (mean -0.61° , s.d. 0.98) groups. Differences between the two groups were significant ($t_{44} = 2.19$, $p < 0.05$, two-tailed). A linear regression analysis (figure 1b, right panel) revealed that lower interoceptive sensitivity predicted larger decreases in skin temperature ($r^2 = 0.04$, $b = 1.65$, $p < 0.05$, one-tailed, based on an *a priori* hypothesis, see [5]).

The main effect of visuo-tactile stimulation on the averaged ratings of the eight RHI statements, collected after both the synchronous and asynchronous visuo-tactile stimulation phases was significant ($F_{1,44} = 101$, $p < 0.05$), with no between-groups differences (see grand mean in table 1). We also performed a regression analysis that focused on the questionnaire item 'it seemed like the rubber hand was my hand', which has been previously shown to be the largest component loading in the experience of body-ownership during the RHI [12]. Higher affirmative ratings to this ownership statement were predicted by lower interoceptive sensitivity ($r^2 = 0.06$, $b = -3.56$, $p < 0.05$, two-tailed; figure 1c).

4. DISCUSSION

The results show that interoceptive sensitivity predicts the malleability of body-ownership during the RHI manipulation. Indeed, behavioural and autonomic measures of body-ownership malleability following exteroceptive stimulation were significantly predicted by interoceptive awareness, with low interoceptive sensitivity resulting in a stronger sense of body-ownership over a fake hand (i.e. larger proprioceptive drifts and larger skin temperature decrease after synchronous visuo-tactile stimulation). Overall, the magnitude of differences in introspective evidence (RHI statements) was not as strong as the one observed in the behavioural (proprioceptive drift) and autonomic measures (skin temperature). However, the ratings to the ownership question that has been previously shown to have the largest component loading in the phenomenology of the illusion (i.e. 'I felt as if the rubber hand was my own hand', see [12]) were predicted by interoceptive awareness, with lower interoceptive sensitivity scores resulting in higher affirmative ratings to this question.

Could the differences between the two groups be explained by differences in proprioception or autonomic body-states prior to multi-sensory stimulation? The inspection of proprioceptive awareness prior to the visuo-tactile stimulation suggests not, as both groups showed comparable and minimal proprioceptive errors during the pre-induction proprioceptive judgments. The inspection of skin temperature prior to the visuo-tactile stimulation also failed to show any significant difference between groups. Finally, the BIQ ratings that reflect body-image dissatisfaction, again, showed no significant differences between groups, and similarly there were no significant differences in the mean BMI of the two groups, ruling out that any observed differences are owing to differences in the perception or weight of the participant's actual body. Therefore, the observed differences in the behavioural and physiological measures between the two groups following the induction of the RHI reflect the active modulatory role of interoceptive sensitivity in

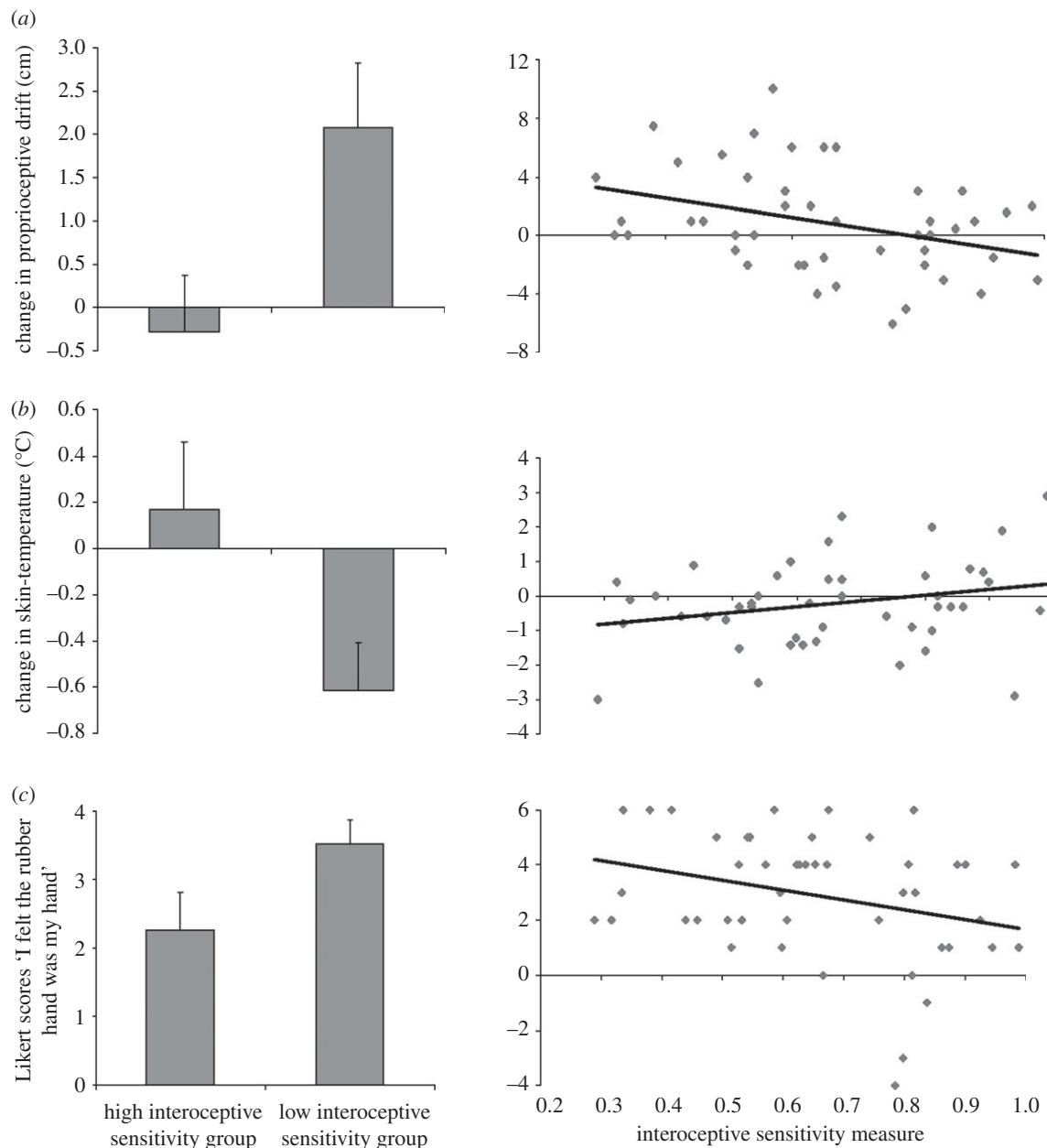


Figure 1. (a) Mean proprioceptive shifts (i.e. difference between synchronous and asynchronous stimulation) and s.e.m. for each group on the left panel, and negative correlation with interoceptive sensitivity on the right panel. (b) Mean skin-temperature shifts (i.e. difference between synchronous and asynchronous stimulation) and s.e.m. for each group, on the left panel, and positive correlation with interoceptive sensitivity measure, on the right panel. (c) Mean difference in subjective ratings (i.e. difference between synchronous and asynchronous stimulation) and s.e.m. for the question 'I felt as if the rubber hand was my own hand' on the left panel, and negative correlation with interoceptive sensitivity measure on the right panel.

the multi-sensory integration of body-related visual and tactile percepts.

The literature on the sense of body-ownership suggests that the main cause of the RHI is the integration of seen and felt touches that occur in close peripersonal space [14]. However, multi-sensory integration in peripersonal hand space by itself is not sufficient to maintain a coherent representation of one's body. Instead, other factors such as the visual form congruency, the anatomical congruency, the volumetric congruency, the postural congruency and the spatial relationship between viewed and felt body-part, modulate the induction of the RHI and the experience of body-ownership (for a review see [2]).

More recently, it has been shown that, in addition to changes on proprioceptive representations of one's body, the experience of ownership during RHI is also accompanied by significant changes in the homeostatic regulation of the real hand. In particular, skin temperature of the real hand decreased when participants experienced the RHI [5], suggesting that cognitive processes that change the awareness of our physical self may in turn change the physiological regulation of the body. The changes caused in the physiological regulation of the body as a result of the experience of body-ownership over a fake hand suggest that processes other than multi-sensory integration may be involved in

Table 1. The mean ratings for each questionnaire item (\pm s.d., italics) across conditions. (Participants rated the statements using a seven-item Likert scale (i.e. +3 indicated that they ‘strongly agreed’, –3 that they ‘strongly disagreed’ and 0 that they ‘neither agreed nor disagreed’, though any intermediate value could be used).)

	‘during the experiment there were times when...’	all participants ($n = 46$)		high interoceptive sensitivity group ($n = 23$)		low interoceptive sensitivity group ($n = 23$)	
		sync.	async.	sync.	async.	sync.	async.
ownership questions	... ‘it seemed like I was looking directly at my own hand, rather than at a rubber hand’	1.08 (0.27)	–1.34 (0.24)	1.00 (0.36)	–1.34 (0.35)	1.17 (0.41)	–1.34 (0.34)
	... ‘it seemed like the rubber hand was part of my body’	0.80 (0.26)	–1.76 (0.22)	0.52 (0.37)	–1.65 (0.33)	1.08 (0.37)	–1.86 (0.29)
	... ‘it seemed like the rubber hand was my hand’	0.97 (0.25)	–1.91 (0.21)	0.52 (0.39)	–1.73 (0.36)	1.43 (0.31)	–2.08 (0.22)
	... ‘it seemed like the rubber hand belonged to me’	0.86 (0.27)	–1.91 (0.21)	0.52 (0.39)	–1.73 (0.36)	1.21 (0.36)	–2.08 (0.22)
	... ‘it seemed like the rubber hand began to resemble my real hand’	1.26 (0.22)	–1.45 (0.23)	1.00 (0.29)	–1.34 (0.35)	1.52 (0.32)	–0.156 (0.27)
location questions	mean ownership questions	1.00 (0.21)	–1.68 (0.19)	0.72 (0.32)	–1.59 (0.32)	1.27 (0.29)	–1.77 (0.23)
	... ‘it seemed like the touch I felt was caused by the paintbrush touching the rubber hand’	1.41 (0.23)	–1.58 (0.23)	1.04 (0.33)	–1.52 (0.34)	1.78 (0.33)	–1.65 (0.31)
	... ‘it seemed like the rubber hand was in the location where my hand was’	0.28 (0.30)	–1.86 (0.23)	0.04 (0.37)	–1.95 (0.33)	0.52 (0.48)	–1.78 (0.37)
	... ‘it seemed like my hand was in the location where the rubber hand was’	0.65 (0.27)	–1.84 (0.23)	0.39 (0.38)	–2.00 (0.33)	0.91 (0.39)	–1.69 (0.34)
	mean location questions	0.78 (0.21)	–1.76 (0.21)	0.49 (0.25)	–1.82 (0.29)	1.07 (0.33)	–1.71 (0.30)
grand mean		0.89 (0.19)	–1.72 (0.19)	0.60 (0.24)	–1.70 (0.29)	1.17 (0.29)	–1.74 (0.25)

generating, maintaining or disrupting the awareness of the bodily self. Given the primacy of interoception for the integration of visceral and somatosensory information as well as for several higher order representations of self [6,15], the present study provides, to our knowledge, the first direct evidence for an active modulatory role of interoception on the experience of the body *from the outside*.

Interoceptive awareness is usually considered a trait, and as such it may also be linked to specific personality traits. For example, previous studies have shown that individuals who score higher on neuroticism-related personality measures show greater interoceptive awareness [16–18]. However, other studies have suggested a link between interoceptive awareness and blood pressure, with untreated newly diagnosed hypertensives showing higher interoceptive sensitivity [19]. Given that blood pressure cannot be considered a trait, this observation questions the characterization of interoceptive awareness as a trait.

Our particular focus here was to consider the effect of interoceptive awareness, as a trait, on the malleability of body-representations. The interpretation we put forward takes into account two key findings. First, the present study shows that interoceptive sensitivity plays an active role while the brain integrates body-related multi-sensory percepts. This modulatory role is further supported by the observation that different levels of interoceptive sensitivity are not linked to different levels of proprioceptive awareness or skin temperature in the absence of multi-sensory stimulation (e.g. prior to it). Second, the right insular lobe has been shown to underpin both interoceptive awareness [18] and the experience of body-ownership during the RHI [20]. Taken together, these observations suggest that the interaction between the perception of the body from *within* and from the *outside* is instantiated in the convergence zone of the right insular lobe.

What can account for the finding that low interoceptive sensitivity results in greater malleability of body-representations following multi-sensory stimulation? There are two possible explanations. First, it might be possible that individuals with low interoceptive sensitivity can allocate more attentional resources to multi-sensory processing because they are less aware of their internal states, resulting in a stronger multi-sensory integration and consequently a stronger RHI. A similar account has been proposed from RHI studies on schizophrenic patients [21,22]. However, it was recently shown that, if anything, high interoceptive awareness positively correlates with better performance in attention tasks [23]. A second explanation would suggest that high interoceptive sensitivity might contribute to an overall more efficient processing of body-related sensory percepts by the co-weighting of both interoceptive and exteroceptive signals during body-perception, in contrast to individuals with low interoceptive sensitivity who might rely mainly on exteroceptive signals. People with high interoceptive sensitivity may display enhanced monitoring of the origins of body-related percepts, and may map these percepts against the available interoceptive representations of the internal milieu. This hypothesis is supported by recent neurophysiological models of interoception and its neural underpinnings. High interoceptive sensitivity might optimize internal predictive models used in sensory self-monitoring [15], consistent with the

functional role of the right insula in integrating bodily, environmental and neural systems to optimize homeostatic efficiency [6] and represent the 'material me' in a global way. On this view, the insular lobe would instantiate a collective representation of one's body produced by the continuous monitoring, weighting and integration of different signals. Interestingly, neurological damage in the right insula results in neurological deficits in sensory self-monitoring [24], such as somatoparaphrenia [25], while a neuroimaging study in neurologically healthy volunteers during the RHI showed that activity in the right mid-posterior insula correlated with the experience of body-ownership [20].

Given the importance of interoception for all bodily feelings (for reviews see [6,15]), and its effect on exteroceptive body-awareness as shown in the present study, affective changes in the explicit representation of one's body (e.g. body-image), may critically rely on the modulatory effect of interoceptive awareness on exteroception of one's body. Intriguingly, anorexic patients display decreased interoceptive awareness [13], and their body-image dissatisfaction is correlated with activity in the right insular lobe [26]. The finding that interoceptive awareness can modulate exteroceptive representations of the body has important implications for impairments of body-awareness where the integration of the body as experienced from *within* and from the *outside* may be severely disrupted. Future studies should clarify the exact weighting of interoceptive and exteroceptive signals in forming a coherent representation of one's body.

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