

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

Journal:	<i>Proceedings B</i>
Manuscript ID:	RSPB-2010-2547.R1
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Tsakiris, Manos; Royal Holloway, University of London, Psychology Tajadura- Jiménez, Ana; Royal Holloway, University of London, Psychology Costantini, Marcello; University "G. d'Annunzio,"
Subject:	Behaviour < BIOLOGY, Cognition < BIOLOGY, Neuroscience < BIOLOGY
Keywords:	interoception, multisensory, body-awareness
Proceedings B category:	Behaviour

SCHOLARONE™
Manuscripts

1 **Just a heartbeat away from one's body: Interoceptive**
2 **sensitivity predicts malleability of body-representations**
3
4
5
6

7 Manos Tsakiris^{1*}, Ana Tajadura- Jiménez¹, Marcello Costantini²
8

9 ¹Department of Psychology, Royal Holloway, University of London

10 ²Laboratory of Neuropsychology and Cognitive Neuroscience, Department of
11 Neuroscience and imaging, University G. d'Annunzio, Chieti, Italy & Institute for
12 Advanced Biomedical Technologies - ITAB, Foundation University G. d'Annunzio,
13 Chieti, Italy.
14

15
16 *Corresponding author: Dr Manos Tsakiris, Department of Psychology, Royal Holloway,
17 University of London, Egham, Surrey, UK, manos.tsakiris@rhul.ac.uk
18
19
20

21 Word Count: 4,253 (incl. references and captions)
22

Running Title: *Just a heartbeat away from one's body* 2

1 **Abstract**

2 Body-awareness relies on the representation of both interoceptive and exteroceptive
3 percepts coming from one's body. However, the exact relation and possible interaction
4 of interoceptive and exteroceptive systems for body-awareness remain unknown. We
5 sought to understand for the first time the interaction between interoceptive and
6 exteroceptive awareness of the body. First, we measured interoceptive awareness with an
7 established heartbeat monitoring task. We, then, used a multisensory-induced
8 manipulation of body-ownership (e.g. Rubber Hand Illusion) and we quantified the extent
9 to which participants experienced ownership over a foreign body-part using behavioural,
10 physiological and introspective measures. The results suggest that interoceptive
11 sensitivity predicts the malleability of body representations, that is, people with low
12 interoceptive sensitivity experienced a stronger illusion of ownership in the Rubber Hand
13 Illusion. Importantly, this effect was not simply due to poor proprioceptive representation
14 or differences in autonomic states of one's body prior to the multisensory stimulation,
15 suggesting that interoceptive awareness modulates the on-line integration of multisensory
16 body-percepts.

17

18

19 Word count: 157

1 Awareness of one's body is intimately linked to self-identity, the sense of being
2 "me" (Bermúdez, Marcel & Eilan, 1995). A key question is how the brain integrates
3 different sensory signals from the body to produce the experience of this body as *mine*,
4 known as sense of body-ownership. Converging evidence suggests that the integration of
5 exteroceptive signals related to the body, such as vision and touch, produces or even
6 alters the sense of body-ownership (Tsakiris, 2010). For example, in the Rubber Hand
7 Illusion (RHI), watching a rubber hand being stroked synchronously with one's own
8 unseen hand causes the rubber hand to be attributed to one's own body, to "feel like it's
9 my hand" (Botvinick & Cohen, 1998). This feeling of body-ownership can be quantified
10 behaviorally as a drift in the perceived location of one's own hand towards the rubber
11 hand (Tsakiris & Haggard, 2005), as well as physiologically, as a drop in skin
12 temperature of one's own hand (Moseley et al., 2008).

13 However, multisensory integration conveys information about the body as
14 perceived *from the outside*, and hence, represents only one channel of information
15 available for self-awareness. Interoception, defined here as the sense of the physiological
16 condition of the body, is a ubiquitous information channel used to represent one's body
17 *from within* (Craig, 2007). A renewed interest in the functional role of basic homeostatic
18 processes (Damasio, 1999) has emphasized the primary role of interoception for the
19 representation of one's body from within (Craig, 2009), and for the more general
20 awareness of the "material me" (Sherrington, 1900).

21 While the effects of exteroception on the physiological regulation of the body
22 have been recently documented (Moseley et al., 2008), no study has directly investigated
23 whether interoceptive awareness may influence exteroceptive representations of one's
24 body. We, therefore, sought to understand for the first time the interaction between
25 interoceptive and exteroceptive awareness of the body. We combined an interoceptive
26 sensitivity task with a multisensory task that evokes a bodily illusion to test whether
27 interoceptive awareness can predict the malleability of body-representations. First, we
28 measured interoceptive awareness with an established heartbeat monitoring task
29 (Schandry, 1981). We, then, used a multisensory-induced manipulation of body-
30 ownership (RHI) and we quantified the extent to which participants experienced
31 ownership over a fake hand using behavioural, autonomic and psychometric measures.

1 Our focus was on the relation between interoceptive awareness and the magnitude of the
2 changes in body-representations induced with the RHI.

3

4 **Methods**

5 *Participants*

6 Forty-six female neurologically-healthy volunteers (mean age 21.5, SD 2.8)
7 participated. The study was approved by the Department of Psychology Ethics
8 Committee, Royal Holloway. After giving their informed consent, participants reported
9 their age, height and weight. The reported height and weight were used to calculate the
10 Body Mass Index (BMI) for each participant. Participants were also asked to complete
11 the Body Image Questionnaire (BIQ) that assesses body-image dissatisfaction (Cash &
12 Szymanski, 1995).

13 *Experimental Procedure and Apparatus*

14 First, participants performed a heartbeat monitoring task. Heart rate was
15 monitored with a piezo-electric pulse transducer attached to the participant's non-
16 dominant index finger (PowerLab 26T, AD Instruments, UK). Heartbeat perception was
17 measured using the Mental Tracking Method (Schandry, 1981) that has been widely used
18 to assess interoceptive awareness, has good test-retest reliability (e.g.81%) and
19 correlates highly with other heartbeat detection tasks (Knoll & Hodapp, 1992).
20 Participants were instructed to start silently counting their own heartbeat on an
21 audiovisual start cue, and until they received an audiovisual stop cue. After one brief
22 training session (15 s), the actual experiment started. This consisted of four different time
23 intervals of 100 s, 45 s, 35 s and 25 s, presented in a random order across participants.
24 Participants were asked to type in the number of heartbeats counted at the end of each
25 interval. Throughout, participants were not permitted to take their pulse, and no feedback
26 on the length of the counting phases or the quality of their performance was given.

27 Participants were, then, exposed to the RHI phase. They sat at a table across from
28 the experimenter, with their left hand placed inside a specially constructed box,
29 measuring 36.5 cm in width, 19 cm in height, and 29 cm in depth. One hole was cut in
30 front, through which the participant placed their hand; another hole was cut on top,
31 through which the participant could see a life sized prosthetic left hand; and most of the

1 back of the box was removed, allowing the experimenter to brush both hands. A black
2 cover (59.5 cm by 29 cm) was connected to the box by two hinges. When the cover was
3 open, the rubber hand could be seen by the participant, but the experimenter was hidden
4 from view; when it was closed, the opposite was true. Participants wore a cloth smock,
5 such that their arms were out of view throughout the experiment.

6 The RHI phase consisted of two blocks, completed by all participants in a
7 counterbalanced order. At the beginning of each block, the cover was lowered and
8 participants were asked to place their left hand inside the box. A pre-induction
9 proprioceptive location judgment was obtained by asking participants to indicate the felt
10 location of their left index finger. Participants were asked, “Where do you feel your left
11 index finger is?” and in response, they verbally reported a number on the ruler. They
12 were instructed to judge the position of their finger by projecting a parasagittal line from
13 the center of their fingertip to the ruler laid across the box top, parallel to their frontal
14 plane. A random ruler offset varied from trial to trial to discourage participants from re-
15 using values from prior trials. Following the pre-induction proprioceptive judgment, skin
16 temperature at the knuckle of the participants’ left index finger was measured with an
17 Infrared Thermometer (Maplin, UK). Next, the cover was raised and a 120-s induction
18 phase began in which the index fingers of the rubber hand and the participant’s hand
19 were brushed with two identical paintbrushes with a frequency of approximately 1 Hz. In
20 the synchronous condition, the hands were brushed at the same time, while in the
21 asynchronous condition they were brushed 180° out of phase. After 120 s, the cover was
22 lowered and a post-induction temperature measurement was taken, followed by a post-
23 induction proprioceptive location judgment performed in the same manner as before,
24 while ensuring a random ruler offset that varied from trial to trial was used to discourage
25 participants from re-using remembered verbal labels from prior trials. Participants were,
26 then, asked to remove their hand from the box and to complete an 8-item questionnaire
27 that assessed their subjective experience during visuotactile stimulation (adapted from
28 Longo, Schuur, Kammers, Tsakiris & Haggard, 2008). The eight items in the
29 questionnaire were a subset of the questions used in Longo et al.’s (2008) study. The first
30 five questions were previously shown to form the component of ownership associated
31 with the RHI, and the remaining questions formed the component of location, associated

Running Title: *Just a heartbeat away from one's body* 6

1 with the RHI. The second block of the RHI took place shortly after the completion of the
2 questionnaire, with the same measurements and order of events as described above for
3 the first block. The presentation of the synchronous and asynchronous visuo-tactile
4 blocks was counterbalanced across participants.

5

6 **Results**

7 *Interoceptive sensitivity measure*

8 Heartbeat perception was calculated as the mean score of four heartbeat
9 perception intervals according to the following transformation (see Pollatos et al., 2008;
10 Schandry, 1981):

$$11 \quad \frac{1}{4} \sum (1 - (|\text{recorded heartbeats} - \text{counted heartbeats}|) / \text{recorded heartbeats})$$

12 According to this transformation, the heartbeat perception score can vary between
13 0 and 1, with higher scores indicating small differences between recorded and counted
14 heartbeats (i.e., higher interoceptive sensitivity). The median value of interoceptive
15 sensitivity was 0.64 (SD 0.18). Using a median split method, the group of 46 participants
16 were split into two groups of high interoceptive sensitivity (HIGH group, mean heartbeat
17 perception 0.81, SD 0.1, n=23) and low interoceptive sensitivity (LOW group, mean
18 heartbeat perception 0.49, SD 0.01, n=23).

19 *Body Mass Index and Body-Image Ideals Questionnaire (BIQ)*

20 The BMI and BIQ scores were recorded to ensure that there were not between-
21 group differences in the weight (e.g. pathological underweight, see BMI) and perception
22 (e.g., body-image dissatisfaction, see BIQ) of the real body, that could potentially
23 confound performance in the interoceptive sensitivity task (see Pollatos et al., 2008). The
24 mean body mass index (BMI) for the HIGH group was 20.4 kg/m² (SD 1.9), and for the
25 LOW group was 21.7 kg/m² (SD 2.7), with no significant differences observed between
26 groups ($t(44)=1.7$, $p>0.05$). The mean BIQ (Cash & Szymanski, 1995) score for the
27 HIGH group was 1.80 (SD 0.33) and for the LOW group was 2.07 (SD 0.33), with no
28 significant differences observed between groups ($t(44)=-0.58$, $p>0.05$).

29 *Rubber Hand Illusion*

30 The mean proprioceptive mislocalization prior to the induction period was -1.24
31 cm (SD 3.16) for the HIGH group and -0.82 cm (SD 2.59) for the LOW group, and the

1 between-groups difference was not significant ($t(44)=-0.48$, $p>0.05$). The absence of a
2 significant difference suggests that both the HIGH and the LOW groups had comparable
3 proprioceptive representations prior to the induction period.

4 Proprioceptive drifts were calculated as the difference between the pre-induction
5 proprioceptive judgments and the post-induction judgments. Positive values represent a
6 mislocalization toward the rubber hand. The mean proprioceptive drifts were submitted in
7 a mixed ANOVA, with the within-subjects factor of visuo-tactile stimulation, and the
8 between-subjects factor of HIGH or LOW interoceptive sensitivity. The effect of visuo-
9 tactile stimulation (i.e., synchronous vs. asynchronous) on proprioception was significant
10 ($F(1,44)=4.52$, $p<0.05$), as well as the interaction of stimulation by interoceptive group
11 ($F(1,44)=4.3$, $p<0.05$). Independent samples t-test were used to compare the
12 proprioceptive drift between the two groups for each visuo-tactile stimulation. Following
13 synchronous visuo-tactile stimulation, the difference in proprioceptive drifts between the
14 HIGH (mean 0.113 cm) and LOW (mean 1.978 cm) groups was significant ($t(44)=-2.57$,
15 $p<0.05$, 2-tailed). Following asynchronous visuo-tactile stimulation, the difference in
16 proprioceptive drifts between the HIGH (mean 0.391 cm) and LOW (mean -0.108 cm)
17 groups was not significant ($t(44)=0.77$, $p>0.05$). Therefore, the interaction was due to the
18 two groups differing in the synchronous, but not in the asynchronous, condition.

19 In addition, to directly compare the two groups, we focused on the part of the
20 proprioceptive drift due to visual-tactile integration (Tsakiris & Haggard, 2005). This
21 integration component, called proprioceptive shift, can be defined as the increase in
22 proprioceptive drift when visual and tactile stimulation are correlated (i.e., synchronous
23 conditions), over and above the drift caused by the same stimuli when they are not
24 correlated (i.e., asynchronous conditions). We calculated these shifts by subtracting the
25 proprioceptive drifts obtained in the asynchronous conditions from the proprioceptive
26 drifts obtained in the synchronous conditions (Tsakiris & Haggard, 2005). Figure 1A (left
27 panel) shows the mean proprioceptive shifts of the HIGH (mean -0.27, SD 3.13) and
28 LOW (mean 2.08, SD 3.55) groups. Differences between the two groups were significant
29 ($t(44)=2.39$, $p<0.05$, 2-tailed). Furthermore, a linear regression analysis (Figure 1B, right
30 panel) revealed that lower interoceptive sensitivity predicted larger proprioceptive shifts
31 towards the rubber hand ($r^2=.12$, $b=-6.5$, $p<0.05$, 2-tailed).

Running Title: *Just a heartbeat away from one's body* 8

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

10 To directly compare the two groups, we focused on the part of the temperature
11 change due to visual-tactile integration, calculated by subtracting the change in skin
12 temperature obtained in the asynchronous condition from the change obtained in the
13 synchronous condition. Figure 1B (left panel) shows the mean temperature shifts of the
14 HIGH (mean 0.16°, SD 1.36) and the LOW (mean -0.61°, SD 0.98) groups. Differences
15 between the two groups were significant ($t(44)=2.19$, $p<0.05$, 2-tailed). A linear
16 regression analysis (Figure 1B, right panel) revealed that lower interoceptive sensitivity
17 predicted larger decreases in skin temperature ($r^2=.04$, $b=1.65$, $p<0.05$, 1-tailed, based on
18 an a priori hypothesis, see Moseley et al., 2008).

19 The main effect of visuo-tactile stimulation on the averaged ratings of the eight
20 RHI statements, collected after both the synchronous and asynchronous visuo-tactile
21 stimulation phases was significant ($F(1,44)=101$, $p<0.05$), with no between-groups
22 differences (see Grand Mean in Table 1). We also performed a regression analysis that
23 focused on the questionnaire item “it seemed like the rubber hand was my hand”, which
24 has been previously shown to be the largest component loading in the experience of
25 body-ownership during the RHI (Longo et al., 2008). Higher affirmative ratings to this
26 ownership statement were predicted by lower interoceptive sensitivity ($r^2=.06$, $b=-3.56$,
27 $p<0.05$, 2-tailed, see Figure 1C).

28 29 **Discussion**

30 The results show that interoceptive sensitivity predicts the malleability of body-
31 ownership during the RHI manipulation. Indeed, behavioral and autonomic measures of

1 body-ownership malleability following exteroceptive stimulation were significantly
2 predicted by interoceptive awareness, with low interoceptive sensitivity resulting in a
3 stronger sense of body-ownership over a fake hand (i.e. larger proprioceptive drifts and
4 larger skin temperature decrease after synchronous visuo-tactile stimulation). Overall, the
5 magnitude of differences in introspective evidence (RHI statements) was not as strong as
6 the one observed in the behavioral (proprioceptive drift) and autonomic measures (skin
7 temperature). However, the ratings to the ownership question that has been previously
8 shown to have the largest component loading in the phenomenology of the illusion (i.e.,
9 “I felt as if the rubber hand was my own hand”, see Longo et al., 2008) were predicted by
10 interoceptive awareness, with lower interoceptive sensitivity scores resulting in higher
11 affirmative ratings to this question.

12 Could the differences between the two groups be explained by differences in
13 proprioception or autonomic body-states prior to multisensory stimulation? The
14 inspection of proprioceptive awareness prior to the visuo-tactile stimulation suggests not,
15 as both groups showed comparable and minimal proprioceptive errors during the pre-
16 induction proprioceptive judgments. The inspection of skin temperature prior to the
17 visuo-tactile stimulation also failed to show any significant difference between groups.
18 Finally, the BIQ ratings that reflect body-image dissatisfaction, again, showed no
19 significant differences between groups, and similarly there were no significant
20 differences in the mean BMI of the two groups, ruling out that any observed differences
21 are due to differences in the perception or weight of the participant's actual body.
22 Therefore, the observed differences in the behavioral and physiological measures
23 between the two groups following the induction of the RHI reflect the active modulatory
24 role of interoceptive sensitivity in the multisensory integration of body-related visual and
25 tactile percepts.

26 The literature on the sense of body-ownership suggests that the main cause of the
27 RHI is the integration of seen and felt touches that occur in close peripersonal space
28 (Makin, Holmes & Ehrsson, 2008). However, multisensory integration in peripersonal
29 hand space by itself is not sufficient to maintain a coherent representation of one's body.
30 Instead, other factors such as the visual form congruency, the anatomical congruency, the
31 volumetric congruency, the postural congruency and the spatial relation between viewed

Running Title: *Just a heartbeat away from one's body* 10

1 and felt body-part, modulate the induction of the RHI and the experience of body-
2 ownership (for a review see Tsakiris, 2010). More recently, it has been shown that in
3 addition to changes on proprioceptive representations of one's body, the experience of
4 ownership during RHI is also accompanied by significant changes in the homeostatic
5 regulation of the real hand. In particular, skin temperature of the real hand decreased
6 when participants experienced the RHI (Moseley et al., 2008), suggesting that cognitive
7 processes that change the awareness of our physical self may in turn change the
8 physiological regulation of the body. The changes caused in the physiological regulation
9 of the body as a result of the experience of body-ownership over a fake hand suggest that
10 processes other than multisensory integration may be involved in generating, maintaining
11 or disrupting the awareness of the bodily self. Given the primacy of interoception for the
12 integration of visceral and somatosensory information as well as for several higher-order
13 representations of self (Craig, 2009; Critchley, 2005), the present study provides the first
14 direct evidence for an active modulatory role of interoception on the experience of the
15 body *from the outside*.

16 Interoceptive awareness is usually considered as a trait, and as such it may also be
17 linked to specific personality traits. For example, previous studies have shown that
18 individuals who score higher on neuroticism-related personality measures show greater
19 interoceptive awareness (Critchley, Wiens, Rothstein, Ohman, & Dolan, 2004; Ehlers &
20 Breuer, 1992; Stewart et al., 2001). However, other studies have suggested a link
21 between interoceptive awareness and blood pressure, with untreated newly diagnosed
22 hypertensives showing higher interoceptive sensitivity (Koroboki et al., 2010). Given that
23 blood pressure cannot be considered as a trait, this observation questions the
24 characterization of interoceptive awareness as a trait.

25 Our particular focus here was to consider the effect of interoceptive awareness, as
26 a trait, on the malleability of body-representations. The interpretation we put forward
27 takes into account two key findings. First, the present study shows that interoceptive
28 sensitivity plays an active role while the brain integrates body-related multisensory
29 percepts. This modulatory role is further supported by the observation that different
30 levels of interoceptive sensitivity are not linked to different levels of proprioceptive
31 awareness or skin temperature in the absence of multisensory stimulation (e.g., prior to

1 it). Second, the right insular lobe has been shown to underpin both interoceptive
2 awareness (Critchley et al., 2004) and the experience of body-ownership during the RHI
3 (Tsakiris et al., 2007). Taken together, these observations suggest that the interaction
4 between the perception of the body from *within* and from the *outside* is instantiated in the
5 convergence zone of the right insular lobe.

6 What can account for the finding that low interoceptive sensitivity results in
7 greater malleability of body-representations following multisensory stimulation? There
8 are two possible explanations. First, it might be possible that individuals with low
9 interoceptive sensitivity can allocate more attentional resources to multisensory
10 processing because they are less aware of their internal states, resulting in stronger
11 multisensory integration and consequently a stronger RHI. A similar account has been
12 proposed from RHI studies on schizophrenic patients (Morgan et al., 2010; Peled et al.,
13 2000). However, it was recently shown that, if anything, high interoceptive awareness
14 positively correlates with better performance in attention tasks (Matthias, Schandry,
15 Duschek, & Pollatos, 2009). A second explanation would suggest that high interoceptive
16 sensitivity might contribute to an overall more efficient processing of body-related
17 sensory percepts by the co-weighting of both interoceptive and exteroceptive signals
18 during body-perception, in contrast to individuals with low interoceptive sensitivity who
19 might rely mainly on exteroceptive signals. People with high interoceptive sensitivity
20 may display enhanced monitoring of the origins of body-related percepts, and may map
21 these percepts against the available interoceptive representations of the internal milieu.
22 This hypothesis is supported by recent neurophysiological models of interoception and its
23 neural underpinnings. High interoceptive sensitivity might optimize internal predictive
24 models used in sensory self-monitoring (Critchley, 2005), consistent with the functional
25 role of the right insula in integrating bodily, environmental and neural systems to
26 optimize homeostatic efficiency (Craig, 2009) and represent the “material me” in a global
27 way. On this view, the insular lobe would instantiate a collective representation of one's
28 body produced by the continuous monitoring, weighting and integration of different
29 signals. Interestingly, neurological damage in the right insula results in neurological
30 deficits in sensory self-monitoring (Spinazzola, Pia, Folegatti, Marchetti & Berti, 2008),
31 such as somatoparaphrenia (Baier & Karnath, 2008), while a neuroimaging study in

Running Title: *Just a heartbeat away from one's body* 12

1 neurologically healthy volunteers during the RHI showed that activity in the right mid-
2 posterior insula correlated with the experience of body-ownership (Tsakiris, Hesse, Boy,
3 Haggard & Fink, 2007).

4 Given the importance of interoception for all bodily feelings (for reviews see
5 Craig, 2009; Critchley, 2005), and its effect on exteroceptive body-awareness as shown
6 in the present study, affective changes in the explicit representation of one's body (e.g.,
7 body-image), may critically rely on the modulatory effect of interoceptive awareness on
8 exteroception of one's body. Intriguingly, anorexic patients display decreased
9 interoceptive awareness (Pollatos et al., 2008), and their body-image dissatisfaction is
10 correlated with activity in the right insular lobe (Friederich et al., 2010). The finding that
11 interoceptive awareness can modulate exteroceptive representations of the body has
12 important implications for impairments of body-awareness where the integration of the
13 body as experienced from *within* and from the *outside* may be severely disrupted. Future
14 studies should clarify the exact weighting of interoceptive and exteroceptive signals in
15 forming a coherent representation of one's body.

16
17 **Acknowledgments:** We would like to thank Stephanie Kyriacou, Ania Kreisel and
18 Francesca Pearce for data collection. The study was supported by ESRC First Grant RES-
19 061-25-0233 to MT.

20 21 **References**

- 22 Baier, B., & Karnath, H. O. (2008). Tight link between our sense of limb ownership and
23 self-awareness of actions. *Stroke*, *39*, 486–488.
- 24 Bermúdez, J. L., Marcel, A. J., & Eilan, N. (Eds.). (1995). *The body and the self*.
25 Cambridge, Mass. ; London: MIT Press.
- 26 Botvinick, M., & Cohen, J. (1998). Rubber hands “feel” touch that eyes see. *Nature*, *391*,
27 756.
- 28 Cash, T. F., & Szymanski, M. L. (1995). The development and validation of the Body-
29 Image Ideals Questionnaire. *Journal of Personality Assessment*, *64*, 466-477.
- 30 Critchley, H. D. (2005). Neural mechanisms of autonomic, affective, and cognitive
31 integration. *Journal of Comparative Neurology*, *493*, 154-166.

- 1 Craig, A. D. (2009). How do you feel – now? The anterior insula and human awareness.
2 *Nature Reviews Neuroscience*, *10*, 59-70.
- 3 Craig, A. D. (2010). The sentient self. *Brain Structure and Function*, *214*, 563-577.
- 4 Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R. J. (2004). Neural
5 systems supporting interoceptive awareness. *Nature Neuroscience*, *7*, 189-95.
- 6 Damasio, A. (1999). *The Feeling of What Happens: Body and Emotion in the Making of*
7 *Consciousness*. New York: Harcourt Brace.
- 8 Ehlers, A., & Breuer, P. (1992). Increased cardiac awareness in panic disorder. *Journal of*
9 *Abnormal Psychology*, *101*, 371-382.
- 10 Friederich, H-C., Brooks, S., Uhera, R., Campbell, I. C., Giampietro, V., Brammer, M.,
11 Williams, S. C. R., Herzog, W., & Treasure, J. (2010). Neural correlates of body
12 dissatisfaction in anorexia nervosa. *Neuropsychologia*, *48*, 2878-2885.
- 13 Knoll, J. F., & Hodapp, V. (1992). A comparison between two methods for assessing
14 heartbeat perception. *Psychophysiology*, *29*, 218–222.
- 15 Koroboki, E., Zakopoulos, N., Manios, E., Rotas, V., Papadimitriou, G., Papageorgiou,
16 C. (2010) Interoceptive awareness in essential hypertension. *International Journal of*
17 *Psychophysiology*, *78*, 158-162.
- 18 Longo, M. R., Schuur, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What
19 is embodiment? A psychometric approach. *Cognition*, *107*, 978-998.
- 20 Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands
21 and peripersonal space. *Behavioral Brain Research*, *191*, 1-10.
- 22 Matthias, E., Schandry, R., Duschek, S., Pollatos, O. (2009). On the relationship between
23 interoceptive awareness and the attentional processing of visual stimuli. *International*
24 *Journal of Psychophysiology*, *72*, 154-159.
- 25 Morgan, H. L., Turner, D. C., Corlett, P. R., Absalom, A. R., Adapa, R., Arana, F. S.,
26 Pigott, J., Gardner, J., Everitt, J., Haggard, P., Fletcher, P.C. (2010). Exploring the impact
27 of the Ketamine on the experience of illusory body ownership. *Biological Psychiatry*.
28 2010 Oct 12. [Epub ahead of print]PMID: 20947068 .
- 29 Moseley, G. L., Olthof, N., Venema, A., Don, S., Wijers, M., Gallace, A., & Spence C.
30 (2008). Psychologically induced cooling of a specific body part caused by the illusory
31 ownership of an artificial counterpart. *PNAS*, *105*, 13168-13172.

Running Title: *Just a heartbeat away from one's body* 14

- 1 Peled, A., Ritsner, M., Hirschmann, S., Geva, A. B., Modai, I. (2000). Touch feel illusion
2 in schizophrenic patients. *Biological Psychiatry*, *48*, 1105-1108.
- 3 Pollatos, O., Kurz, A. L., Albrecht, J., Schreder, T., Kleeman, A. M., Schopf, V.,
4 Kopietz, R., Wiesmann, M., & Schandry, R. (2008). Reduced perception of bodily
5 signals in anorexia nervosa. *Eating Behaviours*, *9*, 381-388
- 6 Schandry, R. (1981). Heart beat perception and emotional experience. *Psychophysiology*,
7 *18*, 483-488.
- 8 Sherrington, C. S. (1900). Cutaneous sensations. In Schafer, E. A. (Ed.), *Text-book of*
9 *physiology* (pp 920-1001). Edinburgh: Pentland.
- 10 Spinazola, L., Pia, L., Folegatti, A., Marchetti, C., & Berti, A. (2008). Modular structure
11 of awareness for sensorimotor disorders: Evidence from anosognosia for hemiplegia and
12 anosognosia for hemianopia. *Neuropsychologia*, *46*, 915-926.
- 13 Stewart, S. H., Buffett-Jerrott, S. E., Kokaram, R. (2001). Heartbeat awareness and heart
14 rate reactivity in anxiety sensitivity: A further investigation. *Anxiety Disorders*, *15*, 535-
15 553.
- 16 Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership.
17 *Neuropsychologia*, *48*, 703-12.
- 18 Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile
19 integration and self-attribution. *Journal of Experimental Psychology: Human Perception*
20 *and Performance*, *31*, 80-91.
- 21 Tsakiris, M., Hesse, M., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural correlates of
22 body-ownership: A sensory network for bodily self-consciousness, *Cerebral Cortex*, *17*,
23 2235-2244.

1 **Tables and Figure Captions**

2

3 **Table 1:** Table 1 shows the mean ratings for each questionnaire item (\pm SD) across
4 conditions. Participants rated the statements using a 7-item Likert scale (i.e., +3 indicated
5 that they “strongly agreed”, -3 that they “strongly disagreed”, and 0 that they “neither
6 agreed nor disagreed”, though any intermediate value could be used).

7

8 **Figure 1:** (A) Mean proprioceptive shifts (i.e. difference between synchronous and
9 asynchronous stimulation) and S.E.M. for each group on the left panel, and negative
10 correlation with interoceptive sensitivity on the right panel. (B) Mean skin-temperature
11 shifts (i.e. difference between synchronous and asynchronous stimulation) and S.E.M. for
12 each group, on the left panel, and positive correlation with interoceptive sensitivity
13 measure, on the right panel. (C) Mean difference in subjective ratings (i.e. difference
14 between synchronous and asynchronous visuo-tactile stimulation) and S.E.M. for the
15 question “I felt as if the rubber hand was my own hand” on the left panel, and negative
16 correlation with interoceptive sensitivity measure on the right panel.

17

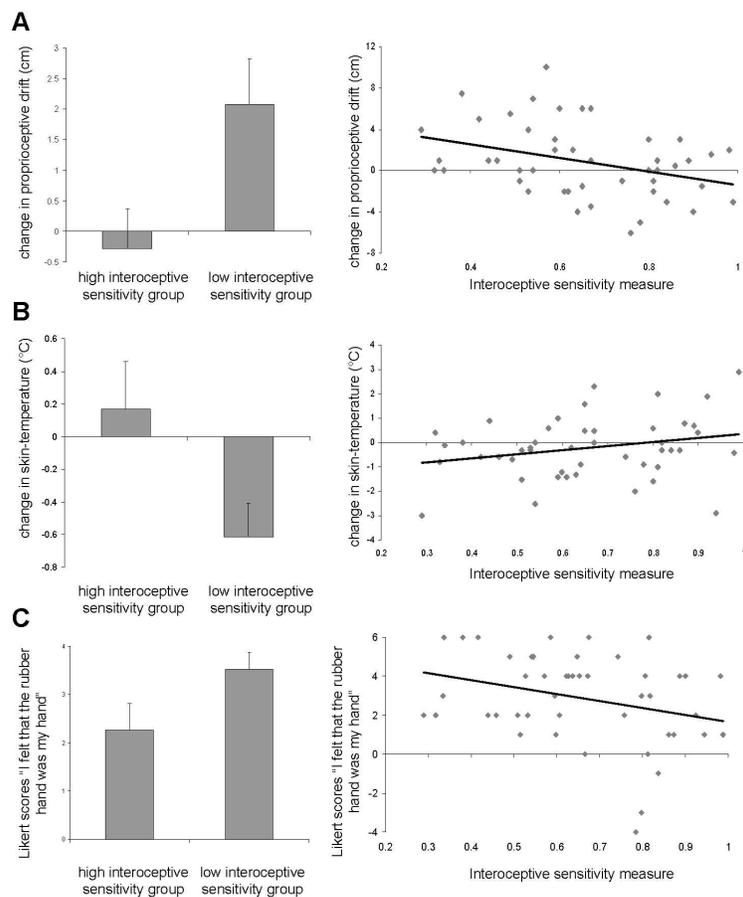
18

19

1 Table 1

2

	“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)	-1.56 (0.27)
	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)
Location Questions	... 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)



(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) 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.

209x296mm (200 x 200 DPI)

Table 1

	“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)	-1.56 (0.27)
	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)
Location Questions	... 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)