Turning body and self inside out: Visualized heartbeats alter bodily self-consciousness and tactile perception

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Research Article

Turning body and self inside out:

Visualized heartbeats alter bodily self-consciousness and tactile perception

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Abstract

Prominent theories highlight the importance of bodily perception for self-consciousness, but it is currently not known whether this is based on interoceptive or exteroceptive signals or on integrated signals from these anatomically distinct systems. Here, we combined both types of signals, providing participants with visual exteroceptive information about their heartbeat: a real-time video image of a periodically illuminated silhouette outlining the participant’s (“virtual”) body and flashing in synchrony with their heartbeat. We investigated whether these “cardio-visual” signals could modulate bodily self-consciousness and tactile perception, and report two main findings. First, synchronous cardio-visual signals increased self-identification with and self-location towards the virtual body, and, secondly, altered the perception of tactile stimuli applied to participants’ backs, so that touch was mislocalized towards the virtual body. We argue that the integration of signals from the inside and the outside of the human body is a fundamental neurobiological process underlying self-consciousness.

Introduction

Neurological, neuroimaging, and psychological data have highlighted the importance of bodily perception for a neurobiological model of the self and subjectivity. Inspired by early neurological research on the body schema (Head & Holmes, 1911; Schilder, 1935), recent clinical research described alterations of the self in cases of disturbed multisensory integration (Blanke, Landis, Spinelli, & Seeck, 2004; Brugger, Regrad, & Landis, 1997; Heydrich, Dieguez, Grunwald, Seeck, & Blanke, 2010; Vallar & Ronchi, 2009). These clinical insights inspired the use of multisensory conflicts to systematically alter the perception of the body and self (Blakemore, Wolpert, & Frith, 1998; Botvinick & Cohen, 1998; Dieguez, Mercier, Newby, & Blanke, 2009; Fourneret & Jeannerod, 1998; Lenggenhager, Tadi, Metzinger, & Blanke, 2007).

Alterations of the self and the generation of illusory own body perceptions through multisensory conflicts have mostly affected isolated body parts such as fingers (Dieguez et al., 2009), hands (Botvinick & Cohen, 1998), arms (Fourneret & Jeannerod, 1998), or the face (Sforza, Bufalari, Haggard, & Aglioti, 2010), but can also induce changes in the perception of the entire body (Ehrsson, 2007; Lenggenhager et al., 2007). In one such illusion (Lenggenhager et al., 2007) participants viewed their own body from behind through a head mounted display while their back was stroked. With synchronous stroking, participants self-identified with the 'virtual' body and mislocalized their self towards where the virtual body was seen.

These studies on the bodily self manipulated only exteroceptive sensory sources of information about the body (i.e. vision and touch). However, prominent evidence has been put forward that the brain's representations of internal bodily states (e.g. the heartbeat

(Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004)) are equally important or even more important for the self (A. D. Craig, 2002; Damasio, 2000). Although recent patient work suggests that exteroceptive and interoceptive signals can be integrated (in visceral perception (Khalsa, Rudrauf, Feinstein, & Tranel, 2009)), until now, no one has investigated how these two signals might interact to jointly affect bodily self-consciousness. This is surprising given what is known about the convergence of visceral and somatosensory signals in single neurons in the spinal cord, brain stem, and thalamus (Foreman, Blair, & Weber, 1984; Takahashi & Yokota, 1983) and clinical data from patients with coronary heart disease and referred pain (Ruch, 1965).

We therefore developed an experimental setup that investigated whether a conflict between an interoceptive signal (the heartbeat) and an exteroceptive (visual) signal would modulate bodily self-consciousness and whether this cardio-visual conflict would also alter exteroception (tactile perception). We thus presented cardio-visual illumination of the virtual body so that a flashing silhouette was either temporally synchronous or asynchronous with respect to the subject’s heartbeats. We predicted that participants would feel greater self-identification with the virtual body, would self-locate more towards the virtual body, and that tactile stimuli would be mislocalised towards the virtual body more in the synchronous than the asynchronous condition. Our data show that synchronous cardio-visual signals increased self-identification with and self-location towards the virtual body and also altered the perception of tactile stimuli (relative to the asynchronous condition).

Methods

Participants

A total of 17 healthy right-handed participants took part (9 females, mean age 26.7±5.6 years). All participants had no previous experience with the task or related experimental paradigms. All participants had normal or corrected to normal vision and had no history of neurological or psychiatric conditions. All participants gave written informed consent and were compensated for their participation. The study protocol was approved by the local ethics research committee – La Commission d'éthique de la recherche Clinique de la Faculté de Biologie et de Médecine – at the University of Lausanne, Switzerland and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Materials and procedure

Setup, electrocardiogram (ECG), signal analysis

The present protocol adapted an experimental setup that has been used previously to study bodily self-consciousness and visuo-tactile integration (Aspell, Lenggenhager, & Blanke, 2009; Ehrsson, 2007; Lenggenhager et al., 2007). Participants stood with their backs facing a video camera placed 2 meters behind. The video, showing the participant's body (virtual body) was projected in the body conditions in real time onto a head mounted display (HMD), see Figure 1. While filming the video we also recorded the participant's ECG throughout the entire experiment. Raw data (ECG) were acquired with the BioSemi Active II™ system (Biosemi, The Netherlands) at a sampling rate of 2048Hz. In-house software was developed to detect, in real time, the peak of each R-wave from the recorded ECG data and to trigger an additional visual stimulus (e.g. a flashing outline surrounding the participant's virtual body) that flashed on and off synchronously or asynchronously with respect to the participant's heartbeat (for further details please refer to the Supplementary Material and Supplementary Figure S1). There were 4 different blocks corresponding to 4 different conditions: (1) Body with flashing outline synchronous with the heartbeat (body synchronous, BS); (2) Body with flashing outline asynchronous with the heartbeat (body asynchronous, BAS); (3) Object with flashing outline synchronous with the heartbeat (object synchronous, OS); (4) Object with flashing outline asynchronous with the heartbeat (object asynchronous, OAS).

Self-identification and self-location

Participants' subjective responses were assessed at the end of each block by an eleven-item questionnaire adapted from (Lenggenhager et al., 2007); see Table 1) that allowed us to quantify self-identification with the virtual body. The questions were randomly ordered and rated on a 7-point Likert scale between -3 to 3, in which -3 indicated complete disagreement and +3 complete agreement.

At the end of each block (duration ~6 min) we measured self location as described previously (Lenggenhager et al., 2007). To do this we first passively displaced the participant backwards by 1.5 meters (the experimenter gently guided the participants - who had their eyes closed - while they took very small steps backwards). They were then asked to walk back to their initial position (while keeping their eyes closed) with normal sized steps. The distance between the original position and the position estimated by the participant (drift) was measured.

Tactile perception - the cross modal congruency effect

To measure the effect of cardio-visual stimulation on tactile perception, we adapted our previous setup and paradigm that allowed us to measure visuo-tactile CCEs (Aspell et al., 2009); for further details please refer to the Supplementary Material). Participants were instructed to keep their eyes open, to fixate a location in the middle of their backs as viewed via the HMD and to stand still while waiting for the first vibro-tactile and LED stimuli (presented one minute after the start of the trial). For the measurement of the visuo-tactile CCE, participants had to indicate with their right hand, by pressing one of two buttons as fast as possible whether they felt a vibration at the top (an upper device) or at the bottom (a lower device) of their backs (regardless of side), while trying to ignore the light flashes. Four conditions (with 25 trials each) were thus presented, which differed in the relative locations of the target vibrator and the distractor LED: (1) same side, congruent elevation; (2) same side, incongruent elevation; (3) different side, congruent elevation; (4) and different side, incongruent elevation. We analyzed reaction times (RTs) and accuracies in each condition.

Statistical analysis

In order to asses the illusion strength we first compared the subjective ratings in the illusion questions (question 1-3) with the ratings in the control question (question 4-11) in the 4 experimental conditions using a two-tailed 3-way repeated-measures ANOVA with within-subject factors body (body/object), synchrony (synchronous/asynchronous) and question type (illusion/control) as described previously (Morgan et al., 2011; Palluel, Aspell, Lavanchy, & Blanke, 2012; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008). In order to follow up on the results of the ANOVA, we carried out planned-comparisons using a paired t-test. Based on previous work using visuo-tactile stimulation (Botvinick & Cohen, 1998; Ionta et al., 2011; Lenggenhager et al., 2007), we postulated the *a priori* hypothesis of higher subjective ratings in the illusion questions in the BS condition as compared to the BAS condition and no such difference for the object conditions (OS and OAS) and the control questions. The significance level (alpha) used was adjusted for multiple comparisons using the Bonferroni method (p=0.0125).

In a second step we focused in more detail on the differences of the ratings from the illusion questions (in particular question 3 “I felt as if the virtual body/object was my body”), performing planned-comparisons between BS-BAS, OS-OAS, BS-OS and BAS-OAS using a paired t-test. Again, we postulated the *a priori* hypothesis of higher ratings in the BS condition as compared to the BAS condition and of generally higher ratings in the body conditions as compared to the object conditions (contrasts BS-OS and BAS-OAS) but no significant difference between the object conditions (OS and OAS). Moreover, in order to make sure that the observed effects are not due to the subjects being aware of the manipulation, question 8 (“It seemed as if the flashing semi-transparent template was my heartbeat”) was analyzed using the same contrasts. Accordingly, the significance level used (alpha) was adjusted using the Bonferroni method (p=0.003).

The drift (self-location) measures (calculated relative to the initial position = 0) were analyzed using repeated measures analyses of variance (ANOVA) with the factors body (body/object) and synchrony (synchronous/asynchronous). The RTs and the accuracy data of the CCE were analyzed using the factors body (body/object), synchrony (synchronous/asynchronous), side (same side/different side) and congruency (congruent/incongruent). We here focus mainly on the RT data rather than accuracy, as this has been shown to be more sensitive for CCE analysis (Austen, Soto-Faraco, Enns, & Kingstone, 2004; Shore, Barnes, & Spence, 2006; Spence, Pavani, & Driver, 2004). Fisher LSD

(Last significant difference) test was used for post-hoc testing and the significance (alpha) level used was $p=0.05$. Three participants had to be excluded from CCE analysis (one because of chance level performance and two because of technical problems, e.g. less than half of the trials were recorded in one condition). This resulted in a total $N=14$ for the CCE analysis. Trials with incorrect responses and trials in which participants failed to respond within 1500 msec were discarded from reaction time (RT) analysis following the methods in previous studies (Aspell et al., 2009; Spence et al., 2004). We also determined heart rate variability from the ECG by calculating the average standard deviation of the average RR intervals (SDANN) for each condition (Cowan, 1995)using repeated measures analyses of variance (ANOVA) with factors body (body/object) and synchrony (synchronous/asynchronous).

Results

Self-identification

The mean responses to Q3 ("I felt as if the virtual body/object was my body") are shown in Figure 2A. The effects of seeing a body and synchronous stroking on the illusion strength (average of responses to questions 1-3) was investigated using a 2x2x2 repeated measures ANOVA. We found a significant main effect of body ($N=17$, $F_{1,16}=38.11$, $p<0.001$, $\eta_p^2=0.704$) and question type ($N=17$, $F_{1,16}=13.14$, $p=0.02$, $\eta_p^2=0.451$), as well as an interaction between body and question type ($N=17$, $F_{1,16}=20.1$, $p<0.001$, $\eta_p^2=0.557$) and between body, synchrony and question type ($N=17$, $F_{1,16}=4.36$, $p=0.053$, $\eta_p^2=0.214$). Further analysis using planned-comparisons showed that the overall illusion was stronger during the BS as compared to the BAS condition ($p=0.01$, one-tailed). No significance difference between the average score of the control questions during the BS and BAS conditions nor for any type of question during the object conditions could be found (all $p>0.08$, one-tailed).

Subsequent analysis focusing on mean responses to questions 1 through 3 (illusion questions see Table 1), revealed that self-identification with the virtual body (question 3, see Figure 2A) was stronger during the BS condition (mean=0.88) as compared to the BAS condition (mean=-0.12; $p=0.002$, one-tailed) and the OS condition (mean=-2.29, $p<0.001$, one-tailed), as well as between the BAS and the OAS condition (mean=-2.41, $p<0.001$, one-tailed). No significant difference was found between the OS and OAS condition ($p=0.33$, one-tailed). These data, using cardio-visual conflict, and thus an intero-exteroceptive conflict, are comparable to earlier data using purely exteroceptive, visuo-tactile, conflicts (7, 8, 13, 14). Analysis of Q8 ("It seemed as if the flashing semi-transparent template was my heartbeat") revealed that participants were not aware of the experimental manipulation (mean ratings across all conditions were negative and no significant difference could be observed between the conditions; all $p>0.07$, one-tailed; see Figure 2B).

Self-location

Cardio-visual signals also altered self-location (as shown in Figure 2C): it was modulated by cardio-visual synchrony, but only in the body conditions as predicted (based on work using pure exteroceptive conflicts, i.e. greater change of self-location in the BS than the BAS condition (Aspell et al., 2009; Lenggenhager et al., 2007)). Statistical analysis revealed neither a significant main effect of body ($N=17$, $F_{1,16}=1.10$, $p=0.31$, $\eta_p^2=0.064$) nor of synchrony ($N=17$, $F_{1,16}=0.38$, $p=0.54$, $\eta_p^2=0.023$), but did, crucially, reveal a significant two-way interaction between body and synchrony ($N=17$, $F_{1,16}=8.93$, $p<0.01$, $\eta_p^2=0.358$). This was caused by a significant difference between the BS (mean =10.0cm+/-24.6cm) and the BAS conditions (mean =-1.0cm+/-20.3 cm, p=0.02). Further analysis revealed that self-location differed from 0 only in the BS condition (p=0.05), but not in the BAS condition p=0.41). In contrast, in the object conditions, self-location changes were generally smaller and did not differ from 0 (all p>0.24); they also did not differ between the OS (mean =-3.2cm+/-22.9cm) and OAS conditions (mean =3.9cm+/-22.4cm, p=0.11).

Tactile perception

By measuring the magnitude of the visuo-tactile CCE during cardio-visual stimulation we directly tested whether and how the cardio-visual signals altered the perception of exteroceptive tactile cues that we applied to the body surface of our participants during the illusion. Based on previous work showing that visuo-tactile stroking alters CCE magnitude (Aspell et al., 2009; Zopf, Savage, & Williams, 2010) in conditions that induce changes in self-identification and self-location, we here predicted that cardio-visual illumination should induce similar changes. Because exteroceptive as well as interoceptive signals are involved in bodily self-consciousness (as indicated by the present changes in self-identification and self-location) we expected greater mislocalization of touch (as reflected in CCE magnitude) towards the virtual body in the BS condition during cardio-visual stimulation. The critical test is thus whether the visuo-tactile CCE varied as a function of cardio-visual synchrony.

Figure 2D plots this effect and shows that CCEs were larger during cardio-visual synchrony. This effect was more pronounced if the vibration and the visual distractor were on the same side than on the different side (three-way interaction between synchrony, congruency and side; $F_{1,13}$=7.57, p=0.02, η_p^2=0.368; see Figure S2A and B in the Supplementary Material). Statistical analysis also revealed significant main effects of body

(N=14, $F_{1,13}$=8.73, p=0.01, η_p^2=0.402) and congruency ($F_{1,13}$=69.097, p<0.001, η_p^2=0.842) as well as a significant two-way interaction between side and congruency ($F_{1,13}$=40.75, p<0.001, η_p^2=0.758). No significant interactions between body and synchrony ($F_{1,13}$=2.224, p=0.16), body, synchrony, and congruency ($F_{1,13}$=0.827, p=0.38), body, synchrony, and side ($F_{1,13}$=0.029, p=0.87), and no significant 4-way interaction between congruency, side, synchrony, and body ($F_{1,13}$=0.0302, p=0.87) were found. For further discussion of CCE data see Supplementary material and Figures S2A and B.

As the magnitude of these CCE effects (RTs) due to cardio-visual illumination is comparable to those observed for CCEs during visuo-tactile stroking (Aspell et al., 2009; Spence et al., 2004; Zopf et al., 2010), this finding shows that a cardio-visual conflict modulates how irrelevant visual signals interfere with the perception of tactile cues on one’s body surface. Further analysis revealed that these differences in touch perception (CCE) and bodily self-consciousness (self-identification, self-location) are not related to more elementary changes in heart physiology, such as differences in heart frequency and variability: An ANOVA comparing the heart variability (SDANN) across conditions did not reveal any significant main effects or interactions between BS (59±49 ms), BAS (44±14 ms), OS (59±58 ms) and OAS (69±85 ms) (all p>0.33); see figure S2C in the Supplementary Material.

Our finding of an alteration in the perception of tactile stimuli applied to one’s body surface while viewing a heartbeat-locked illumination of the virtual body suggests that cardio-visual signals interfere with how tactile signals are integrated in the human brain. In addition to their relevance for self-consciousness, the present behavioral data therefore also extend data on viscero-somatic convergence (and in particular cardio-tactile convergence that has previously been observed in spinal cord, brainstem, and thalamus) to cardiac signals and their integration with exteroceptive signals at higher, most likely cortical levels of processing (see Discussion).

Discussion

The present study allows us to draw several conclusions. Our data are compatible with evidence that has accumulated within two separate traditions in the neurosciences pointing to the importance of exteroceptive *and* interoceptive systems for self-consciousness. We show that signals from these systems – despite their anatomical, physiological and functional differences – can be integrated. Since these integrated extero-interoceptive (cardio-visual) signals are modulators of two crucial aspects of bodily self-consciousness, we argue that the integration of signals from the inside and the outside of the human body is a fundamental neurobiological process underlying self-consciousness.

The present data demonstrate stronger self-identification and a greater shift in self-location (as compared to the asynchronous condition) when an illuminating silhouette surrounding a video image of the participant's own body flashed on and off synchronously with the participant's heartbeat. This is the first time that an extero-interoceptive conflict has been used to modulate bodily self-consciousness. Earlier studies used purely exteroceptive (e.g. visuo-tactile) conflicts (Aspell et al., 2009; Lenggenhager et al., 2007; Zopf et al., 2010). Our findings are compatible with earlier proposals that exteroceptive (Blanke et al., 2004; Blanke & Metzinger, 2009) and interoceptive signals (A. D. Craig, 2002; Damasio, 2000; M. Tsakiris, Jimenez, & Costantini, 2011) are important for the representation of the self in the brain.

It has been proposed that ownership of rubber hands and self-identification with virtual bodies (Botvinick & Cohen, 1998; Lenggenhager et al., 2007; Moseley, Gallace, & Spence, 2011) is at least partly explained by the fact that tactile input (stroking) is inherently self-specifying sensory information (Bermudez, 1995) because tactile stimuli *necessarily* provide information about one's own body (whereas, e.g., visual and auditory signals do not). Interoceptive (e.g. heartbeat) signals are also self-specifying sensory signals and in addition, are 're-afferent' signals as they originate from the organism's visceral motor control processes (Christoff, Cosmelli, Legrand, & Thompson, 2011). Given this, we argue that when synchronous heartbeat timing information is presented to the participant, albeit via an unusual route (vision), it serves to increase self-identification with the virtual body, relative to the condition in which the visual information is asynchronous.

It is notable that these cardio-visual effects on bodily self-consciousness are only found when the flashing outline is viewed on a video image of the participant's body, not when it is viewed on a control object. The cardio-visual synchrony effect is therefore not sufficient on its own to cause changes in bodily self-consciousness: the visual object must resemble a body. Similar findings were reported using visuo-tactile stimulation of whole bodies (Lenggenhager et al., 2007) and hands (Haans, Ijsselsteijn, & de Kort, 2008; Manos Tsakiris, Carpenter, James, & Fotopoulou, 2010; M Tsakiris & Haggard, 2005). Top-down mechanisms, which refer to stored information about typical human body form, are likely to be recruited in order for these illusions, including the present cardio-visual illusion one, to occur: multisensory congruence alone is not sufficient (Makin, Holmes, & Ehrsson, 2008; Manos Tsakiris et al., 2010).

By measuring the magnitude of visuo-tactile CCEs during cardio-visual stimulation we show that cardio-visual signals also alter the perception of exteroceptive tactile cues: we observed a greater mislocalization of touch during synchronous cardio-visual illumination. These changes were of similar magnitude to those observed when the full body illusion was induced using purely exteroceptive conflicts (Aspell et al., 2009). This alteration in the spatial perception of tactile stimuli indicates that task irrelevant cardio-visual signals can selectively alter tactile spatial perception (possibly via the integration of cardio-visual signals with tactile signals). Concerning the underlying brain mechanisms, these CCE data suggest that the interfering effects of the cardio-visual synchrony were conveyed to the somatosensory system, thereby modulating tactile processing.

Collectively, our data show that internal and external states of the body are integrated and suggest that they converge within a common system representing the bodily self. Viscero-somatic convergence has been described in the dorsal horn of the spinal cord, the brain stem and the thalamus by revealing single neurons with tactile receptive fields that also receive afferent cardiac input (Foreman et al., 1984; Takahashi & Yokota, 1983). Such convergence has been proposed to account for the referred location of visceral sensations, most notoriously of heart pain (angina pectoris) that may be felt on the trunk, face, and upper extremities (referred pain (Ruch, 1965)). Thus, afferent signals from the viscera converge with somatosensory afferents from specific body parts (Foreman et al., 1984; Holzl, Moltner, & Neidig, 1998). Our data shows that not only viscero-somatic but also viscero-visual information can be integrated. Based on the anatomy of the visceral and visual pathways we suggest that the present cardio-visual integration is supported by cortical (or thalamic) structures rather than other subthalamic or spinal structures. Cortical convergence is further supported by our finding that illusory self-identification and self-location due to cardio-visual synchrony were only observed when participants viewed a body, but not when they viewed an object. Since awareness of cardiac signals has been shown to rely on somatosensory signals conveyed through parietal cortex (e.g. chest wall; (Khalsa et al., 2009)), and since posterior parietal areas 5 and 7 have been shown to contain bimodal neurons responding to visual and tactile input (Iriki, Tanaka, & Iwamura, 1996; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975), we suggest that cardio-visual signals might be integrated in posterior parietal cortex and are thus able to modulate bodily self-consciousness and somatosensory processing.

The observed behavioral changes in somatosensory cortex may have also occurred as a consequence of signals arriving from different brain regions such as the insula or the parietal cortex (e.g. SII). The insula (Khalsa et al., 2009) has been shown to be recruited during the perception of cardiac signals. Cardio-visual signals could thus also have been integrated in the insula first and these integrated signals could then have modulated tactile processing and bodily self-consciousness. The insula is a key area for interoception, is important for heartbeat awareness (Critchley et al., 2004), and has been proposed to be crucial for subjective bodily feelings (A. Craig, 2010; A. D. Craig, 2002). It is a highly multisensory brain region that is also activated by visual, tactile, and auditory cues (Kondo & Kashino, 2007; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Pressnitzer & Hupe, 2006). Both the posterior parietal cortex and the insula have been implicated in a number of studies on self-attribution of a fake or virtual hand (Press, Heyes, Haggard, & Eimer, 2008), (Ehrsson, Spence, & Passingham, 2004; Farrer & Frith, 2002; M Tsakiris, Hesse, Boy, Haggard, & Fink, 2007).

In conclusion, the present data on changes in self-identification, self-location and tactile perception suggest that neural mechanisms for detecting correlations between the timing of a flashing visual stimulus and the heartbeat are highly sensitive and are powerful modulators of bodily self-consciousness. The brain's detection of correlations among multisensory signals is an important basis for distinguishing self from non-self (Botvinick & Cohen, 1998; Rochat & Striano, 2000; van den Bos & Jeannerod, 2002). The current heartbeat illumination paradigm brought interoceptive cues to the 'outside' and allowed us to induce a number of different fine-grained behavioral changes. Given that our data show that exteroceptive and interoceptive signals are combined and that they are potent modulators of bodily self-consciousness, we propose that signals from the inside and the outside of the human body form an integrated cortical system for bodily self-consciousness.

Authorship

J.A. L.H. and O.B. designed the experiment. L.H., G.M., T.L. and B.H. conducted the experiment. J.A. L.H. and O.B wrote the paper. All authors approved the final version of the paper for submission.

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References

Aspell, J. E., Lenggenhager, B., & Blanke, O. (2009). Keeping in touch with one's self: multisensory mechanisms of self-consciousness. *PLoS One, 4*(8), e6488. doi: 10.1371/journal.pone.0006488

Austen, E. L., Soto-Faraco, S., Enns, J. T., & Kingstone, A. (2004). Mislocalizations of touch to a fake hand. *Cogn Affect Behav Neurosci, 4*(2), 170-181.

Bermudez, J. L. (1995). Ecological perception and the notion of a nonconceptual point of view. In J. L. Bermudez, A. Marcel & N. Eilan (Eds.), *The body and the self*. Boston: MIT Press.

Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nat Neurosci, 1*(7), 635-640. doi: 10.1038/2870

Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopy of neurological origin. *Brain, 127*(Pt 2), 243-258. doi: 10.1093/brain/awh040

awh040 [pii]

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends Cogn Sci, 13*(1), 7-13. doi: S1364-6613(08)00250-7 [pii]

10.1016/j.tics.2008.10.003

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*(6669), 756. doi: 10.1038/35784

Brugger, P., Regrad, M., & Landis, T. (1997). Illusory reduplication of own's own body: phenomenology and classification of autoscopic phenomena. *Cogn. Neuropsychiatr.*(2), 19-38.

Christoff, K., Cosmelli, D., Legrand, D., & Thompson, E. (2011). Specifying the self for cognitive neuroscience. *Trends Cogn Sci, 15*(3), 104-112. doi: S1364-6613(11)00002-7 [pii]

10.1016/j.tics.2011.01.001

Cowan, M. J. (1995). Measurement of heart rate variability. *West J Nurs Res, 17*(1), 32-48; discussion 101-111.

Craig, A. (2010). The sentient self. *Brain Structure and Function, 214*(5), 563-577. doi: 10.1007/s00429-010-0248-y

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nat Rev Neurosci, 3*(8), 655-666. doi: 10.1038/nrn894

nrn894 [pii]

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nat Neurosci, 7*(2), 189-195. doi: 10.1038/nn1176

nn1176 [pii]

Damasio, A. R. (2000). *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*: Harcourt Brace, New York.

Dieguez, S., Mercier, M. R., Newby, N., & Blanke, O. (2009). Feeling numbness for someone else's finger. *Curr Biol, 19*(24), R1108-1109. doi: S0960-9822(09)01917-4 [pii]

10.1016/j.cub.2009.10.055

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science, 317*(5841), 1048. doi: 317/5841/1048 [pii]

10.1126/science.1142175

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science, 305*(5685), 875-877. doi: 10.1126/science.1097011

1097011 [pii]

Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage, 15*(3), 596-603. doi: 10.1006/nimg.2001.1009

S1053811901910092 [pii]

Foreman, R. D., Blair, R. W., & Weber, R. N. (1984). Viscerosomatic convergence onto T2-T4 spinoreticular, spinoreticular-spinothalamic, and spinothalamic tract neurons in the cat. *Exp Neurol, 85*(3), 597-619.

Fourneret, P., & Jeannerod, M. (1998). Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia, 36*(11), 1133-1140. doi: S0028393298000062 [pii]

Haans, A., Ijsselsteijn, W. A., & de Kort, Y. A. W. (2008). The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image, 5*(4), 389-394. doi: DOI: 10.1016/j.bodyim.2008.04.003

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain, 34*(2-3), 102-254. doi: 10.1093/brain/34.2-3.102

Heydrich, L., Dieguez, S., Grunwald, T., Seeck, M., & Blanke, O. (2010). Illusory own body perceptions: case reports and relevance for bodily self-consciousness. *Conscious Cogn, 19*(3), 702-710. doi: S1053-8100(10)00130-3 [pii]

10.1016/j.concog.2010.04.010

Holzl, R., Moltner, A., & Neidig, C. W. (1998). Somatovisceral interactions in visceral perception: abdominal masking of colonic stimuli. *Integr Physiol Behav Sci, 33*(3), 246-279.

Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., . . . Blanke, O. (2011). Multisensory Mechanisms in Temporo-Parietal Cortex Support Self-Location and First-Person Perspective. *Neuron, 70*(2), 363-374.

Iriki, A., Tanaka, M., & Iwamura, Y. (1996). Coding of modified body schema during tool use by macaque postcentral neurones. *NeuroReport, 7*(14), 2325-2330.

Khalsa, S. S., Rudrauf, D., Feinstein, J. S., & Tranel, D. (2009). The pathways of interoceptive awareness. *Nat Neurosci, 12*(12), 1494-1496. doi: nn.2411 [pii]

10.1038/nn.2411

Kondo, H. M., & Kashino, M. (2007). Neural mechanisms of auditory awareness underlying verbal transformations. [10.1016/j.neuroimage.2007.02.024]. *Neuroimage, 36*, 123-130.

Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. [10.1016/j.neuroimage.2004.09.024]. *Neuroimage, 24*, 704-714.

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: manipulating bodily self-consciousness. *Science, 317*(5841), 1096-1099. doi: 317/5841/1096 [pii]

10.1126/science.1143439

Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research, 191*(1), 1-10.

Morgan, H. L., Turner, D. C., Corlett, P. R., Absalom, A. R., Adapa, R., Arana, F. S., . . . Fletcher, P. C. (2011). Exploring the Impact of Ketamine on the Experience of Illusory Body Ownership. *Biological Psychiatry, 69*(1), 35-41. doi: 10.1016/j.biopsych.2010.07.032

Moseley, G. L., Gallace, A., & Spence, C. (2011). Bodily illusions in health and disease: Physiological and clinical perspectives and the concept of a cortical 'body matrix'. *Neurosci Biobehav Rev*. doi: S0149-7634(11)00064-9 [pii]

10.1016/j.neubiorev.2011.03.013

Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol, 38*(4), 871-908.

Palluel, E., Aspell, J. E., Lavanchy, T., & Blanke, O. (2012). Experimental changes in bodily self-consciousness are tuned to the frequency sensitivity of proprioceptive fibres. *NeuroReport, 23*(6), 354-359 310.1097/WNR.1090b1013e328351db328314.

Press, C., Heyes, C., Haggard, P., & Eimer, M. (2008). Visuotactile Learning and Body Representation: An ERP Study with Rubber Hands and Rubber Objects. *Journal of Cognitive Neuroscience, 20*(2), 312-323. doi: doi:10.1162/jocn.2008.20022

Pressnitzer, D., & Hupe, J. M. (2006). Temporal dynamics of auditory and visual bistability reveal common principles of perceptual organization. [10.1016/j.cub.2006.05.054]. *Curr. Biol., 16*, 1351-1357.

Rochat, P., & Striano, T. (2000). Perceived self in infancy. *Infant Behavior and Development, 23*(3-4), 513-530.

Ruch, T. C. (1965). Pathophysiology of Pain. In T. C. Ruch & H. D. Patton (Eds.), *Physiology and Biophysics*. Philadelphia: W.B. Saunders Company.

Schilder, P. (1935). *The image and appearance of the human body*. London: Kegan Paul, Trench, Trubner.

Sforza, A., Bufalari, I., Haggard, P., & Aglioti, S. M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. *Soc Neurosci, 5*(2), 148-162. doi: 915712549 [pii]

10.1080/17470910903205503

Shore, D. I., Barnes, M. E., & Spence, C. (2006). Temporal aspects of the visuotactile congruency effect. *Neurosci Lett, 392*(1-2), 96-100. doi: S0304-3940(05)01043-8 [pii]

10.1016/j.neulet.2005.09.001

Slater, M., Perez-Marcos, D., Ehrsson, H. H., & Sanchez-Vives, M. V. (2008). Towards a Digital Body: The Virtual Arm Illusion. *Frontiers in Human Neuroscience, 2*, 6.

Spence, C., Pavani, F., & Driver, J. (2004). Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cogn Affect Behav Neurosci, 4*(2), 148-169.

Takahashi, M., & Yokota, T. (1983). Convergence of cardiac and cutaneous afferents onto neurons in the dorsal horn of the spinal cord in the cat. *Neurosci Lett, 38*(3), 251-256.

Tsakiris, M., Carpenter, L., James, D., & Fotopoulou, A. (2010). Hands only illusion: multisensory integration elicits sense of ownership for body parts but not for non-corporeal objects. *Experimental Brain Research, 204*(3), 343-352. doi: 10.1007/s00221-009-2039-3

Tsakiris, M., & Haggard, P. (2005). The rubber hand illusion revisited: Visuotactile integration and self-attribution. *Journal of Experimental Psychology-Human Perception and Performance, 31*(1), 80-91.

Tsakiris, M., Hesse, M., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural Signatures of Body Ownership: A Sensory Network for Bodily Self-Consciousness. *Cerebral Cortex, 17*(10), 2235-2244. doi: 10.1093/cercor/bhl131

Tsakiris, M., Jimenez, A. T., & Costantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. *Proc Biol Sci, 278*(1717), 2470-2476. doi: rspb.2010.2547 [pii]

10.1098/rspb.2010.2547

Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. *Exp Brain Res, 192*(3), 533-551. doi: 10.1007/s00221-008-1562-y

van den Bos, E., & Jeannerod, M. (2002). Sense of body and sense of action both contribute to self-recognition. *Cognition, 85*(2), 177-187. doi: Doi: 10.1016/s0010-0277(02)00100-2

Zopf, R., Savage, G., & Williams, M. A. (2010). Crossmodal congruency measures of lateral distance effects on the rubber hand illusion. *Neuropsychologia, 48*(3), 713-725. doi: S0028-3932(09)00435-7 [pii]

10.1016/j.neuropsychologia.2009.10.028

Figure legends

Figure 1. Setup. Participants (*a*) stood with their backs facing a video camera placed 200 cm behind them (*b*). An electrocardiogram was recorded (*a*) and R-Peaks were detected in real-time (*c*), triggering a flashing silhouette outlining the participant's body (virtual body) (*d*). The video, showing the virtual body was projected in real time onto a head mounted display (HMD) (*body condition)*. It appeared visually that the virtual body was standing 200 cm in front of the participant (*e*). After each block participants were passively displaced 150 cm backwards to the camera and instructed to walk back to the original position. See also Supplementary Figure S1 and Movie S1.

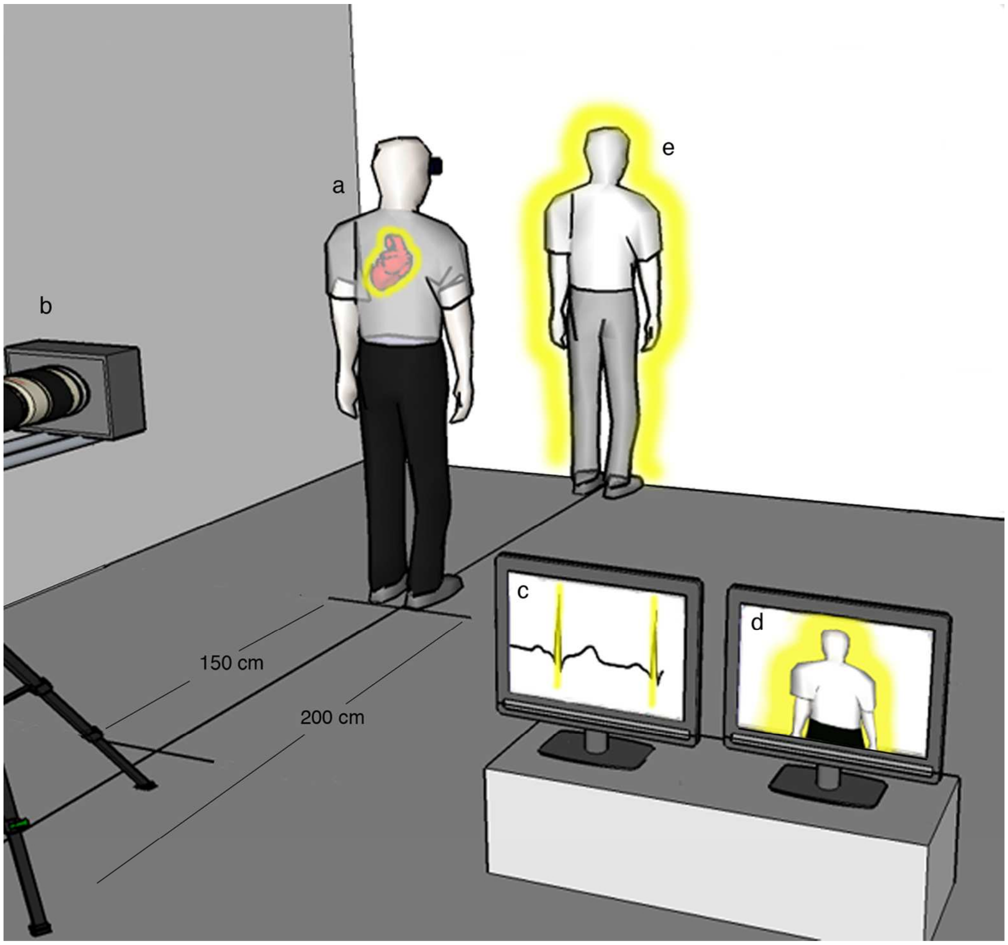
Figure 2. a. Self-identification (Q3: ‘I felt as if the body/object was my body’) significantly differed between the body synchronous condition (BS; mean=0.88) and the body asynchronous condition (BAS; mean=-0.12); and object synchronous condition (OS; mean=-2.29). Importantly, no difference between the object synchronous (OS; mean=-2.29) and object asynchronous condition (OAS; mean = -2.41) was found (N=17). White bars represent synchronous conditions, grey bars represent asynchronous conditions. Error bars indicate standard errors of the mean

b. Heartbeat awareness was not significantly different between the four conditions (Q8: ‘It seemed as if the flashing semi-transparent template was my heartbeat**’**).

c. Self-location was modulated by cardio-visual synchrony in the body condition only, with a greater change of self-location towards the virtual body in BS than in BAS. No significant difference was found between the OS and OAS (N=17).

d. CCE The CCE (N=14) was larger during cardio-visual synchrony and had greater magnitude when the vibration and the visual distractor were on the same side (three-way interaction between synchrony, congruency and side; $F_{1,13}$ =7.57, p =0.02).. See also Figure S2 in Supplementary Material.

Table 1 Questionnaire items



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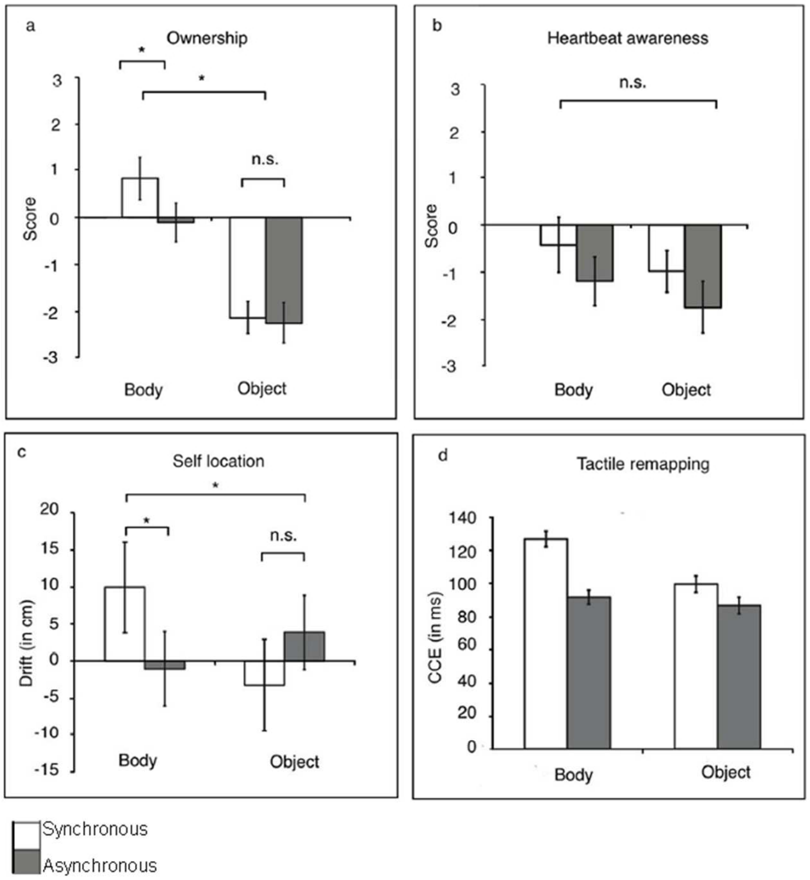

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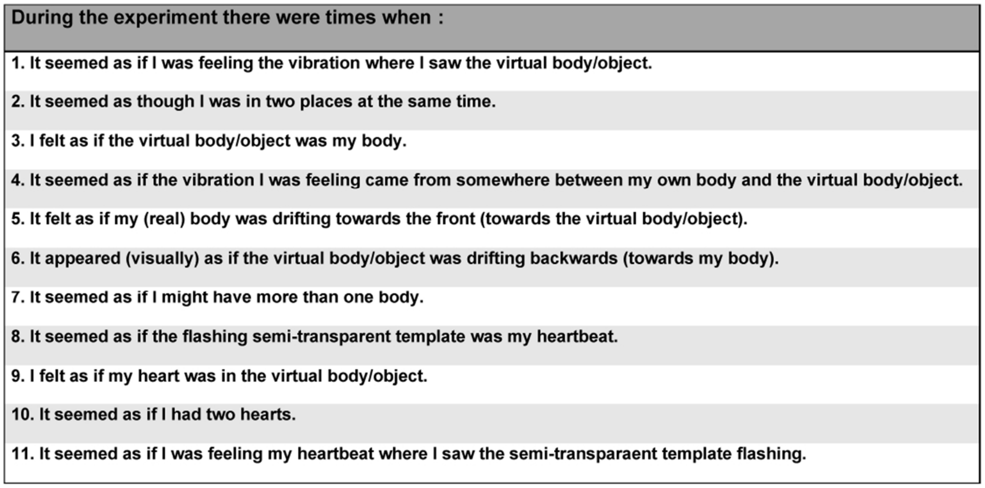

During the experiment there were times when :
1. It seemed as if I was feeling the vibration where I saw the virtual body/object.
2. It seemed as though I was in two places at the same time.
3. I felt as if the virtual body/object was my body.
4. It seemed as if the vibration I was feeling came from somewhere between my own body and the virtual body/object.
5. It felt as if my (real) body was drifting towards the front (towards the virtual body/object).
6. It appeared (visually) as if the virtual body/object was drifting backwards (towards my body).
7. It seemed as if I might have more than one body.
8. It seemed as if the flashing semi-transparent template was my heartbeat.
9. I felt as if my heart was in the virtual body/object.
10. It seemed as if I had two hearts.
11. It seemed as if I was feeling my heartbeat where I saw the semi-transparaent template flashing.

289x149mm (100 x 100 DPI)