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Title

Heartfelt Self: Cardio-visual integration affects self-face recognition and interoceptive cortical processing

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Running title

Heartfelt Self

Abstract

The sense of body-ownership relies on the representation of both interoceptive and exteroceptive signals coming from one's body. However, it remains unknown how the integration of bodily signals coming from *outside* and *inside* the body is instantiated in the brain. Here we used a modified version of the Enfacement Illusion to investigate whether the integration of visual and cardiac information can alter self-face recognition (Experiment 1) and neural responses to heartbeats (Experiment 2). We projected a pulsing shade, that was synchronous or asynchronous with the participant's heartbeat, onto a picture depicting the participant's face morphed with the face of an unfamiliar other. Results revealed that synchronous (vs. asynchronous) cardio-visual stimulation led to increased self-identification with the other's face (Experiment 1), while during stimulation, synchronicity modulated the amplitude of the Heartbeat Evoked Potential, an electrophysiological index of cortical interoceptive processing (Experiment 2). Importantly, the magnitude of the illusion-related effects was dependent of, and increased linearly, with the participants' Interoceptive Accuracy. These results provide the first direct neural evidence for the integration of interoceptive and exteroceptive signals in bodily self-awareness.

Keywords: Body Ownership, Heartbeat Evoked Potential, Interoception, Predictive Coding, Self recognition.

Introduction

The sense of body-ownership, that is, the sense of owning and identifying with a particular body, is a fundamental aspect of self-awareness (Blanke and Metzinger 2009). Body-ownership has been typically studied through the use of bodily illusions that rely upon the multisensory integration of exteroceptive signals, such as vision and touch, focusing therefore on how the body is perceived *from the outside.* More recently, it has been suggested that interoceptive signals, that is the perception of internal physiological states of the body as perceived *from within,* may also play an important role for body-ownership (Craig 2009; Tsakiris et al. 2011). While the effects of exteroceptive signals on producing or altering the sense of body-ownership have been well documented (for a review see Tsakiris 2010), the process of integrating interoceptive and exteroceptive signals and the effects that their integration has on self-awareness are less well understood.

A large body of empirical evidence has shown that the integration of exteroceptive information such as vision and touch can alter the sense of body-ownership for body-parts and full bodies (see Blanke 2012 and Tsakiris 2010 for reviews). For example, in the now classic Rubber Hand Illusion (RHI), observing an artificial hand being stroked in synchrony with strokes applied to one's own hand leads to the subjective incorporation of the rubber hand as part of one's own body, to "feel like it's my hand" (Botvinick and Cohen 1998). Beyond ownership over body-parts, other studies have used the same method of multisensory integration[1] (i.e. visuo-tactile stimulation) to ask whether similar changes would occur in the representation of one's own face. In the Enfacement Illusion (Tsakiris, 2008; Sforza et al. 2010; Apps et al. 2015), watching another person's face being touched synchronously with

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[1] The use of the term "integration" follows the past literature of bodily illusions that typically rely on the presentation of synchronous or asynchronous multisensory stimuli to alter body-representations (Tsakiris 2010; Blanke 2012). In this literature the term integration is taken to reflect the cause that gives rise to a change in body representations. It should be noted that, in this context, temporal synchrony is a necessary but not sufficient condition for integration to take place. Integration does not occur, for example, when synchronous multisensory stimulation is applied over body parts in anatomically incongruent positions or over on-corporeal objects (Tsakiris, 2010).

one's own face evokes changes in self-face recognition, so that we perceive the other person's face as more similar to one's own. This extension from bodies to faces, which are arguably the most distinctive features of one's body, suggests that multisensory integration is a shared critical mechanism for the construction of body-ownership and self-face recognition.

Beyond the known role of exteroceptive information, the role that interoceptive information may play in body-awareness has remained largely unexplored. The first study to link the perception of the body *from the outside* with the perception of the body *from the inside* showed that the illusory sense of ownership of an artificial hand, (i.e. RHI, elicited by exteroceptive information) is negatively correlated with the individual's interoceptive accuracy (IAcc), which refers to the ability to detect interoceptive signals, such as one's heartbeats (Tsakiris et al. 2011). This study provided the first empirical evidence for the influence of interoception on the integration of body-related sensory signals arising from different exteroceptive domains. Interestingly, in a way analogous to the effects of IAcc on the RHI, individual traits of IAcc were shown to predict changes in self-other boundaries during the Enfacement Illusion (Tajadura-Jimenez et al. 2012a; 2012b). More recently, direct evidence for the integration of exteroceptive and interoceptive information in body-ownership comes from two virtual reality studies (Suzuki et al. 2013; Aspell et al. 2013). Suzuki and colleagues (2013) demonstrated that watching a virtual depiction of the participant's hand pulsing in synchrony with their own heartbeats induced the subjective experience of ownership over the virtually projected hand. This effect was not observed when the cardiac signals were presented out-of-synchrony with the participant's heartbeats. Interestingly, participants with higher IAcc experienced a stronger illusory sense of ownership over the virtual hand than participants with lower IAcc. Similarly, Aspell and colleagues (2013) showed that watching a projection of the participants' body (virtual body) surrounded by an illuminating silhouette flashing synchronously, as opposed to asynchronously, with their own heartbeat led to enhanced self-identification and greater shift in self-location towards the virtual body. These studies indicate that the integration of sensory information across the interoceptive and exteroceptive domains via cardio-visual synchrony can alter body-ownership.

We here capitalise on these recent findings to investigate for the first time the neural dynamics underpinning this integration of multisensory bodily signals coming from *outside* and from *within* the body. To explore this question, we first provide a proof of concept behavioural study that tests the effect of cardio-visual stimulation on self-recognition using a modified version of the Enfacement Illusion. Next, we used electroencephalography (EEG) to investigate if the neural responses to own heartbeats are modulated by the integration of interoceptive and exteroceptive signals.

In Experiment 1, we projected a pulsing shade, that was synchronous or asynchronous with the participant's heartbeats, onto a picture that depicted the face of an unfamiliar other morphed with the participant's own face. Before and after this cardio-visual stimulation, participants carried out a self-other face recognition task to assess the changes that cardio-visual stimulation caused in the mental representation of their own face. In experiment 2 we used a similar procedure and, in addition, during the cardio-visual stimulation we measured participants' heartbeat evoked potential (HEP) – an electrophysiological index of cortical processing of cardiac signals (Pollatos and Schandry 2004). This allowed us to investigate changes in the brain mechanisms associated with cardiac processing during the cardio-visual stimulation. Based on past results (Tsakiris et al. 2011; Suzuki et al. 2013) that highlight the critical role of interoceptive accuracy in the integration of exteroceptive and interoceptive information we measured the participants levels of IAcc using the mental tracking task (Schandry 1981), an established measure of the ability to monitor heartbeats.

We hypothesised that synchronous (as opposed to asynchronous) cardio-visual stimulation would lead to changes in the mental representation of one's face (Aspell et al. 2013; Suzuki et al. 2013; Tajadura-Jimenez et al. 2012a). Behaviourally this would be reflected in changes in the self-face recognition task after synchronous stimulation, as well as by explicit reports in the subjective questionnaire. Moreover, the effects of synchronous cardio-visual stimulation would be greater in those individuals with higher levels of IAcc (Suzuki et al. 2013; Azevedo et al. 2016), as measured by the mental tracking task. We also hypothesised that shifts in self-face representation due to cardio-visual stimulation would lead to changes in the cortical response to cardiac signals, i.e. the HEP component. Moreover, HEP amplitude changes would rely on the individuals' trait IAcc, such that HEP modulation was expected to be greater in individuals with higher as opposed to lower IAcc.

Experiment 1:

Material and Methods

Participants

A total of 36 (24 females; mean age=21, s.d.=3.1) healthy volunteers took part in this experiment. Data from 4 participants was excluded from analyses due to incorrect interpretation of the visual analogue scale (VAS) used to collect ratings in the self-face recognition task. Additionally, analyses looking at changes in the Point of Subjective Equality (see below) for each condition revealed the presence of 3 outliers (+/- 2.5 s.d. from the mean). Thus, the final sample comprised 29 (18 females; mean age=21.2, s.d.=3.3) participants.

Stimuli

Stimuli used during the *cardio-visual stimulation* period consisted of photos of the participant's face with a neutral expression morphed with the face of a same gender unfamiliar other. The stimulus set comprised 8 different unfamiliar models (4 females; 4 males), selected from our in-house database, that had never been seen by the participants prior to the experiment. To avoid carry over effects from one condition to the other, each participant was presented with two unfamiliar gender-matched models, one presented in the synchronous condition, one presented in the asynchronous condition (see below). Models associated with the synchronous and asynchronous condition were randomly used across participants. That is, each participant was presented only with 2 of these faces, and each face was randomly presented to some participants in the synchronous conditions and to other participants in the asynchronous conditions. The photographs of the participant's face were taken in a separate session, prior to the experimental session. These non-mirror-reversed photos were morphed with Fantamorph (v4.0.8 Abrosoft, http://www.fantamorph.com) and edited with Photoshop software (Adobe Systems, San Jose, CA). Pictures presented during the stimulation period included hair, ears and upper torso. The presentation of coloured pictures aimed to present participants with highly realistic images to maximise the effect of the enfacement illusion (Tsakiris, 2008; Sforza et al. 2010; Paladino et al. 2010; Tajadura-Jimenez et al. 2012a, 2013). Conversely, pictures shown in the self-recognition task were desaturated (i.e. black and white) and cropped to hide hair, ears, and neck (Figure 1). This was done to prevent features unrelated to face morphology from interfering with judgments of self-recognition. It is worth noting that this is the common procedure in enfacement illusion studies (e.g. Tajadura-Jimenez et al. 2013). Two degrees of morphing were used during the stimulation period: 40%-self/60%-other (hereafter referred to as 40/60) and 60%-self/40%-other (hereafter referred to as 60/40). The 40/60 morphed stimulus served as the experimental condition because this stimulus contained a greater percentage of the other's face, and we were principally interested in testing whether synchronous cardio-visual stimulation with that stimulus would alter self-recognition performance. The 60/40 morphed stimulus served as the control condition as it contained a larger percentage of the self, and we did not expect self-face recognition performance to be affected in this case.

Experimental procedure

Participants were comfortability sited in an armchair with a standard 3-lead electrocardiogram (ECG) attached to their chest to monitor their heart activity throughout the session (Powerlab, ADInstrumens, www.adinstruments.com). A hardware-based function detected each R-wave to synchronise stimuli presentation with the participants' heartbeats.

The main experimental procedure was organised in four blocks, each comprising the following sequence of tasks: *Pre-Stimulation Face Recognition Task – Cardio-Visual Stimulation – Post-Stimulation Face Recognition Task – Questionnaire* (Figure 1A). Each block began with the presentation of the participant's photo (100% self) for 5 seconds, followed by the photo of a same gender unfamiliar other (100% other) for 5 seconds. Participants were instructed that a set of morphing images of these two photos would be presented in that block.

Stimulation consisted of periodic pulses of decreased luminosity over the upper torso and face leaving constant the luminosity of the background (see Figure 1C). Each of these pulses had a duration of 100ms and they could be presented either synchronously or asynchronously with the participant's own heartbeats. During the synchronous stimulation, pulses were presented 200ms after each ECG's R-wave. This time window was selected to coincide with the period of maximum subjective perception of heartbeats (Brener et al. 1993; Suzuki et al. 2013). In the asynchronous conditions, pulses mimicked the rhythm of another person's previously recorded heart at rest with a heart rate 10% faster or slower than the participant's heart rate (estimated from the 20 heartbeats immediately preceding the onset of the cardio-visual stimulation period of each block). Faster or slower asynchronous rhythms were counterbalanced across participants. Thus, each of the four blocks was characterised by the synchronicity of the stimulation and degree of morphing: *synchronous 40/60; synchronous 60/40; asynchronous 40/60; asynchronous 60/40.* Information regarding the cardio-visual synchrony stimulation was never mentioned to participants. Instead, they were told that the ECG recordings had the purpose of measuring cardiac responses to the perception of faces with different degrees of self-other morphing.

Before and after the cardio-visual stimulation, participants carried out the face recognition task. They were presented with a randomised series of black and white photos reflecting different degrees of morphing - from 20% self/ to 80% self in steps of 2%. A black template was imposed to these photos to remove non-facial attributes (e.g., background, hair, ears) (Figure 1). Participants were asked to rate each photo on a VAS (ranging from 0-100) "*how similar is this face to your own?*" Extremes of the scale were anchored with "*mostly similar to me*" (100) and "*least similar to me*" (0). This task allowed to estimate the degree of morphing for which participants judged to equally represent "other" and "self" traits, hereafter referred to as *point of subjective equality* (PSE). PSE was estimated by fitting the participants' ratings for each picture into a logistic function, and corresponds to the central point, 50%, of this fitted psychometric curve. The comparison of the PSEs assessed previously and subsequently to cardio-visual stimulation allows estimating changes in self-other mental representation due to the stimulation (Sforza et al. 2010; Tajadura-Jimenez et al. 2012b). It should be noted that by combining pre and post stimulation PSE measurements with between-participants randomised counterbalancing of faces used in synchronous and asynchronous conditions we were able to control, or at least greatly minimise, any general non-specific effects of similarity differences between self and other face at baseline.

The *questionnaire* consisted in 5 questions (see Table 1), 3 of which related to changes in self-other face representation due to visual stimulation (Q1, Q2, Q3) (Tajadura-Jimenez et al.

2012a) and two related to the pulsing rhythm (Q4, Q5) (cf. Aspell et al. 2013). Participants answered on a VAS (ranging from 0-100) with the labels "*I disagree*" and "*I agree*" presented at the two extremes of the scales.

After the completion of the 4 experimental blocks, participants carried out the *mental tracking task* (Schandry 1981), a standard measure of the IAcc that reflects the ability to accurately identify and perceive heartbeats. Participants were asked to silently count their heartbeats, without feeling their pulse, during four trials of 25, 35, 45 and 100 seconds. Reported and measured heartbeats were compared to estimate an index of IAcc using the following equation (Schandry 1981):

$$(1 \div 4)\times \sum_{i=0}^{4} [1 - ((recorded\ items - counted\ items) \div recorded\ items)]$$

Debriefing

To understand if participants detected or had any suspicion about the synchrony between the pulses and their own heartbeats, at the end of the experimental session, we asked them the following questions: "*What do you think the purpose of this experiment was?*" and "*Did anything about the experiment seem strange to you, or was there anything you were wondering about?*" Only one participant mentioned a possible contingency between heartbeats and pulses, confirming that the processes mediating cardio-visual integration are largely implicit (Azevedo et al. 2016). We did not disclosure the relationship between heartbeats and pulses so that participants remained naïve for the EEG session.

Results

Point of Subjective Equality (PSE)

Our main analyses was focused on changes in the representation of self-other faces due to cardio-visual stimulation as measured by the change in the PSE at each condition. Data was submitted to a repeated measures ANOVA with 2 Time (Pre-stimulation; Post-stimulation) x 2 Synchrony (Synchronous; Asynchronous) x 2 Morphing (40/60; 60/40) as within-subject factors. The analysis revealed a main effect of Time (F(1,28)=12.21, p=0.002), and a main effect of Synchrony (F(1,28)=5.84, p=0.022), as well as an interaction Time x Morphing (F(1,28)=5.44, p=0.027), and an interaction Synchrony x Morphing (F(1,28)=5.0, p=0.034). However, the critical 3-way interaction Time x Synchrony x Morphing (F(1,28)=0.17, p=0.68) and the interaction Time x Synchrony (F(1,28)=0.85, p=0.36) were not significant. Because trait ability to monitor heartbeats may moderate participants' susceptibility to cardio-visual synchronicity effects (Suzuki et al. 2013) analyses were re-run with individual IAcc scores as covariates in the ANOVA. Indeed, the analysis showed that IAcc moderated the 3-way interaction - Time x Synchrony x Morphing x IAcc (F(1,27)=7.96, p=0.009), that was now significant (F(1,27)=7.14, p=0.013). The Time x Synchrony x IAcc (F(1,27)=4.80, p=0.038) was also significant. These results show that the ability to monitor own heartbeats modulates changes in one's own representation of self-other faces due to cardio-visual stimulation. To follow up on this effect, we subtracted pre-stimulation values from post-stimulation (ΔPSE) ratings and performed planned comparisons in separate ANCOVAs for the 40/60 and 60/40 conditions, with Synchrony (Synchronous; Asynchronous) as single within-subject factor and IAcc as covariate. Results revealed an effect of Synchrony in the 40/60 condition (F(1,27)=14.1, p=0.001; effect of IAcc: F(1,27)=16.6, p<0.001) but not in the 60/40 (F(1,27)=0.04, p=0.84; effect of IAcc: F(1,27)=0.08, p=0.9). This effect is illustrated by the correlation between IAcc and the ΔPSE for the synchronous minus the asynchronous 40/60 condition (r=0.617, p<0.001; Figure 2C).

Questionnaires

Separate analyses were carried out for the questions referring to enfacement effects (Questions 1-3) and questions referring to the subjective experience of the flashing (Questions 4-5). In the former case, an ANOVA with 3 Questions (Q1; Q2; Q3) x 2 Synchrony (Synchronous; Asynchronous) x 2 Morphing (40/60; 60/40) was carried out. The analysis showed a main effect of the factor Questions ($F(1,28)=6.45$, $p=0.003$) and an interaction Questions x Synchrony ($F(1,28)=4.6$, $p=0.014$). There were no other main effects or interactions (all $ps>0.05$). Thus, responses to the two Morphing conditions were averaged for each question. Planned comparisons between responses to the synchronous and asynchronous conditions for each question were performed. Synchrony had an effect on responses to Q2 ($t(1,28)=2.69$, $p=0.012$), but not responses to Q1 ($t(1,28)=-0.27$, $p=0.79$) neither to Q3 ($t(1,28)=-1.6$, $p=0.12$). To further explore the relation between the subjective responses and participants' IAcc, we included IAcc as covariate in the ANOVA. However, we did not observe any interaction of IAcc with Synchrony effects (all $ps>0.05$). Analyses on Questions 4-5 did not reveal a significant effect or interaction with Synchrony (all $ps>0.05$).

Discussion – Experiment 1

We observed that synchronous (vs. asynchronous) cardio-visual stimulation induced changes in the participant's recognition of their own face. In particular, the comparison between PSE values obtained before and after the cardio-visual stimulation in the synchronous, as opposed the asynchronous condition, reveals that the cardio-visual stimulation increased the perceived similarity between self and other faces. This pattern of results is comparable to the effects of visuo-tactile induction of the Enfacement illusion (Tsakiris 2008; Tajadura-Jimenez et al. 2012a; Sforza et al. 2010). These studies demonstrated unidirectional changes in the self-other distinction, showing changes in self-face recognition, but not in the recognition of the other's face. Self-recognition judgements depend on a comparison between the visual percept and a stored mnemonic representation of how a particular person (or the self) looks like

(Apps et al. 2012; Legrain et al. 2011). As with previous studies, the observed changes in self-recognition performance seem to reflect an updating in the mental representation of one's own facial appearance. Moreover, these results are in line with previous studies that reported feelings of body ownership of a virtual reality avatar and a virtual hand (Aspell et al. 2013; Suzuki et al. 2013) under conditions of cardio-visual stimulation. Overall, the results support the view that the integration of interoceptive and exteroceptive information is a critical mechanism for self-other distinction and for the construction or updating of self-face mental representations.

Interestingly, the effect of synchronous cardio-visual stimulation on self-recognition was dependent on individual trait levels of IAcc. Specifically, these stimulation-induced changes in self-other distinction increased linearly with IAcc. Thus, cardio-visual stimulation was particularly effective among those individuals who are, as a trait, better able to accurately perceive their own heartbeats. Even if participants were not aware of the contingency between their heartbeats and the pulses (as confirmed during debriefing), the presumably great sensitivity that individuals with higher IAcc have to interoceptive bodily signals facilitated the implicit integration of their cardiac activity with the visual stimulus depicting the other's face.

While both the behavioural task and the questionnaire data revealed that cardio-visual synchrony induces changes in self-face representation similar to those experienced with the classical enfacement illusion, we observed that trait levels of IAcc only correlated with behavioural changes, but not with subjective reports. This can be explained by the fact that while the face-recognition task (used to estimate ΔPSE) measures fine-grained shifts in self-face perception, the questionnaires rely on introspective evaluations to quantify the subjective experience of the illusion and thus constitute a coarser measure.

Having established a behavioural effect, we next investigated, for the first time, if this change in the mental representation of self- faces caused by the integration of interoceptive with exteroceptive (i.e. visual) signals is reflected at the level of cortical interoceptive processing, by focusing on changes in the neural responses to heartbeats, i.e. HEP, during the cardio-visual stimulation.

Experiment 2:

Material and Methods

Participants

Participants from Experiment 1 were contacted and invited to take part in Experiment 2. A total of 24 participants agreed to participate. Participants were neurologically unimpaired and received reimbursement for their participation. One participant was excluded from the sample due to excess of artifacts in the EEG signal (see EEG analysis) resulting in a total of 23 participants (9 males; mean age=21.9; s.d=3.71). Participants gave their informed consent, with approval by the Ethics Committee, Department of Psychology, Royal Holloway University of London. Experiment 2 was performed 1.5-5 months after Experiment 1.

Experimental procedure

Participants were seated in a dimly lit, sound-attenuated and electrically shielded chamber in front of a monitor at a distance of 80 cm. Participants' ECG was recorded following the same procedure as in Experiment 1. The ECG was recorded throughout all the experimental phases where there was cardio-visual stimulation.

Stimuli consisted of morphed pictures of the participants' upper torso and a face containing 40% of the participants' facial features and 60 % of the features of a gender-matched unfamiliar other (i.e., 40/60 degree of morphing). The 40/60 pictures were selected from Experiment 1 because, as expected, the effect of synchronous cardio-visual stimulation on the

PSE ratings was observed in the 40/60 synchronous (experimental) condition but not in the 60/40 synchronous (control) condition. There were 8 unfamiliar models (4 male, 4 female). Participants' face was morphed with faces of two randomly assigned models, one used in the synchronous condition and the other in the asynchronous condition. Besides, the stimulus set included pictures of the upper body and face of two owls. Pictures were approximately 1200 x 960 size and they were presented in a white background. As in Experiment 1, stimulation consisted of periodic pulses of decreasing luminosity of the upper torso and face leaving constant the luminosity of the background. The pulse length was 100ms and was presented either synchronously or asynchronously with the participant's own heartbeats.

The experiment contained 48 blocks of 90 seconds length, presented randomly. There were 4 block types, each presented 12 times. The experiment consisted of 2 experimental conditions, where participants were presented with the 40/60 morphed faces either in synchrony (synchronous experimental block) or asynchrony with their own heartbeats (asynchronous experimental block). In addition, there were 2 control conditions, where participants were presented with pictures of owls presented in synchrony (synchronous control block) or asynchrony (asynchronous control block) with their heartbeats. After each block, participants were presented with one question of a 6 item questionnaire, including the 3 questions related to changes in self-other face representation due to the visual stimulation (Tajadura-Jimenez et al. 2012a), and the 2 questions related to the pulsing rhythm used in Experiment 1. The additional question "*How distracted were you during this block?*" anchored by the expressions "*not at all*" and "*very much*" was also included to control for attention to the stimuli. Participants answered to each question twice for each condition, in a fully randomised way.

EEG and ECG recording

EEG was recorded with Ag-AgCl electrodes from 64 active scalp electrodes mounted on an elastic electrode cap, according to the International 10/20 system, using ActiveTwo system (AD-box) and Actiview software (BioSemi, Amsterdam, Netherlands; 512 Hz sampling rate; band-pass filter 0.16-100Hz (down 3 dB); 24 bit resolution). Electrodes were referenced to the Common Mode Sense and Driven Right Leg electrodes and rereferenced to the average reference off-line. As in the behavioural study, the ECG signal was recorded with a standard 3-lead ECG attached to participants' chest (Powerlab, ADInstrumens, www.adinstruments.com). The R-peaks of the EGC were identified using a hardware-based detection algorism. The onset of the R-waves were marked in the EEG recording. The average number of trials (heartbeats) contributing to the HEP were 1039 in the experimental synchronous condition; 1044.74 in the experimental asynchronous condition; 1050.91 in the control synchronous condition; and 1053.7 in the control asynchronous condition. Importantly, there were no significant differences in number of heartbeats between conditions (F(3,66)=0.597, p>0.05).

EEG data analysis

Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts). The data was digitally low-pass-filtered at 30 Hz. The data was then submitted to ICA as implemented in Vision Analyzer to correct for ocular and cardiac-field artifacts (CFAs) (Terhaar et al. 2014). The CFAs were corrected by removing the independent components (most often one, or two) whose timing and topography resembled the characteristics of the CFAs. The CFA represents a challenge to the analysis of the HEP because the averaging of the data around the R-peak amplifies the CFA becoming time-locked to the heartbeat (Luft and Bhattacharya, 2015). However, the ICA method has been shown to be of high efficiency in the removal of the independent components representing cardiac-field artifacts from the EEG signal, specifically within the time window where the HEP typically occurs, i.e. 200-

400ms (e.g. Terhaar et al. 2014; Park et al. 2014; Luft and Bhattacharya 2015) (see also figure 3D). To compute the HEP the EEG signal was epoched into 750ms segments, starting 150ms before the R-wave onset. Segments were baseline corrected using an interval from -150 to -50ms before the R-wave onset. The period ranging from -50ms to 0ms was not considered to avoid the inclusion of artifacts related to the QRS complex of the ECG signal when computing the baseline correction of the signal (e.g. Canales-Johnson et al. 2015). Moreover, in the present experimental design, longer baseline periods should be avoided as, for participants with faster heart rates, this period may partially overlap with late components of visual evoked responses to the pulsing stimulus of the immediately preceding trial. Automatic artifact rejection was combined with visual inspection for all participants (±100 μV threshold; 0.05% mean percentage of the data was rejected due to excessive amplitude). The minimum percentage of trials per condition included in the analysis was 82% (percentage of trials did not significantly differ between conditions; $p>0.05$). The signal was re-referenced to the arithmetic average of all electrodes. Single-subject ERP for each Condition (Experimental; Control) and Synchrony (Synchronous; Asynchronous) were calculated and used to compute ERP grand averages across subjects.

The HEP has a frontal-to-parietal distribution with higher amplitudes over the right, as opposed to the left, hemisphere (Dirlich et al. 1997; Pollatos and Schandry 2004; Kern et al. 2013; Schulz et al. 2015). Previous studies have defined the HEP as a positive deflection in fronto-central sites. However, the polarity of the HEP seems to vary across studies according to factors such as the task, sites, and time window analysed (Gray et al. 2007; Couto et al. 2014; Canales-Johnson et al. 2015). In the current study, analyses were restricted to 6 regions of interests (ROIs) (Figure 3A), defined according to the widespread distribution of the HEP topography and on the basis of the aforementioned studies. To estimate the effects of the cardio-visual stimulation on neural responses to heartbeats, mean voltages of the HEPs time-locked to R-wave onset were computed at the group level using a non-parametric randomisation test controlling for multiple-comparisons (Maris and Oostenveld 2007). Subject-wise activation time courses were extracted at the selected ROIs and were passed to analysis procedure of FieldTrip, the details of which are described by Maris and Oostenveld (2007). Subject-wise activation time courses were compared to identify statistically significant temporal clusters using a FieldTrip-based analysis (Oostenveld et al. 2011) of one ROI at a time (Canales-Johnson et al. 2015; Couto et al. 2014).

To test for the interaction effects between the Synchrony effect and the group (experimental vs. control) on HEP amplitudes, and the possibility that this effect is mediated by the participants' IAcc (as shown in experiment 1), we first computed the Synchrony effect (calculated by subtraction of amplitudes at each time point on the asynchronous trials from the synchronous trials) in both the experimental and control group. Then we calculated the difference linked to the Synchrony effect in the experimental vs. the control group at each time point, and we called it "difference Synchrony effect". We then passed the subject-wise activation time courses to the analysis procedure of Fieldtrip. In brief, this procedure regresses the "difference Synchrony effect" (computed as described above) on the predictor, i.e. participants' IAcc, at each corresponding temporal point in the subject-wise activation time courses using the independent sample regression coefficient T-statistics. FieldTrip uses a nonparametric method (Bullmore et al. 1999) to address the multiple comparison problem. t-values of adjacent temporal points whose p-values were less than 0.05 were clustered by adding their t-values, and this cumulative statistic is used for inferential statistics at the cluster level. This procedure, that is, the calculation of t-values at each temporal point followed by clustering of adjacent t-values was repeated 5000 times, with randomised swapping and resampling of the subject-wise averages before each repetition. This Monte

Carlo method results in a nonparametric estimate of the P-value representing the statistical significance of the identified cluster.

Results

Modulation of HEP amplitudes

The results of the cluster-based permutation test revealed significant modulations of the HEP amplitude as indicated by a significant negative cluster between 195 and 289ms after the R-wave onset (p=0.005) in the right centro-parietal ROI (Figure 3A). This time window is in accordance with the latencies reported in previous HEP studies, i.e. 200-400ms, where the cortical processing of cardiac signals takes place (Schandry, et al. 1986; Pollatos and Schandry 2004; Yuan et al. 2007; Fukushima et al. 2011; Kern et al. 2013; Canales-Johnson et al. 2015). Moreover, it minimises overlapping between the HEP and the VEP associated to the visual pulse staring at 120ms after the onset of the pulse (i.e., 200ms after the R wave). Based on the results of the cluster-based permutation analysis, we performed a correlation analysis (2-tailed) between IAcc and the HEP difference linked to the Synchrony effect (i.e. Synchronous vs Asynchronous) in the experimental vs. the control condition in the right centroparietal ROI between 195 and 289ms. This analysis revealed that the higher the IAcc the greater the HEP difference of the Synchrony effect in the experimental synchronous condition (r= -0.632, p=0.001; Figure 3E).

In addition, to ensure that the differences observed between conditions in the HEP cannot be explained by differences in the ECG signal, we analysed the ECG trace mimicking the analysing procedure followed in the HEP analysis. The results of the cluster-based permutation test on the ECG did not reveal any significant cluster of significant interactions at p<0.05, corrected for multiple comparisons.

Overall, these results show that the presentation of a 40/60 morphed face (i.e., containing 40% of the participants' features) whose luminosity changed in rhythmic pulses synchronously to the participants' heartbeats led to amplitude changes of the HEP component in the 195-289ms time window at centro-parietal sites in the right hemisphere. The interaction shown in Figure 3A,D illustrates the changes in HEP amplitude during the synchronous compared to asynchronous experimental cardio-visual stimulation, and to the control conditions, in which visual stimulation was perceived over the face of an owl. In other words, it demonstrates the distinct effect that synchronous cardio-visual stimulation has on HEP amplitudes when perceiving someone else's face vs an owl face. Importantly, such modulation of HEP amplitude was dependent on the individuals' trait levels of IAcc. Furthermore, the correlation analysis showed that the stimulation-induced changes on the HEP amplitude increased linearly with IAcc (see Figure 3E).

Questionnaires

In line with Experiment1, we carried out separate analyses for the questions referring to the enfacement effects (Questions 1-3), the subjective experience of the pulsing (Questions 4-5) and attention to the task (Question 6). Regarding the enfacement questions, the interaction between 3 Questions (Q1; Q2; Q3) x 2 Synchrony (Synchronous; Asynchronous) x 2 Condition (Experimental; Control) was not significant (F(1,44)=0.01, p=0.99). However, the critical interaction Synchrony x Condition was significant (F(1,22)=4.46,p=0.046), as well as the main effects of Synchrony (F(1,22)=10.13, p=0.004) and Condition (F(1,22)=102.83, p<0.001). Given that the analysis did not show a main effect of Question, nor in interaction (ps>0.05), we collapsed responses to Q1, Q2 and Q3 and performed planned comparisons between the synchronous and asynchronous cardio-visual stimulation in both the experimental and the control condition. Results showed significant differences between synchronous and asynchronous trials in the experimental condition (t(1,22)=2.88, p=0.009) but not in the control condition (t(1,22)=0.78, p=0.44). Regarding the questions about the subjective experience of pulsing (Q4-Q5), there were not significant main effects of the factors Condition (F(1,22)=0.37,p=0.55), nor Synchrony (F(1,22)=3.48,p=0.076), neither significant interactions (all ps>0.05). Likewise, there was no significant main effect, nor in interaction, for the question referring to attention to the task (all ps>0.05).

We also explored a possible relationship between subjective reports of enfacement and i) the magnitude of HEP changes and ii) individual levels of IAcc. For that, HEP changes and IAcc scores were included, in separate analyses, as covariates in the Condition x Synchrony ANOVA on the subject reports of enfacement (average responses to Questions 1-3). Neither IAcc (ps>0.05) nor HEP changes (ps>0.05) were found to have an effect over any main effect or interaction.

Discussion - Experiment 2

Experiment 2 shows that synchronous cardio-visual stimulation resulted in significant changes in the participants' subjective reports, as well as changes in the electrophysiological processing of cardiac signals. We observed reduced HEP amplitude during the synchronous, as opposed to the asynchronous, stimulation in the experimental condition, while no effects were observed in the control condition. In accordance with earlier findings (Gray et al. 2007; Couto et al. 2014; Canales-Johnson et al. 2015), the pattern of interaction in Figure 3A shows an HEP component represented by a deflection across parietal sites in the right hemisphere. This might reflect the importance of the right hemisphere in the integration of interoceptive and exteroceptive bodily related signals (Craig, 2009) and in self-recognition extending previous evidence on the key role of the right hemisphere to process information relative to the self (Keenan et al. 2000).

Furthermore, the effects of cardio-visual synchrony on HEP amplitude were dependent on individual trait levels of IAcc. In particular, the amplitude reduction of the HEP increased linearly with IAcc. Past studies have shown a link between individual differences in IAcc and

HEP amplitudes, such that individuals with higher IAcc show greater HEP amplitude than those with lower IAcc when they focus on their heartbeat (Pollatos and Schandry 2004; Yuan et al 2007). We here show IAcc-dependent modulations of HEP amplitudes when the brain integrates interoceptive and exteroceptive signals.

General discussion

Across two experiments, we focused on the mechanisms underpinning the integration of information originating from *outside* and from *within* our bodies, through cardio-visual stimulation. We investigated how this integration relates to changes in the mental representation of one's self, as assessed by changes in self-recognition. We report three key findings. First, we show that cardio-visual stimulation, i.e. perceiving a pulsing stimulus in synchrony with one's own heart over someone else's face, leads to changes in self-recognition and increases self-other perceived similarity. Second, we reveal that synchronous cardio-visual stimulation over another person's face was associated with the modulation of the HEP amplitude, an index of cortical representation of cardiac processing. Third, these changes in HEP were dependent on individual trait levels of IAcc, so that participants with higher IAcc exhibit greater changes on HEP amplitude, in comparison to participants with lower IAcc.

How does the change of neural activation locked to heartbeats reflects the experimentally induced changes of bodily self-consciousness? In the classic exteroceptive ways of inducing illusions of ownership, there is an initial inter-sensory conflict (e.g. between felt and seen touch). To solve this conflict, the brain attenuates the importance of incoming proprioceptive and somatosensory inputs and assigns greater salience to visual information (Tsakiris 2010; Apps and Tsakiris 2014; Zeller et al. 2015). This results in a recalibration of visual-tactile coordinates (i.e. touch referral) that leads to an updated sense of body-ownership. In support of this idea, neuroimaging data shows that ownership of an artificial hand in the RHI, or with a virtual body in the full body illusion, is linked to changes in neural activity in the somatosensory cortex (Tsakiris et al. 2007; Zeller et al. 2015; Evans and Blanke 2013; Aspell et al. 2012; Lenggenhager et al. 2011). In particular, Tsakiris and colleagues (2007) found that the degree of proprioceptive drift, an objective index of strength of the illusion, was linearly correlated with decreased activity in the somatosensory cortex. Moreover, Zeller and colleagues (2015) demonstrated an amplitude reduction of the somatosensory evoked potentials (SEPs) to brushstrokes delivered to the participants' hand synchronously to brushstrokes delivered to the artificial hand placed in an anatomically congruent, vs. incongruent, position. This reduction in SEP was interpreted as decreased processing of own somatosensory signals allowing to solve the multisensory conflict experienced by the RHI.

In our study, we observed changes in HEP amplitude when one's heartbeat sensations were congruent with the visual cues originating from someone else's face, creating the subjective experience of self-other merging. These results suggest that during cardio-visual stimulation, i.e. one's heartbeat projected onto someone else's face, the external representation of what seems to be inherently private information to the self creates a conflict (i.e. heartbeats being simulated by an external agent). Consistently with previous research, this conflict may be solved by attenuating the salience of interoceptive sensations leading to reduced HEP amplitudes relative to the control conditions. Overall, these findings complement and advance previous evidence on cortical attenuation during classical bodily illusions, demonstrating that the cortical processing of interoceptive signals may be subject to the same principles as somatosensory signals (Zeller et al. 2015).

Our findings add to the growing body of literature suggesting the HEP as an important index of cortical processing of afferent cardiovascular activity (Leopold and Schandry 2001). The magnitude of HEPs has been consistently associated to the representation of the bodily aspects of emotional processing (Müller et al. 2015; Fukushima et al. 2011; Couto et al. 2014; Luft and Bhattacharya 2015) and self-processing (Schulz et al. 2015; Pollatos and Schandry 2004; Canales-Johnson et al. 2015). Of particular relevance for the present study is the recent finding of reduced HEP amplitudes among individuals suffering from depersonalisation/ derealisation disorder (Schulz et al. 2015). In this study, the authors established a close link between altered experiences of bodily self and the cortical processing of heartbeats. Our results expand these findings by showing that *dynamic* and *on-line* modulations of heartbeat processing are related to shifts in the mental representation of one's self in healthy individuals. In specific, HEP modulation is likely to reflect a mechanism by which the brain attempts to reduce the multisensory conflict by attenuating the cortical representation of own heartbeat signals to allow the updating of self-representations. Overall, our results support the idea of plasticity of self-representations under circumstances of simultaneous integration of exteroceptive and interoceptive signals related to the body. They provide a direct link between the brain mechanisms processing on-line interoceptive bodily signals and the process of identifying with a face, a crucial aspect of self-awareness.

Could there be alternative explanations to our results? Recent studies have shown bidirectional links between the amplitude of neural responses to heartbeats and visual processing (Park et al. 2014, Salomon et al., 2016; Fukushima et al. 2011; Couto et al. 2014; Luft and Bhattacharya 2015). Interestingly, recent research showed reduced cortical processing (van Elk et al., 2014) and reduced insula activity (Salomon et al., 2016), a key region in the processing of interoceptive signals, to stimuli presented synchronously with the participant's heartbeats. Could therefore the modulation of the HEP observed in our study reflect a purely visual effect driven by synchrony? Crucially, we did not find any significant changes in the HEP amplitude in the synchronous control condition, i.e. synchronous stimulation over the owl's face. This therefore suggests that the HEP amplitude reduction observed in the synchronous experimental condition cannot be explained by pure visual effects. It is also worth noting that previous physiological and electrophysiological data has shown a partial overlap between the HEP and the electrocardiac field up to 450ms after the R-wave (Dirlich et al. 1997) suggesting that the observed HEP amplitude changes could be partially explained by the differences in the temporal occurrence of the CFA between synchronous *vs.* asynchronous stimulation. Although we cannot entirely rule out this possibility, there are three reasons why this is unlikely. Firstly, the temporal dynamics of the CFA were identical in both the experimental and the control synchronous condition. However, the modulation of HEP was only observed in the former. Secondly, we submitted the EEG data to ICA, which has been shown to be highly efficient to remove CFA from HEPs (Terhaar et al. 2014; Park et al. 2014; Luft and Bhattacharya 2015). Moreover, analyses of the ECG did not reveal significant differences between the conditions. Thus, we are confident that the observed HEP reduction is a consequence of the illusory experience of self-other merging due to cardio-visual integration.

Previous research by our group has shown that individuals with lower IAcc are particularly susceptible to bodily illusions relying on exteroceptive cues, such as the RHI (Tsakiris et al. 2011) and the enfacement illusion (Tajadura-Jimenez et al. 2013). Then, we suggested that individuals with lower IAcc displayed a more malleable self- representation in response to exteroceptive cues. Interestingly, here, and in line with the findings of Suzuki and colleagues (2013; see also Azevedo et al. 2016), we observed the opposite pattern. Specifically, individuals with higher IAcc revealed greater incorporation of other's features related to the integration between one exteroceptive signal and one interoceptive signal. These results may initially seem at odds with the former. However, the role played by IAcc in the classic methods of induction of the illusion (Tsakiris et al. 2011; Tajadura-Jimenez et al. 2013) and in the cardio-visual adaptations (see present experiments, and Suzuki et al. 2013; Aspell et al.

2014) is likely to be very different. While cardiac information is not directly involved in the induction of visual-tactile illusions, in cardio-visual stimulation paradigms interoceptive cues are part of the induction mechanism. Moreover, because heart sensations are considerably faint and people differ greatly in their ability to attend, monitor and process cardiac signals at a higher cortical level (e.g. HEPs), IAcc crucially determines the extent to which the illusion is experienced. Individuals with higher IAcc, presumably, have greater access to their cardiac signals. This would facilitate the integration of their cardiac signals with the other's face leading to a greater incorporation of the other's facial features in the mental representation of their own face in comparison to lower IAcc. Furthermore, the greater HEP amplitude reduction observed in individuals with higher IAcc seems to indicate high flexibility in the process of interoceptive signals at the cortical level (Barrett and Simons 2015).

Recent theoretical proposals have suggested that self-processing can be characterised by the principles of Predictive Coding (PC) (Fotopoulou 2012; Apps and Tsakiris 2014; Seth 2014; Sel 2014; Barrett and Simons 2015). According to this view, the sensory input is compared with internal models, which are constantly updated by compiling the statistical regularities of past inputs (Friston and Kiebel 2009). Within predictive coding models of self-awareness (Apps and Tsakiris 2014; Seth 2014) one's body is processed in a Bayesian manner as the most likely to be "me". That is, one's own body is the one which has the highest probability of being "mine" as other objects are probabilistically less likely to evoke the same sensory inputs. This information can be considered as highly abstract with respect to the low-level properties of the stimuli and it can only be represented as "self" when different streams of multisensory information are integrated. That is, the self-face will only be recognised as "self" when a visual stimulus has been processed hierarchically for its low level visual properties, its configural features and then its identity. The self-face will therefore be represented as an abstract, supramodal representation of visual input e.g. this is a face, that I have seen before, that I am familiar with, and that is associated with congruent corollary discharge, vestibular, somatosensory and interoceptive information. Such probabilistic representation arises through the integration of information from hierarchically organised unimodal systems in higher-level multimodal areas. This process entails that probabilistic representations are created through the integration of top-down "predictions" about the body and of bottom-up "prediction errors" (PEs) from unimodal sensory systems that are then explained away. Importantly, within predictive coding, priors, predictions and associated predictions errors are all represented in terms of precision. "Precision" refers to the inverse variance associated with each probability distribution and is thus a measure of their relative salience and reliability (Friston 2009). Precision operates both within and between modalities. Within any modality, at each level of the hierarchy and taking account of the given context, the brain weighs the relative precision of PEs that informs or revises expectations at higher level of the hierarchy (Hohwy 2012; Brown et al. 2013).

The use of cardio-visual stimulation employed in the present experiments allowed us to test empirically whether the brain will attenuate the visual or the interoceptive information. The neural evidence presented in Experiment 2 that is indicative of a reduction of the HEP in the critical test condition suggests that interoceptive information is attenuated. In a way these results are comparable to the attenuation of somatosensory signals in the classic visuo-tactile stimulation during the Rubber Hand Illusion (Zeller et al. 2015; Limanowski and Blankenburg 2015). Importantly, predictive coding models allow us to test how contextual factors influence information processing as the precision of predictions and predictions errors may vary considerably across different contexts (see also Apps and Tsakiris 2014). For example, visual information may be more precise in the context of self-recognition, while in the absence of visual input or at night, when vision becomes imprecise, the relative precision of interoceptive signals necessarily increases (Pezzulo 2014). Therefore, the relative precision of PEs and priors across sensory modalities is constantly being updated. Thus, as shown here, in contexts that rely heavily on visual information, i.e. self-recognition, interoceptive signals are attenuated, possibly at higher order cortical areas, under conditions of cardio-visual synchrony. In accordance, the HEP amplitude reduction provides evidence of a neurophysiological mechanism throughout which the sensory input is attenuated to update the mental representations of one's self according to the external evidence.

In conclusion, this study provides new insights on the integration of multisensory bodily signals coming from *outside* and from *within* the body and its influence in self-face representation. We designed two experiments that investigated whether synchronous cardio-visual stimulation can enhance self-identification with the face of another and the cortical processing of such an altered experienced. Our data showed that multisensory integration of heartbeat sensations with the visual exteroceptive information of the face of another leads to an illusory sense of identification with the other's face, and to an amplitude reduction of the HEP component. No such effects were found when the interoceptive and exteroceptive signals were presented in an asynchronous manner. We therefore provide direct neural evidence for the integration of interoceptive and exteroceptive signals in bodily self-awareness.

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Figures:

Figure 1

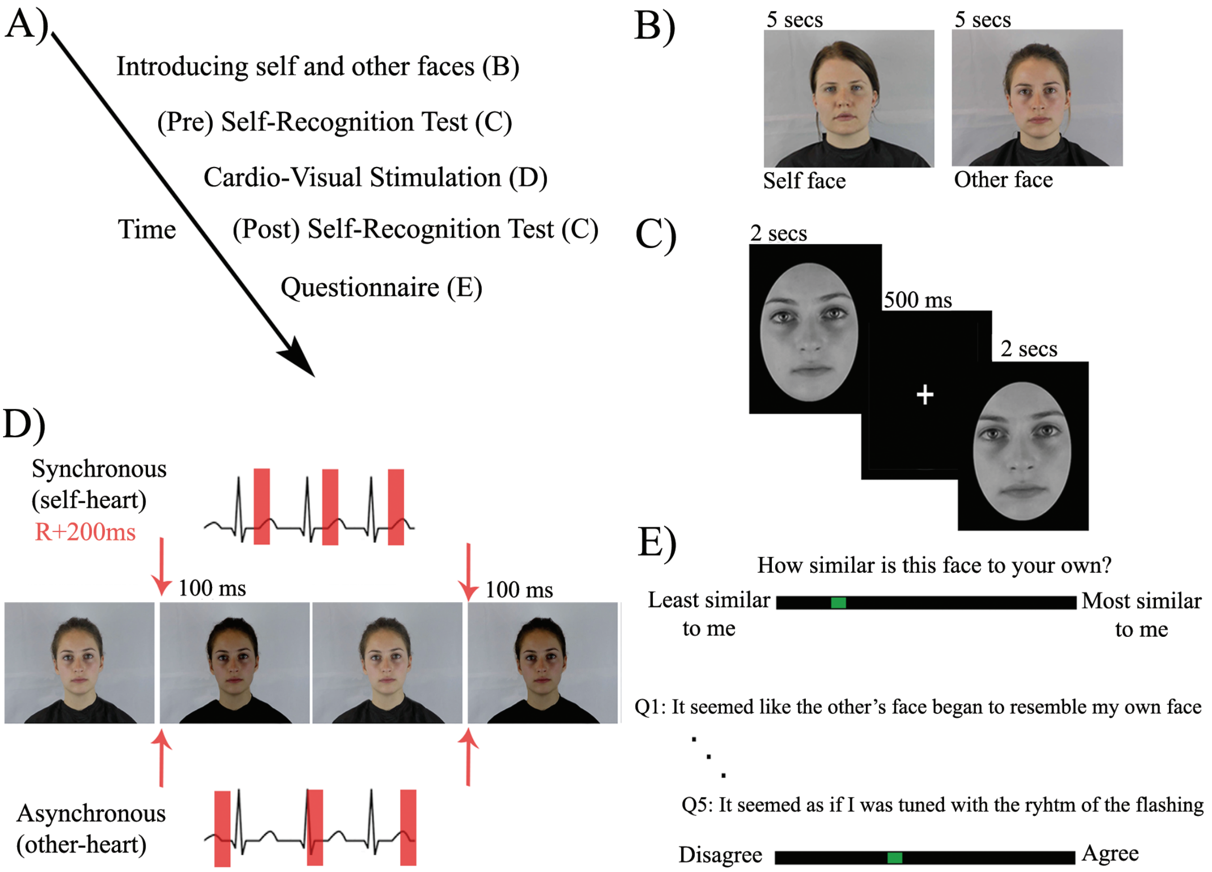

Figure 2

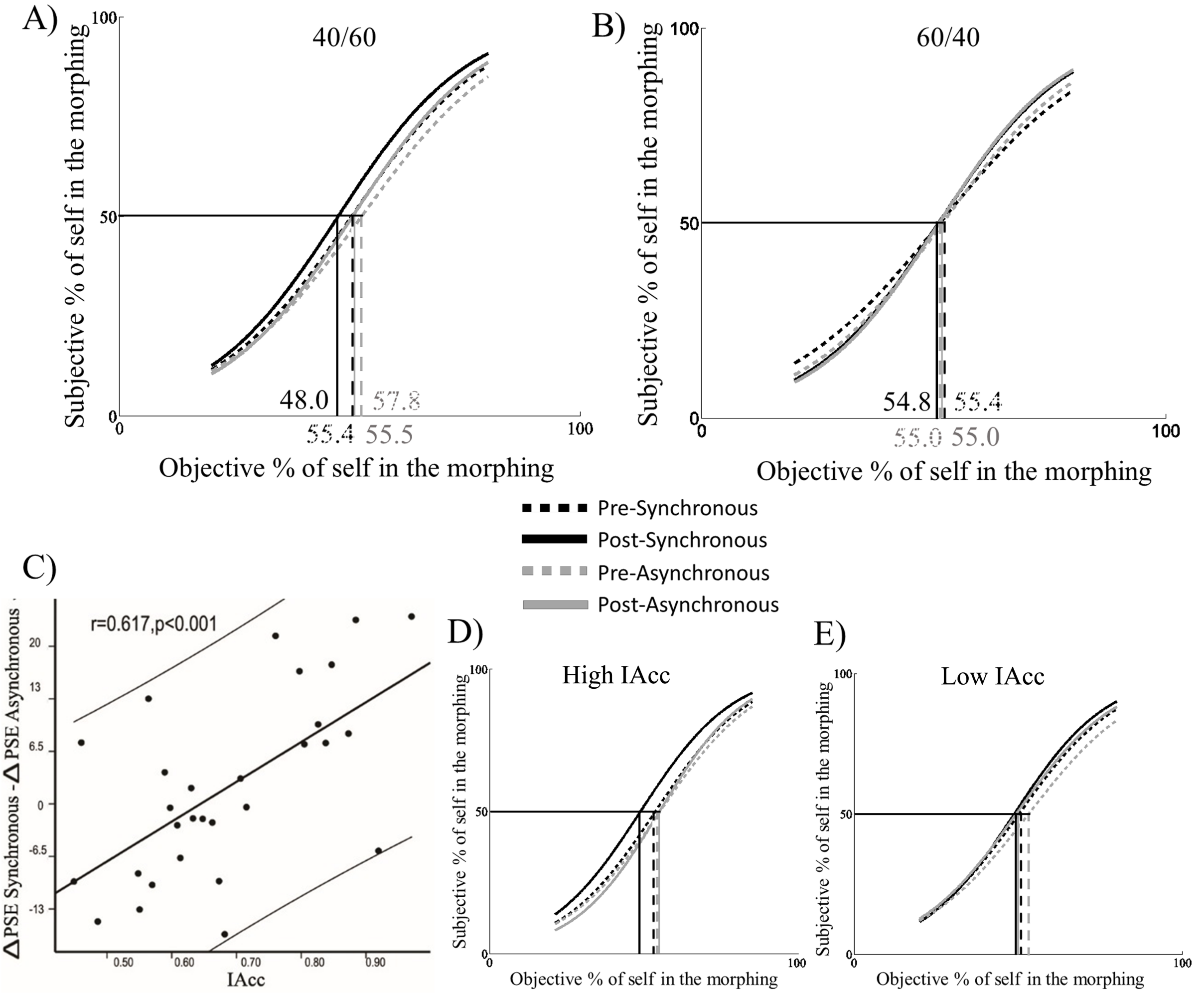
A)
40/60
Subjective % of self in the morphing
Objective % of self in the morphing
0
50
100
48.0
57.8
55.4
55.5
B)
60/40
Subjective % of self in the morphing
Objective % of self in the morphing
54.8
55.4
55.0
55.0
Pre-Synchronous
Post-Synchronous
Pre-Asynchronous
Post-Asynchronous
C)
r=0.617,p<0.001
Δ PSE Synchronous - Δ PSE Asynchronous
IAcc
20
13
6.5
0
-6.5
-13
0.50
0.60
0.70
0.80
0.90
D)
High IAcc
E)
Low IAcc
Subjective % of self in the morphing
Objective % of self in the morphing

Figure 3

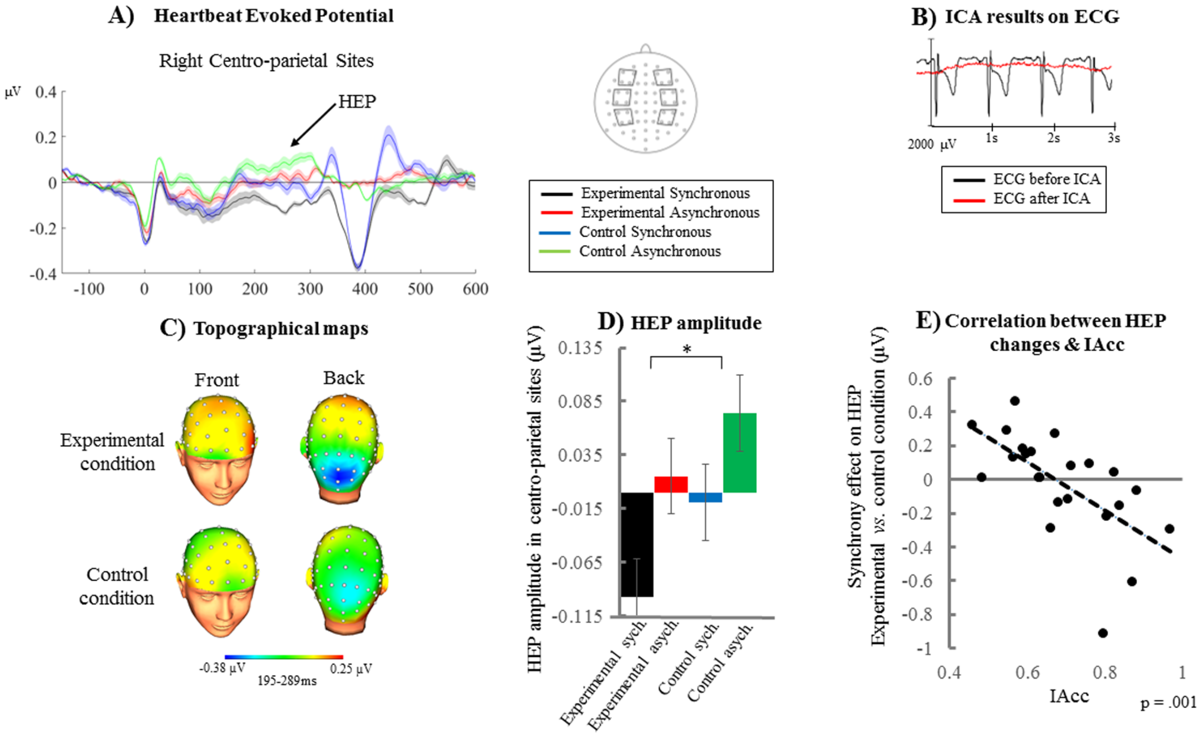
A) Heartbeat Evoked Potential
Right Centro-parietal Sites
µV
0.4
0.2
0
-0.2
-0.4
HEP
-100
0
100
200
300
400
500
600
Experimental Synchronous
Experimental Asynchronous
Control Synchronous
Control Asynchronous
B) ICA results on ECG
2000 µV
1s
2s
3s
ECG before ICA
ECG after ICA
C) Topographical maps
Front
Back
Experimental condition
Control condition
-0.38 µV
0.25 µV
195-289ms
D) HEP amplitude
HEP amplitude in centro-parietal sites (µV)
0.135
0.085
0.035
-0.015
-0.065
-0.115
*
Experimental sych.
Experimental asych.
Control sych.
Control asych.
E) Correlation between HEP changes & IAcc
Synchrony effect on HEP Experimental vs. control condition (µV)
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
0.4
0.6
0.8
1
IAcc
p = .001

Table 1

Questions	**Study 1**				**Study 2**			
	Synchronous		**Asynchronous**		**Synchronous**		**Asynchronous**	
	40/60	60/40	40/60	60/40	Face	Owl	Face	Owl
Q1- It felt like the other`s face was my face	54.2 (32.0)	47.2 (34.2)	48.5 (31.4)	58 (30.4)	59.5 (30.2)	8.5 (17.3)	44.3 (33.8)	7.8 (17.6)
Q2 - It seemed like the other`s face began to resemble my own face	66.4 (27.8)	69.5 (27.9)	58 (28.6)	61.5 (31.8)	59.3 (30.3)	8.3 (16.5)	46.3 (32.9)	6.3 (14.0)
Q3 - It seemed like my own face began to resemble the other person`s face	61.6 (25.9)	63.6 (28.4)	67.0 (26.6)	68 (29.7)	56.3 (30.9)	6.8 (15.5)	44.1 (30.2)	8.2 (16.3)
Q4 - It seemed as if the flashing was inside or going through my body	40.4 (32.6)	35.4 (32.0)	30.4 (26.9)	34.6 (31.4)	54.7 (26.7)	43.3 (29.8)	37.9 (27.0)	37.4 (30.1)
Q5 - It seemed as if I was tuned with the rhythm of the flashing	62.5 (29.8)	52.4 (29.9)	61.2 (29.1)	48.5 (29.0)	55.5 (28.2)	58.3 (27.9)	52.8 (29.4)	54.9 (29.2)
Q6 - How distracted were you during this trial	-	-	-	-	45.8 (27.6)	47.8 (24.6)	44.8 (26.5)	53.1 (24.0)

Caption to figures:

Figure 1. Schematic representation of the experimental protocol. *A*) Timeline of each block; *B*) Self and other faces presented at the beginning of the block; *C*) Self-recognition test carried out before and after the *D*) cardio-visual stimulation procedure; *E*) Questionnaire on the subjective experience associated with the stimulation administered at the end of each block.

Figure 2. *A*) Cardio-visual stimulation induced changes in the mental representation of self/other faces as reflected by a shift in the Point of Subjective Equality (PSE) after synchronous (vs. asynchronous) in the 40/60 condition but *B*) not in the 60/40 condition. In the former condition, participants accepted more facial features of the "other" in the morphed pictures judged to equally represent "self" and "other". Interestingly, this effect was linearly dependent on individual levels of IAcc, such that cardio-visual interaction effects were stronger in higher interoceptors. This relationship is represented by the *C*) positive correlation between IAcc scores and the difference between PSE changes in the synchronous and asynchronous conditions. For illustration purposes PSEs pre- and post-stimulation for each 40/60 condition are represented separately for *D*) Higher and *E*) Lower interoceptors.

Figure 3. *A*) R-locked HEP in the experimental synchronous (black) and asynchronous (red) conditions, and in the control synchronous (blue) and asynchronous (green) conditions, over frontal, central, and parietal sites in the right hemisphere. Although the enhanced reduction of the HEP amplitude seems to be greater in frontal sites, the statistical analysis including IAcc as a covariate shows that the HEP changes occur across all sites in the right hemisphere. *B*) ECG channel of a selected participant before (black) and after (red) applying ICA. This shows the effectiveness of ICA to remove CFA. *C)* Topographical maps showing differential HEP activity (synchronous trials – asynchronous trials) in the experimental and control conditions. *D*) HEP amplitude in the selected frontal ROI. *E*) Negative correlation between

IAcc scores and the synchrony effect (computed as the difference between synchronous and asynchronous trials) in the experimental *vs*. the control condition.

Caption to tables:

Table 1. Questionnaire scores in Experiment 1 and Experiment 2. Average (and SD) ratings for each question.