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.

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2   **Introduction**

3   The sense of body-ownership, that is, the sense of owning and identifying with a particular

4   body, is a fundamental aspect of self-awareness (Blanke and Metzinger 2009). Body-

5   ownership has been typically studied through the use of bodily illusions that rely upon the

6   multisensory integration of exteroceptive signals, such as vision and touch, focusing therefore

7   on how the body is perceived *from the outside.* More recently, it has been suggested that

8   interoceptive signals, that is the perception of internal physiological states of the body as

9   perceived *from within,* may also play an important role for body-ownership (Craig 2009;

10   Tsakiris et al. 2011). While the effects of exteroceptive signals on producing or altering the

11   sense of body-ownership have been well documented (for a review see Tsakiris 2010), the

12   process of integrating interoceptive and exteroceptive signals and the effects that their

13   integration has on self-awareness are less well understood.

14   A large body of empirical evidence has shown that the integration of exteroceptive

15   information such as vision and touch can alter the sense of body-ownership for body-parts

16   and full bodies (see Blanke 2012 and Tsakiris 2010 for reviews). For example, in the now

17   classic Rubber Hand Illusion (RHI), observing an artificial hand being stroked in synchrony

18   with strokes applied to one's own hand leads to the subjective incorporation of the rubber

19   hand as part of one's own body, to "feel like it's my hand" (Botvinick and Cohen 1998).

20   Beyond ownership over body-parts, other studies have used the same method of multisensory

21   integration[1] (i.e. visuo-tactile stimulation) to ask whether similar changes would occur in the

22   representation of one's own face. In the Enfacement Illusion (Tsakiris, 2008; Sforza et al.

23   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).

24   one's own face evokes changes in self-face recognition, so that we perceive the other

25   person's face as more similar to one's own. This extension from bodies to faces, which are

26   arguably the most distinctive features of one's body, suggests that multisensory integration is

27   a shared critical mechanism for the construction of body-ownership and self-face recognition.

28   Beyond the known role of exteroceptive information, the role that interoceptive information

29   may play in body-awareness has remained largely unexplored. The first study to link the

30   perception of the body *from the outside* with the perception of the body *from the inside*

31   showed that the illusory sense of ownership of an artificial hand, (i.e. RHI, elicited by

32   exteroceptive information) is negatively correlated with the individual's interoceptive

33   accuracy (IAcc), which refers to the ability to detect interoceptive signals, such as one's

34   heartbeats (Tsakiris et al. 2011). This study provided the first empirical evidence for the

35   influence of interoception on the integration of body-related sensory signals arising from

36   different exteroceptive domains. Interestingly, in a way analogous to the effects of IAcc on

37   the RHI, individual traits of IAcc were shown to predict changes in self-other boundaries

38   during the Enfacement Illusion (Tajadura-Jimenez et al. 2012a; 2012b). More recently, direct

39   evidence for the integration of exteroceptive and interoceptive information in body-

40   ownership comes from two virtual reality studies (Suzuki et al. 2013; Aspell et al. 2013).

41   Suzuki and colleagues (2013) demonstrated that watching a virtual depiction of the

42   participant's hand pulsing in synchrony with their own heartbeats induced the subjective

43   experience of ownership over the virtually projected hand. This effect was not observed when

44   the cardiac signals were presented out-of-synchrony with the participant's heartbeats.

45   Interestingly, participants with higher IAcc experienced a stronger illusory sense of

46   ownership over the virtual hand than participants with lower IAcc. Similarly, Aspell and

47   colleagues (2013) showed that watching a projection of the participants' body (virtual body)

48   surrounded by an illuminating silhouette flashing synchronously, as opposed to

49   asynchronously, with their own heartbeat led to enhanced self-identification and greater shift

50   in self-location towards the virtual body. These studies indicate that the integration of sensory

51   information across the interoceptive and exteroceptive domains via cardio-visual synchrony

52   can alter body-ownership.

53   We here capitalise on these recent findings to investigate for the first time the neural

54   dynamics underpinning this integration of multisensory bodily signals coming from *outside*

55   and from *within* the body. To explore this question, we first provide a proof of concept

56   behavioural study that tests the effect of cardio-visual stimulation on self-recognition using a

57   modified version of the Enfacement Illusion. Next, we used electroencephalography (EEG) to

58   investigate if the neural responses to own heartbeats are modulated by the integration of

59   interoceptive and exteroceptive signals.

60   In Experiment 1, we projected a pulsing shade, that was synchronous or asynchronous with

61   the participant's heartbeats, onto a picture that depicted the face of an unfamiliar other

62   morphed with the participant's own face. Before and after this cardio-visual stimulation,

63   participants carried out a self-other face recognition task to assess the changes that cardio-

64   visual stimulation caused in the mental representation of their own face. In experiment 2 we

65   used a similar procedure and, in addition, during the cardio-visual stimulation we measured

66   participants' heartbeat evoked potential (HEP) – an electrophysiological index of cortical

67   processing of cardiac signals (Pollatos and Schandry 2004). This allowed us to investigate

68   changes in the brain mechanisms associated with cardiac processing during the cardio-visual

69   stimulation. Based on past results (Tsakiris et al. 2011; Suzuki et al. 2013) that highlight the

70   critical role of interoceptive accuracy in the integration of exteroceptive and interoceptive

71   information we measured the participants levels of IAcc using the mental tracking task

72   (Schandry 1981), an established measure of the ability to monitor heartbeats.

73 We hypothesised that synchronous (as opposed to asynchronous) cardio-visual stimulation

74 would lead to changes in the mental representation of one's face (Aspell et al. 2013; Suzuki

75 et al. 2013; Tajadura-Jimenez et al. 2012a). Behaviourally this would be reflected in changes

76 in the self-face recognition task after synchronous stimulation, as well as by explicit reports

77 in the subjective questionnaire. Moreover, the effects of synchronous cardio-visual

78 stimulation would be greater in those individuals with higher levels of IAcc (Suzuki et al.

79 2013; Azevedo et al. 2016), as measured by the mental tracking task. We also hypothesised

80 that shifts in self-face representation due to cardio-visual stimulation would lead to changes

81 in the cortical response to cardiac signals, i.e. the HEP component. Moreover, HEP amplitude

82 changes would rely on the individuals' trait IAcc, such that HEP modulation was expected to

83 be greater in individuals with higher as opposed to lower IAcc.

84 **Experiment 1:**

85 **Material and Methods**

86 *Participants*

87 A total of 36 (24 females; mean age=21, s.d.=3.1) healthy volunteers took part in this

88 experiment. Data from 4 participants was excluded from analyses due to incorrect

89 interpretation of the visual analogue scale (VAS) used to collect ratings in the self-face

90 recognition task. Additionally, analyses looking at changes in the Point of Subjective

91 Equality (see below) for each condition revealed the presence of 3 outliers (+/- 2.5 s.d. from

92 the mean). Thus, the final sample comprised 29 (18 females; mean age=21.2, s.d.=3.3)

93 participants.

94 *Stimuli*

95 Stimuli used during the *cardio-visual stimulation* period consisted of photos of the

96 participant's face with a neutral expression morphed with the face of a same gender

97   unfamiliar other. The stimulus set comprised 8 different unfamiliar models (4 females; 4

98   males), selected from our in-house database, that had never been seen by the participants

99   prior to the experiment. To avoid carry over effects from one condition to the other, each

100   participant was presented with two unfamiliar gender-matched models, one presented in the

101   synchronous condition, one presented in the asynchronous condition (see below). Models

102   associated with the synchronous and asynchronous condition were randomly used across

103   participants. That is, each participant was presented only with 2 of these faces, and each face

104   was randomly presented to some participants in the synchronous conditions and to other

105   participants in the asynchronous conditions. The photographs of the participant's face were

106   taken in a separate session, prior to the experimental session. These non-mirror-reversed

107   photos were morphed with Fantamorph (v4.0.8 Abrosoft, http://www.fantamorph.com) and

108   edited with Photoshop software (Adobe Systems, San Jose, CA). Pictures presented during

109   the stimulation period included hair, ears and upper torso. The presentation of coloured

110   pictures aimed to present participants with highly realistic images to maximise the effect of

111   the enfacement illusion (Tsakiris, 2008; Sforza et al. 2010; Paladino et al. 2010; Tajadura-

112   Jimenez et al. 2012a, 2013). Conversely, pictures shown in the self-recognition task were

113   desaturated (i.e. black and white) and cropped to hide hair, ears, and neck (Figure 1). This

114   was done to prevent features unrelated to face morphology from interfering with judgments

115   of self-recognition. It is worth noting that this is the common procedure in enfacement

116   illusion studies (e.g. Tajadura-Jimenez et al. 2013). Two degrees of morphing were used

117   during the stimulation period: 40%-self/60%-other (hereafter referred to as 40/60) and 60%-

118   self/40%-other (hereafter referred to as 60/40). The 40/60 morphed stimulus served as the

119   experimental condition because this stimulus contained a greater percentage of the other's

120   face, and we were principally interested in testing whether synchronous cardio-visual

121   stimulation with that stimulus would alter self-recognition performance. The 60/40 morphed

122   stimulus served as the control condition as it contained a larger percentage of the self, and we

123   did not expect self-face recognition performance to be affected in this case.

124   *Experimental procedure*

125   Participants were comfortability sited in an armchair with a standard 3-lead

126   electrocardiogram (ECG) attached to their chest to monitor their heart activity throughout the

127   session (Powerlab, ADInstrumens, www.adinstruments.com). A hardware-based function

128   detected each R-wave to synchronise stimuli presentation with the participants' heartbeats.

129   The main experimental procedure was organised in four blocks, each comprising the

130   following sequence of tasks: *Pre-Stimulation Face Recognition Task – Cardio-Visual*

131   *Stimulation – Post-Stimulation Face Recognition Task – Questionnaire* (Figure 1A). Each

132   block began with the presentation of the participant's photo (100% self) for 5 seconds,

133   followed by the photo of a same gender unfamiliar other (100% other) for 5 seconds.

134   Participants were instructed that a set of morphing images of these two photos would be

135   presented in that block.

136   Stimulation consisted of periodic pulses of decreased luminosity over the upper torso and

137   face leaving constant the luminosity of the background (see Figure 1C). Each of these pulses

138   had a duration of 100ms and they could be presented either synchronously or asynchronously

139   with the participant's own heartbeats. During the synchronous stimulation, pulses were

140   presented 200ms after each ECG's R-wave. This time window was selected to coincide with

141   the period of maximum subjective perception of heartbeats (Brener et al. 1993; Suzuki et al.

142   2013). In the asynchronous conditions, pulses mimicked the rhythm of another person's

143   previously recorded heart at rest with a heart rate 10% faster or slower than the participant's

144   heart rate (estimated from the 20 heartbeats immediately preceding the onset of the cardio-

145   visual stimulation period of each block). Faster or slower asynchronous rhythms were

146 counterbalanced across participants. Thus, each of the four blocks was characterised by the

147 synchronicity of the stimulation and degree of morphing: *synchronous 40/60; synchronous*

148 *60/40; asynchronous 40/60; asynchronous 60/40.* Information regarding the cardio-visual

149 synchrony stimulation was never mentioned to participants. Instead, they were told that the

150 ECG recordings had the purpose of measuring cardiac responses to the perception of faces

151 with different degrees of self-other morphing.

152 Before and after the cardio-visual stimulation, participants carried out the face recognition

153 task. They were presented with a randomised series of black and white photos reflecting

154 different degrees of morphing - from 20% self/ to 80% self in steps of 2%. A black template

155 was imposed to these photos to remove non-facial attributes (e.g., background, hair, ears)

156 (Figure 1). Participants were asked to rate each photo on a VAS (ranging from 0-100) "*how*

157 *similar is this face to your own?*" Extremes of the scale were anchored with "*mostly similar*

158 *to me*" (100) and "*least similar to me*" (0). This task allowed to estimate the degree of

159 morphing for which participants judged to equally represent "other" and "self" traits,

160 hereafter referred to as *point of subjective equality* (PSE). PSE was estimated by fitting the

161 participants' ratings for each picture into a logistic function, and corresponds to the central

162 point, 50%, of this fitted psychometric curve. The comparison of the PSEs assessed

163 previously and subsequently to cardio-visual stimulation allows estimating changes in self-

164 other mental representation due to the stimulation (Sforza et al. 2010; Tajadura-Jimenez et al.

165 2012b). It should be noted that by combining pre and post stimulation PSE measurements

166 with between-participants randomised counterbalancing of faces used in synchronous and

167 asynchronous conditions we were able to control, or at least greatly minimise, any general

168 non-specific effects of similarity differences between self and other face at baseline.

169 The *questionnaire* consisted in 5 questions (see Table 1), 3 of which related to changes in

170 self-other face representation due to visual stimulation (Q1, Q2, Q3) (Tajadura-Jimenez et al.

171 2012a) and two related to the pulsing rhythm (Q4, Q5) (cf. Aspell et al. 2013). Participants

172 answered on a VAS (ranging from 0-100) with the labels "*I disagree*" and "*I agree*"

173 presented at the two extremes of the scales.

174 After the completion of the 4 experimental blocks, participants carried out the *mental*

175 *tracking task* (Schandry 1981), a standard measure of the IAcc that reflects the ability to

176 accurately identify and perceive heartbeats. Participants were asked to silently count their

177 heartbeats, without feeling their pulse, during four trials of 25, 35, 45 and 100 seconds.

178 Reported and measured heartbeats were compared to estimate an index of IAcc using the

179 following equation (Schandry 1981):

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

180 *Debriefing*

181 To understand if participants detected or had any suspicion about the synchrony between the

182 pulses and their own heartbeats, at the end of the experimental session, we asked them the

183 following questions: "*What do you think the purpose of this experiment was?*" and "*Did*

184 *anything about the experiment seem strange to you, or was there anything you were*

185 *wondering about?*" Only one participant mentioned a possible contingency between

186 heartbeats and pulses, confirming that the processes mediating cardio-visual integration are

187 largely implicit (Azevedo et al. 2016). We did not disclosure the relationship between

188 heartbeats and pulses so that participants remained naïve for the EEG session.

189 **Results**

190 *Point of Subjective Equality (PSE)*

191   Our main analyses was focused on changes in the representation of self-other faces due to

192   cardio-visual stimulation as measured by the change in the PSE at each condition. Data was

193   submitted to a repeated measures ANOVA with 2 Time (Pre-stimulation; Post-stimulation) x

194   2 Synchrony (Synchronous; Asynchronous) x 2 Morphing (40/60; 60/40) as within-subject

195   factors. The analysis revealed a main effect of Time ($F(1,28)=12.21$, $p=0.002$), and a main

196   effect of Synchrony ($F(1,28)=5.84$, $p=0.022$), as well as an interaction Time x Morphing

197   ($F(1,28)=5.44$, $p=0.027$), and an interaction Synchrony x Morphing ($F(1,28)=5.0$, $p=0.034$).

198   However, the critical 3-way interaction Time x Synchrony x Morphing ($F(1,28)=0.17$,

199    $p=0.68$) and the interaction Time x Synchrony ($F(1,28)=0.85$, $p=0.36$) were not significant.

200   Because trait ability to monitor heartbeats may moderate participants' susceptibility to

201   cardio-visual synchronicity effects (Suzuki et al. 2013) analyses were re-run with individual

202   IAcc scores as covariates in the ANOVA. Indeed, the analysis showed that IAcc moderated

203   the 3-way interaction - Time x Synchrony x Morphing x IAcc ($F(1,27)=7.96$, $p=0.009$), that

204   was now significant ($F(1,27)=7.14$, $p=0.013$). The Time x Synchrony x IAcc ($F(1,27)=4.80$,

205    $p=0.038$) was also significant. These results show that the ability to monitor own heartbeats

206   modulates changes in one's own representation of self-other faces due to cardio-visual

207   stimulation. To follow up on this effect, we subtracted pre-stimulation values from post-

208   stimulation (ΔPSE) ratings and performed planned comparisons in separate ANCOVAs for

209   the 40/60 and 60/40 conditions, with Synchrony (Synchronous; Asynchronous) as single

210   within-subject factor and IAcc as covariate. Results revealed an effect of Synchrony in the

211   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

212   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

213   by the correlation between IAcc and the ΔPSE for the synchronous minus the asynchronous

214   40/60 condition ($r=0.617$, $p<0.001$; Figure 2C).

215   *Questionnaires*

216   Separate analyses were carried out for the questions referring to enfacement effects

217   (Questions 1-3) and questions referring to the subjective experience of the flashing

218   (Questions 4-5). In the former case, an ANOVA with 3 Questions (Q1; Q2; Q3) x 2

219   Synchrony (Synchronous; Asynchronous) x 2 Morphing (40/60; 60/40) was carried out. The

220   analysis showed a main effect of the factor Questions ($F_{(1,28)}=6.45$, $p=0.003$) and an

221   interaction Questions x Synchrony ($F_{(1,28)}=4.6$, $p=0.014$). There were no other main effects

222   or interactions (all $ps>0.05$). Thus, responses to the two Morphing conditions were averaged

223   for each question. Planned comparisons between responses to the synchronous and

224   asynchronous conditions for each question were performed. Synchrony had an effect on

225   responses to Q2 ($t_{(1,28)}=2.69$, $p=0.012$), but not responses to Q1 ($t_{(1,28)}=-0.27$, $p=0.79$)

226   neither to Q3 ($t_{(1,28)}=-1.6$, $p=0.12$). To further explore the relation between the subjective

227   responses and participants' IAcc, we included IAcc as covariate in the ANOVA. However,

228   we did not observe any interaction of IAcc with Synchrony effects (all $ps>0.05$). Analyses on

229   Questions 4-5 did not reveal a significant effect or interaction with Synchrony (all $ps>0.05$).

230   **Discussion – Experiment 1**

231   We observed that synchronous (vs. asynchronous) cardio-visual stimulation induced changes

232   in the participant's recognition of their own face. In particular, the comparison between PSE

233   values obtained before and after the cardio-visual stimulation in the synchronous, as opposed

234   the asynchronous condition, reveals that the cardio-visual stimulation increased the perceived

235   similarity between self and other faces. This pattern of results is comparable to the effects of

236   visuo-tactile induction of the Enfacement illusion (Tsakiris 2008; Tajadura-Jimenez et al.

237   2012a; Sforza et al. 2010). These studies demonstrated unidirectional changes in the self-

238   other distinction, showing changes in self-face recognition, but not in the recognition of the

239   other's face. Self-recognition judgements depend on a comparison between the visual percept

240   and a stored mnemonic representation of how a particular person (or the self) looks like

241   (Apps et al. 2012; Legrain et al. 2011). As with previous studies, the observed changes in

242   self-recognition performance seem to reflect an updating in the mental representation of one's

243   own facial appearance. Moreover, these results are in line with previous studies that reported

244   feelings of body ownership of a virtual reality avatar and a virtual hand (Aspell et al. 2013;

245   Suzuki et al. 2013) under conditions of cardio-visual stimulation. Overall, the results support

246   the view that the integration of interoceptive and exteroceptive information is a critical

247   mechanism for self-other distinction and for the construction or updating of self-face mental

248   representations.

249   Interestingly, the effect of synchronous cardio-visual stimulation on self-recognition was

250   dependent on individual trait levels of IAcc. Specifically, these stimulation-induced changes

251   in self-other distinction increased linearly with IAcc. Thus, cardio-visual stimulation was

252   particularly effective among those individuals who are, as a trait, better able to accurately

253   perceive their own heartbeats. Even if participants were not aware of the contingency

254   between their heartbeats and the pulses (as confirmed during debriefing), the presumably

255   great sensitivity that individuals with higher IAcc have to interoceptive bodily signals

256   facilitated the implicit integration of their cardiac activity with the visual stimulus depicting

257   the other's face.

258   While both the behavioural task and the questionnaire data revealed that cardio-visual

259   synchrony induces changes in self-face representation similar to those experienced with the

260   classical enfacement illusion, we observed that trait levels of IAcc only correlated with

261   behavioural changes, but not with subjective reports. This can be explained by the fact that

262   while the face-recognition task (used to estimate ΔPSE) measures fine-grained shifts in self-

263   face perception, the questionnaires rely on introspective evaluations to quantify the subjective

264   experience of the illusion and thus constitute a coarser measure.

265   Having established a behavioural effect, we next investigated, for the first time, if this change

266   in the mental representation of self- faces caused by the integration of interoceptive with

267   exteroceptive (i.e. visual) signals is reflected at the level of cortical interoceptive processing,

268   by focusing on changes in the neural responses to heartbeats, i.e. HEP, during the cardio-

269   visual stimulation.

270   **Experiment 2:**

271   **Material and Methods**

272   *Participants*

273   Participants from Experiment 1 were contacted and invited to take part in Experiment 2. A

274   total of 24 participants agreed to participate. Participants were neurologically unimpaired and

275   received reimbursement for their participation. One participant was excluded from the sample

276   due to excess of artifacts in the EEG signal (see EEG analysis) resulting in a total of 23

277   participants (9 males; mean age=21.9; s.d=3.71). Participants gave their informed consent,

278   with approval by the Ethics Committee, Department of Psychology, Royal Holloway

279   University of London. Experiment 2 was performed 1.5-5 months after Experiment 1.

280   ***Experimental procedure***

281   Participants were seated in a dimly lit, sound-attenuated and electrically shielded chamber in

282   front of a monitor at a distance of 80 cm. Participants' ECG was recorded following the same

283   procedure as in Experiment 1. The ECG was recorded throughout all the experimental phases

284   where there was cardio-visual stimulation.

285   Stimuli consisted of morphed pictures of the participants' upper torso and a face containing

286   40% of the participants' facial features and 60 % of the features of a gender-matched

287   unfamiliar other (i.e., 40/60 degree of morphing). The 40/60 pictures were selected from

288   Experiment 1 because, as expected, the effect of synchronous cardio-visual stimulation on the

289 PSE ratings was observed in the 40/60 synchronous (experimental) condition but not in the

290 60/40 synchronous (control) condition. There were 8 unfamiliar models (4 male, 4 female).

291 Participants' face was morphed with faces of two randomly assigned models, one used in the

292 synchronous condition and the other in the asynchronous condition. Besides, the stimulus set

293 included pictures of the upper body and face of two owls. Pictures were approximately 1200

294 x 960 size and they were presented in a white background. As in Experiment 1, stimulation

295 consisted of periodic pulses of decreasing luminosity of the upper torso and face leaving

296 constant the luminosity of the background. The pulse length was 100ms and was presented

297 either synchronously or asynchronously with the participant's own heartbeats.

298 The experiment contained 48 blocks of 90 seconds length, presented randomly. There were 4

299 block types, each presented 12 times. The experiment consisted of 2 experimental conditions,

300 where participants were presented with the 40/60 morphed faces either in synchrony

301 (synchronous experimental block) or asynchrony with their own heartbeats (asynchronous

302 experimental block). In addition, there were 2 control conditions, where participants were

303 presented with pictures of owls presented in synchrony (synchronous control block) or

304 asynchrony (asynchronous control block) with their heartbeats. After each block, participants

305 were presented with one question of a 6 item questionnaire, including the 3 questions related

306 to changes in self-other face representation due to the visual stimulation (Tajadura-Jimenez et

307 al. 2012a), and the 2 questions related to the pulsing rhythm used in Experiment 1. The

308 additional question "*How distracted were you during this block?*" anchored by the

309 expressions "*not at all*" and "*very much*" was also included to control for attention to the

310 stimuli. Participants answered to each question twice for each condition, in a fully

311 randomised way.

312 *EEG and ECG recording*

313   EEG was recorded with Ag-AgCl electrodes from 64 active scalp electrodes mounted on an

314   elastic electrode cap, according to the International 10/20 system, using ActiveTwo system

315   (AD-box) and Actiview software (BioSemi, Amsterdam, Netherlands; 512 Hz sampling rate;

316   band-pass filter 0.16-100Hz (down 3 dB); 24 bit resolution). Electrodes were referenced to

317   the Common Mode Sense and Driven Right Leg electrodes and rereferenced to the average

318   reference off-line. As in the behavioural study, the ECG signal was recorded with a standard

319   3-lead ECG attached to participants' chest (Powerlab, ADInstrumens,

320   www.adinstruments.com). The R-peaks of the EGC were identified using a hardware-based

321   detection algorism. The onset of the R-waves were marked in the EEG recording. The

322   average number of trials (heartbeats) contributing to the HEP were 1039 in the experimental

323   synchronous condition; 1044.74 in the experimental asynchronous condition; 1050.91 in the

324   control synchronous condition; and 1053.7 in the control asynchronous condition.

325   Importantly, there were no significant differences in number of heartbeats between conditions

326   ($F_{(3,66)}=0.597$, $p>0.05$).

327   *EEG data analysis*

328   Off-line EEG analysis was performed using Vision Analyzer software (BrainProducts). The

329   data was digitally low-pass-filtered at 30 Hz. The data was then submitted to ICA as

330   implemented in Vision Analyzer to correct for ocular and cardiac-field artifacts (CFAs)

331   (Terhaar et al. 2014). The CFAs were corrected by removing the independent components

332   (most often one, or two) whose timing and topography resembled the characteristics of the

333   CFAs. The CFA represents a challenge to the analysis of the HEP because the averaging of

334   the data around the R-peak amplifies the CFA becoming time-locked to the heartbeat (Luft

335   and Bhattacharya, 2015). However, the ICA method has been shown to be of high efficiency

336   in the removal of the independent components representing cardiac-field artifacts from the

337   EEG signal, specifically within the time window where the HEP typically occurs, i.e. 200-

338   400ms (e.g. Terhaar et al. 2014; Park et al. 2014; Luft and Bhattacharya 2015) (see also

339   figure 3D). To compute the HEP the EEG signal was epoched into 750ms segments, starting

340   150ms before the R-wave onset. Segments were baseline corrected using an interval from -

341   150 to -50ms before the R-wave onset. The period ranging from -50ms to 0ms was not

342   considered to avoid the inclusion of artifacts related to the QRS complex of the ECG signal

343   when computing the baseline correction of the signal (e.g. Canales-Johnson et al. 2015).

344   Moreover, in the present experimental design, longer baseline periods should be avoided as,

345   for participants with faster heart rates, this period may partially overlap with late components

346   of visual evoked responses to the pulsing stimulus of the immediately preceding trial.

347   Automatic artifact rejection was combined with visual inspection for all participants (±100

348   μV threshold; 0.05% mean percentage of the data was rejected due to excessive amplitude).

349   The minimum percentage of trials per condition included in the analysis was 82%

350   (percentage of trials did not significantly differ between conditions; p>0.05). The signal was

351   re-referenced to the arithmetic average of all electrodes. Single-subject ERP for each

352   Condition (Experimental; Control) and Synchrony (Synchronous; Asynchronous) were

353   calculated and used to compute ERP grand averages across subjects.

354   The HEP has a frontal-to-parietal distribution with higher amplitudes over the right, as

355   opposed to the left, hemisphere (Dirlich et al. 1997; Pollatos and Schandry 2004; Kern et al.

356   2013; Schulz et al. 2015). Previous studies have defined the HEP as a positive deflection in

357   fronto-central sites. However, the polarity of the HEP seems to vary across studies according

358   to factors such as the task, sites, and time window analysed (Gray et al. 2007; Couto et al.

359   2014; Canales-Johnson et al. 2015). In the current study, analyses were restricted to 6 regions

360   of interests (ROIs) (Figure 3A), defined according to the widespread distribution of the HEP

361   topography and on the basis of the aforementioned studies. To estimate the effects of the

362   cardio-visual stimulation on neural responses to heartbeats, mean voltages of the HEPs time-

363   locked to R-wave onset were computed at the group level using a non-parametric

364   randomisation test controlling for multiple-comparisons (Maris and Oostenveld 2007).

365   Subject-wise activation time courses were extracted at the selected ROIs and were passed to

366   analysis procedure of FieldTrip, the details of which are described by Maris and Oostenveld

367   (2007). Subject-wise activation time courses were compared to identify statistically

368   significant temporal clusters using a FieldTrip-based analysis (Oostenveld et al. 2011) of one

369   ROI at a time (Canales-Johnson et al. 2015; Couto et al. 2014).

370   To test for the interaction effects between the Synchrony effect and the group (experimental

371   vs. control) on HEP amplitudes, and the possibility that this effect is mediated by the

372   participants' IAcc (as shown in experiment 1), we first computed the Synchrony effect

373   (calculated by subtraction of amplitudes at each time point on the asynchronous trials from

374   the synchronous trials) in both the experimental and control group. Then we calculated the

375   difference linked to the Synchrony effect in the experimental vs. the control group at each

376   time point, and we called it "difference Synchrony effect". We then passed the subject-wise

377   activation time courses to the analysis procedure of Fieldtrip. In brief, this procedure

378   regresses the "difference Synchrony effect" (computed as described above) on the predictor,

379   i.e. participants' IAcc, at each corresponding temporal point in the subject-wise activation

380   time courses using the independent sample regression coefficient T-statistics. FieldTrip uses a

381   nonparametric method (Bullmore et al. 1999) to address the multiple comparison problem. t-

382   values of adjacent temporal points whose p-values were less than 0.05 were clustered by

383   adding their t-values, and this cumulative statistic is used for inferential statistics at the

384   cluster level. This procedure, that is, the calculation of t-values at each temporal point

385   followed by clustering of adjacent t-values was repeated 5000 times, with randomised

386   swapping and resampling of the subject-wise averages before each repetition. This Monte

387   Carlo method results in a nonparametric estimate of the P-value representing the statistical

388   significance of the identified cluster.

389   **Results**

390   *Modulation of HEP amplitudes*

391   The results of the cluster-based permutation test revealed significant modulations of the HEP

392   amplitude as indicated by a significant negative cluster between 195 and 289ms after the R-

393   wave onset (p=0.005) in the right centro-parietal ROI (Figure 3A). This time window is in

394   accordance with the latencies reported in previous HEP studies, i.e. 200-400ms, where the

395   cortical processing of cardiac signals takes place (Schandry, et al. 1986; Pollatos and

396   Schandry 2004; Yuan et al. 2007; Fukushima et al. 2011; Kern et al. 2013; Canales-Johnson

397   et al. 2015). Moreover, it minimises overlapping between the HEP and the VEP associated to

398   the visual pulse staring at 120ms after the onset of the pulse (i.e., 200ms after the R wave).

399   Based on the results of the cluster-based permutation analysis, we performed a correlation

400   analysis (2-tailed) between IAcc and the HEP difference linked to the Synchrony effect (i.e.

401   Synchronous vs Asynchronous) in the experimental vs. the control condition in the right

402   centroparietal ROI between 195 and 289ms. This analysis revealed that the higher the IAcc

403   the greater the HEP difference of the Synchrony effect in the experimental synchronous

404   condition (r= -0.632, p=0.001; Figure 3E).

405   In addition, to ensure that the differences observed between conditions in the HEP cannot be

406   explained by differences in the ECG signal, we analysed the ECG trace mimicking the

407   analysing procedure followed in the HEP analysis. The results of the cluster-based

408   permutation test on the ECG did not reveal any significant cluster of significant interactions

409   at p<0.05, corrected for multiple comparisons.

410   Overall, these results show that the presentation of a 40/60 morphed face (i.e., containing

411   40% of the participants' features) whose luminosity changed in rhythmic pulses

412   synchronously to the participants' heartbeats led to amplitude changes of the HEP component

413   in the 195-289ms time window at centro-parietal sites in the right hemisphere. The

414   interaction shown in Figure 3A,D illustrates the changes in HEP amplitude during the

415   synchronous compared to asynchronous experimental cardio-visual stimulation, and to the

416   control conditions, in which visual stimulation was perceived over the face of an owl. In

417   other words, it demonstrates the distinct effect that synchronous cardio-visual stimulation has

418   on HEP amplitudes when perceiving someone else's face vs an owl face. Importantly, such

419   modulation of HEP amplitude was dependent on the individuals' trait levels of IAcc.

420   Furthermore, the correlation analysis showed that the stimulation-induced changes on the

421   HEP amplitude increased linearly with IAcc (see Figure 3E).

422   *Questionnaires*

423   In line with Experiment1, we carried out separate analyses for the questions referring to the

424   enfacement effects (Questions 1-3), the subjective experience of the pulsing (Questions 4-5)

425   and attention to the task (Question 6). Regarding the enfacement questions, the interaction

426   between 3 Questions (Q1; Q2; Q3) x 2 Synchrony (Synchronous; Asynchronous) x 2

427   Condition (Experimental; Control) was not significant ($F(1,44)=0.01$, $p=0.99$). However, the

428   critical interaction Synchrony x Condition was significant ($F(1,22)=4.46$, $p=0.046$), as well as

429   the main effects of Synchrony ($F(1,22)=10.13$, $p=0.004$) and Condition ($F(1,22)=102.83$,

430    $p<0.001$). Given that the analysis did not show a main effect of Question, nor in interaction

431   ($ps>0.05$), we collapsed responses to Q1, Q2 and Q3 and performed planned comparisons

432   between the synchronous and asynchronous cardio-visual stimulation in both the

433   experimental and the control condition. Results showed significant differences between

434   synchronous and asynchronous trials in the experimental condition ($t(1,22)=2.88$, $p=0.009$)

435   but not in the control condition ($t(1,22)=0.78$, $p=0.44$). Regarding the questions about the

436   subjective experience of pulsing (Q4-Q5), there were not significant main effects of the

20

437   factors Condition (F(1,22)=0.37,p=0.55), nor Synchrony (F(1,22)=3.48,p=0.076), neither

438   significant interactions (all ps>0.05). Likewise, there was no significant main effect, nor in

439   interaction, for the question referring to attention to the task (all ps>0.05).

440   We also explored a possible relationship between subjective reports of enfacement and i) the

441   magnitude of HEP changes and ii) individual levels of IAcc. For that, HEP changes and IAcc

442   scores were included, in separate analyses, as covariates in the Condition x Synchrony

443   ANOVA on the subject reports of enfacement (average responses to Questions 1-3). Neither

444   IAcc (ps>0.05) nor HEP changes (ps>0.05) were found to have an effect over any main effect

445   or interaction.

446   **Discussion - Experiment 2**

447   Experiment 2 shows that synchronous cardio-visual stimulation resulted in significant

448   changes in the participants' subjective reports, as well as changes in the electrophysiological

449   processing of cardiac signals. We observed reduced HEP amplitude during the synchronous,

450   as opposed to the asynchronous, stimulation in the experimental condition, while no effects

451   were observed in the control condition. In accordance with earlier findings (Gray et al. 2007;

452   Couto et al. 2014; Canales-Johnson et al. 2015), the pattern of interaction in Figure 3A shows

453   an HEP component represented by a deflection across parietal sites in the right hemisphere.

454   This might reflect the importance of the right hemisphere in the integration of interoceptive

455   and exteroceptive bodily related signals (Craig, 2009) and in self-recognition extending

456   previous evidence on the key role of the right hemisphere to process information relative to

457   the self (Keenan et al. 2000).

458   Furthermore, the effects of cardio-visual synchrony on HEP amplitude were dependent on

459   individual trait levels of IAcc. In particular, the amplitude reduction of the HEP increased

460   linearly with IAcc. Past studies have shown a link between individual differences in IAcc and

461 HEP amplitudes, such that individuals with higher IAcc show greater HEP amplitude than

462 those with lower IAcc when they focus on their heartbeat (Pollatos and Schandry 2004; Yuan

463 et al 2007). We here show IAcc-dependent modulations of HEP amplitudes when the brain

464 integrates interoceptive and exteroceptive signals.

465 **General discussion**

466 Across two experiments, we focused on the mechanisms underpinning the integration of

467 information originating from *outside* and from *within* our bodies, through cardio-visual

468 stimulation. We investigated how this integration relates to changes in the mental

469 representation of one's self, as assessed by changes in self-recognition. We report three key

470 findings. First, we show that cardio-visual stimulation, i.e. perceiving a pulsing stimulus in

471 synchrony with one's own heart over someone else's face, leads to changes in self-

472 recognition and increases self-other perceived similarity. Second, we reveal that synchronous

473 cardio-visual stimulation over another person's face was associated with the modulation of

474 the HEP amplitude, an index of cortical representation of cardiac processing. Third, these

475 changes in HEP were dependent on individual trait levels of IAcc, so that participants with

476 higher IAcc exhibit greater changes on HEP amplitude, in comparison to participants with

477 lower IAcc.

478 How does the change of neural activation locked to heartbeats reflects the experimentally

479 induced changes of bodily self-consciousness? In the classic exteroceptive ways of inducing

480 illusions of ownership, there is an initial inter-sensory conflict (e.g. between felt and seen

481 touch). To solve this conflict, the brain attenuates the importance of incoming proprioceptive

482 and somatosensory inputs and assigns greater salience to visual information (Tsakiris 2010;

483 Apps and Tsakiris 2014; Zeller et al. 2015). This results in a recalibration of visual-tactile

484 coordinates (i.e. touch referral) that leads to an updated sense of body-ownership. In support

485   of this idea, neuroimaging data shows that ownership of an artificial hand in the RHI, or with

486   a virtual body in the full body illusion, is linked to changes in neural activity in the

487   somatosensory cortex (Tsakiris et al. 2007; Zeller et al. 2015; Evans and Blanke 2013; Aspell

488   et al. 2012; Lenggenhager et al. 2011). In particular, Tsakiris and colleagues (2007) found

489   that the degree of proprioceptive drift, an objective index of strength of the illusion, was

490   linearly correlated with decreased activity in the somatosensory cortex. Moreover, Zeller and

491   colleagues (2015) demonstrated an amplitude reduction of the somatosensory evoked

492   potentials (SEPs) to brushstrokes delivered to the participants' hand synchronously to

493   brushstrokes delivered to the artificial hand placed in an anatomically congruent, vs.

494   incongruent, position. This reduction in SEP was interpreted as decreased processing of own

495   somatosensory signals allowing to solve the multisensory conflict experienced by the RHI.

496   In our study, we observed changes in HEP amplitude when one's heartbeat sensations were

497   congruent with the visual cues originating from someone else's face, creating the subjective

498   experience of self-other merging. These results suggest that during cardio-visual stimulation,

499   i.e. one's heartbeat projected onto someone else's face, the external representation of what

500   seems to be inherently private information to the self creates a conflict (i.e. heartbeats being

501   simulated by an external agent). Consistently with previous research, this conflict may be

502   solved by attenuating the salience of interoceptive sensations leading to reduced HEP

503   amplitudes relative to the control conditions. Overall, these findings complement and

504   advance previous evidence on cortical attenuation during classical bodily illusions,

505   demonstrating that the cortical processing of interoceptive signals may be subject to the same

506   principles as somatosensory signals (Zeller et al. 2015).

507   Our findings add to the growing body of literature suggesting the HEP as an important index

508   of cortical processing of afferent cardiovascular activity (Leopold and Schandry 2001). The

509   magnitude of HEPs has been consistently associated to the representation of the bodily

510   aspects of emotional processing (Müller et al. 2015; Fukushima et al. 2011; Couto et al. 2014;

511   Luft and Bhattacharya 2015) and self-processing (Schulz et al. 2015; Pollatos and Schandry

512   2004; Canales-Johnson et al. 2015). Of particular relevance for the present study is the recent

513   finding of reduced HEP amplitudes among individuals suffering from depersonalisation/

514   derealisation disorder (Schulz et al. 2015). In this study, the authors established a close link

515   between altered experiences of bodily self and the cortical processing of heartbeats. Our

516   results expand these findings by showing that *dynamic* and *on-line* modulations of heartbeat

517   processing are related to shifts in the mental representation of one's self in healthy

518   individuals. In specific, HEP modulation is likely to reflect a mechanism by which the brain

519   attempts to reduce the multisensory conflict by attenuating the cortical representation of own

520   heartbeat signals to allow the updating of self-representations. Overall, our results support the

521   idea of plasticity of self-representations under circumstances of simultaneous integration of

522   exteroceptive and interoceptive signals related to the body. They provide a direct link

523   between the brain mechanisms processing on-line interoceptive bodily signals and the

524   process of identifying with a face, a crucial aspect of self-awareness.

525   Could there be alternative explanations to our results? Recent studies have shown

526   bidirectional links between the amplitude of neural responses to heartbeats and visual

527   processing (Park et al. 2014, Salomon et al., 2016; Fukushima et al. 2011; Couto et al. 2014;

528   Luft and Bhattacharya 2015). Interestingly, recent research showed reduced cortical

529   processing (van Elk et al., 2014) and reduced insula activity (Salomon et al., 2016), a key

530   region in the processing of interoceptive signals, to stimuli presented synchronously with the

531   participant's heartbeats. Could therefore the modulation of the HEP observed in our study

532   reflect a purely visual effect driven by synchrony? Crucially, we did not find any significant

533   changes in the HEP amplitude in the synchronous control condition, i.e. synchronous

534   stimulation over the owl's face. This therefore suggests that the HEP amplitude reduction

535   observed in the synchronous experimental condition cannot be explained by pure visual

536   effects. It is also worth noting that previous physiological and electrophysiological data has

537   shown a partial overlap between the HEP and the electrocardiac field up to 450ms after the

538   R-wave (Dirlich et al. 1997) suggesting that the observed HEP amplitude changes could be

539   partially explained by the differences in the temporal occurrence of the CFA between

540   synchronous *vs.* asynchronous stimulation. Although we cannot entirely rule out this

541   possibility, there are three reasons why this is unlikely. Firstly, the temporal dynamics of the

542   CFA were identical in both the experimental and the control synchronous condition.

543   However, the modulation of HEP was only observed in the former. Secondly, we submitted

544   the EEG data to ICA, which has been shown to be highly efficient to remove CFA from

545   HEPs (Terhaar et al. 2014; Park et al. 2014; Luft and Bhattacharya 2015). Moreover, analyses

546   of the ECG did not reveal significant differences between the conditions. Thus, we are

547   confident that the observed HEP reduction is a consequence of the illusory experience of self-

548   other merging due to cardio-visual integration.

549   Previous research by our group has shown that individuals with lower IAcc are particularly

550   susceptible to bodily illusions relying on exteroceptive cues, such as the RHI (Tsakiris et al.

551   2011) and the enfacement illusion (Tajadura-Jimenez et al. 2013). Then, we suggested that

552   individuals with lower IAcc displayed a more malleable self- representation in response to

553   exteroceptive cues. Interestingly, here, and in line with the findings of Suzuki and colleagues

554   (2013; see also Azevedo et al. 2016), we observed the opposite pattern. Specifically,

555   individuals with higher IAcc revealed greater incorporation of other's features related to the

556   integration between one exteroceptive signal and one interoceptive signal. These results may

557   initially seem at odds with the former. However, the role played by IAcc in the classic

558   methods of induction of the illusion (Tsakiris et al. 2011; Tajadura-Jimenez et al. 2013) and

559   in the cardio-visual adaptations (see present experiments, and Suzuki et al. 2013; Aspell et al.

560 2014) is likely to be very different. While cardiac information is not directly involved in the

561 induction of visual-tactile illusions, in cardio-visual stimulation paradigms interoceptive cues

562 are part of the induction mechanism. Moreover, because heart sensations are considerably

563 faint and people differ greatly in their ability to attend, monitor and process cardiac signals at

564 a higher cortical level (e.g. HEPs), IAcc crucially determines the extent to which the illusion

565 is experienced. Individuals with higher IAcc, presumably, have greater access to their cardiac

566 signals. This would facilitate the integration of their cardiac signals with the other's face

567 leading to a greater incorporation of the other's facial features in the mental representation of

568 their own face in comparison to lower IAcc. Furthermore, the greater HEP amplitude

569 reduction observed in individuals with higher IAcc seems to indicate high flexibility in the

570 process of interoceptive signals at the cortical level (Barrett and Simons 2015).

571 Recent theoretical proposals have suggested that self-processing can be characterised by the

572 principles of Predictive Coding (PC) (Fotopoulou 2012; Apps and Tsakiris 2014; Seth 2014;

573 Sel 2014; Barrett and Simons 2015). According to this view, the sensory input is compared

574 with internal models, which are constantly updated by compiling the statistical regularities of

575 past inputs (Friston and Kiebel 2009). Within predictive coding models of self-awareness

576 (Apps and Tsakiris 2014; Seth 2014) one's body is processed in a Bayesian manner as the

577 most likely to be "me". That is, one's own body is the one which has the highest probability

578 of being "mine" as other objects are probabilistically less likely to evoke the same sensory

579 inputs. This information can be considered as highly abstract with respect to the low-level

580 properties of the stimuli and it can only be represented as "self" when different streams of

581 multisensory information are integrated. That is, the self-face will only be recognised as

582 "self" when a visual stimulus has been processed hierarchically for its low level visual

583 properties, its configural features and then its identity. The self-face will therefore be

584 represented as an abstract, supramodal representation of visual input e.g. this is a face, that I

585 have seen before, that I am familiar with, and that is associated with congruent corollary

586 discharge, vestibular, somatosensory and interoceptive information. Such probabilistic

587 representation arises through the integration of information from hierarchically organised

588 unimodal systems in higher-level multimodal areas. This process entails that probabilistic

589 representations are created through the integration of top-down "predictions" about the body

590 and of bottom-up "prediction errors" (PEs) from unimodal sensory systems that are then

591 explained away. Importantly, within predictive coding, priors, predictions and associated

592 predictions errors are all represented in terms of precision. "Precision" refers to the inverse

593 variance associated with each probability distribution and is thus a measure of their relative

594 salience and reliability (Friston 2009). Precision operates both within and between

595 modalities. Within any modality, at each level of the hierarchy and taking account of the

596 given context, the brain weighs the relative precision of PEs that informs or revises

597 expectations at higher level of the hierarchy (Hohwy 2012; Brown et al. 2013).

598 The use of cardio-visual stimulation employed in the present experiments allowed us to test

599 empirically whether the brain will attenuate the visual or the interoceptive information. The

600 neural evidence presented in Experiment 2 that is indicative of a reduction of the HEP in the

601 critical test condition suggests that interoceptive information is attenuated. In a way these

602 results are comparable to the attenuation of somatosensory signals in the classic visuo-tactile

603 stimulation during the Rubber Hand Illusion (Zeller et al. 2015; Limanowski and

604 Blankenburg 2015). Importantly, predictive coding models allow us to test how contextual

605 factors influence information processing as the precision of predictions and predictions errors

606 may vary considerably across different contexts (see also Apps and Tsakiris 2014). For

607 example, visual information may be more precise in the context of self-recognition, while in

608 the absence of visual input or at night, when vision becomes imprecise, the relative precision

609 of interoceptive signals necessarily increases (Pezzulo 2014). Therefore, the relative precision

610   of PEs and priors across sensory modalities is constantly being updated. Thus, as shown here,

611   in contexts that rely heavily on visual information, i.e. self-recognition, interoceptive signals

612   are attenuated, possibly at higher order cortical areas, under conditions of cardio-visual

613   synchrony. In accordance, the HEP amplitude reduction provides evidence of a

614   neurophysiological mechanism throughout which the sensory input is attenuated to update the

615   mental representations of one's self according to the external evidence.

616   In conclusion, this study provides new insights on the integration of multisensory bodily

617   signals coming from *outside* and from *within* the body and its influence in self-face

618   representation. We designed two experiments that investigated whether synchronous cardio-

619   visual stimulation can enhance self-identification with the face of another and the cortical

620   processing of such an altered experienced. Our data showed that multisensory integration of

621   heartbeat sensations with the visual exteroceptive information of the face of another leads to

622   an illusory sense of identification with the other's face, and to an amplitude reduction of the

623   HEP component. No such effects were found when the interoceptive and exteroceptive

624   signals were presented in an asynchronous manner. We therefore provide direct neural

625   evidence for the integration of interoceptive and exteroceptive signals in bodily self-

626   awareness.

627 **Acknowledgments**

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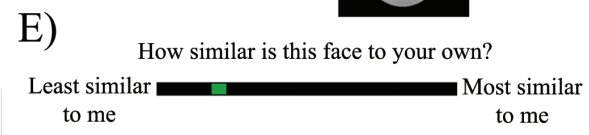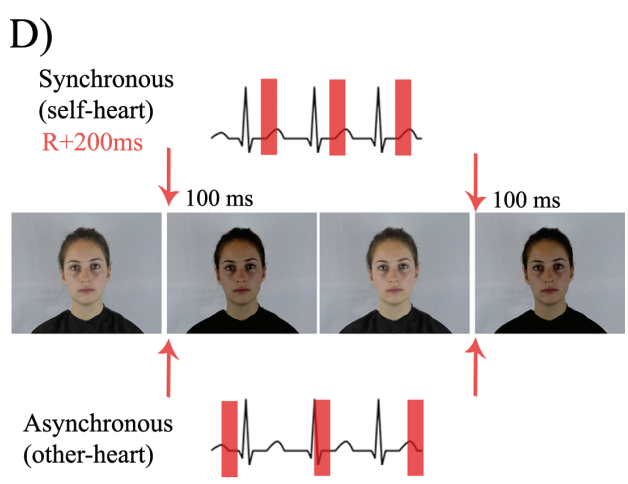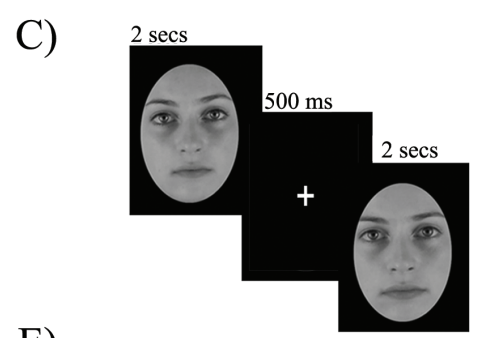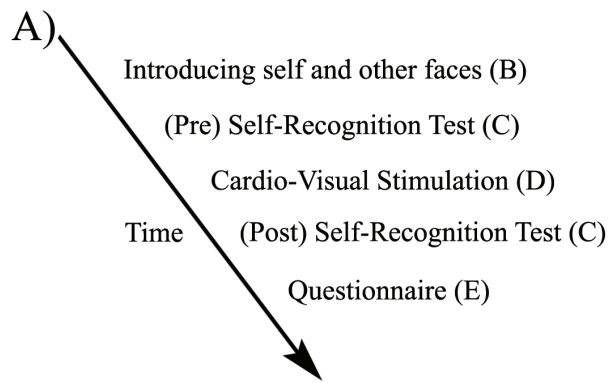
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765

766   **Figures:**

767

768   **Figure 1**

769

770 **Figure 2**

771

A) 40/60

Subjective % of self in the morphing

48.0 57.8

55.4 55.5

Objective % of self in the morphing

B) 60/40

Subjective % of self in the morphing

54.8 55.4

55.0 55.0

Objective % of self in the morphing

■ ■ ■ ■ Pre-Synchronous
▬▬▬ Post-Synchronous
■ ■ ■ ■ Pre-Asynchronous
▬▬▬ Post-Asynchronous

C)

ΔPSE Synchronous - ΔPSE Asynchronous

r=0.617, p<0.001

IAcc

D) High IAcc

Subjective % of self in the morphing

Objective % of self in the morphing

E) Low IAcc

Subjective % of self in the morphing

Objective % of self in the morphing

772 **Figure 3**

773

A) Heartbeat Evoked Potential

Right Centro-parietal Sites

- Experimental Synchronous
- Experimental Asynchronous
- Control Synchronous
- Control Asynchronous

B) ICA results on ECG

- ECG before ICA
- ECG after ICA

C) Topographical maps

Front   Back

Experimental condition

Control condition

-0.38 μV   195-289ms   0.25 μV

D) HEP amplitude

HEP amplitude in centro-parietal sites (μV)

Experimental sych. / Experimental asych. / Control sych. / Control asych.

E) Correlation between HEP changes & IAcc

Synchrony effect on HEP Experimental *vs.* control condition (μV)

IAcc   p = .001

38

774   **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)

775

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

801   IAcc scores and the synchrony effect (computed as the difference between synchronous and

802   asynchronous trials) in the experimental *vs*. the control condition.

803   **Caption to tables:**

804   Table 1. Questionnaire scores in Experiment 1 and Experiment 2. Average (and SD) ratings

805   for each question.