Title: Cardio-visual integration modulates the subjective perception of affectively neutral stimuli

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Abstract

Interoception, which refers to the perception of internal body signals, has been consistently associated with emotional processing and with the sense of self. However, its influence on the subjective appraisal of affectively neutral and body-unrelated stimuli is still largely unknown. Across two experiments we sought to investigate this issue by asking participants to detect changes in the flashing rhythm of a simple stimulus (a circle) that could either be pulsing synchronously with their own heartbeats or following the pattern of another person's heart. While overall task performance did not vary as a function of cardio-visual synchrony, participants were better at identifying trials in which no change occurred when the flashes were synchronous with their own heartbeats. This study adds to the growing body of research indicating that we use our body as a reference point when perceiving the world, and extend this view by focusing on the role that signals coming from inside the body, such as heartbeats, may play in this referencing process. Specifically we show that private interoceptive sensations can be combined with affectively neutral information unrelated to the self to influence the processing of a multisensory percept. Results are discussed in terms of both standard multisensory integration processes and predictive coding theories.

Keywords:

interoception; multisensory integration; heartbeat; neutral stimuli; predictive coding

1. Introduction

In order to perceive and navigate the complexities of the external world, our brain needs to continuously merge information conveyed by the different senses. The integration of signals from multiple sensory modalities allows us to form a robust representation of a particular stimulus and to reconstruct the world in a consistent way (Ernst and Bulthoff, 2004). The fundamental essence of our subjective existence, the sense of the self, is similarly profoundly connected to the continuous integration of body signals from different exteroceptive sensory modalities (Tsakiris, 2007, 2010; Blanke, 2012; Berlucchi and Aglioti, 2010). One way to tap into this mechanism is by inducing controlled bodily illusions (Botvinick & Cohen, 1998; Tsakiris, 2010; Lenggenhager et al., 2007; Tsakiris, 2008; Sforza et al., 2010). Experiencing touch on one's own body whilst perceiving someone else being touched in the same location, in a temporally congruent way, may result in the incorporation of the other person's features into one's own body representation. For example, in the rubber hand illusion, observing an artificial hand being stroked by a paintbrush, in synchrony with strokes applied to our own visually occluded hand, induces a sense of ownership of the artificial hand (Botvinick & Cohen, 1998). Such studies illustrate how the ongoing integration of multisensory information endows us with a stable sense of the bodily self.

However, an often neglected fundamental source of bodily signals is the sensations arising from within the body, i.e. interoceptive information. These signals comprise cues involved in homeostatic control, as well as sensations such as accelerating heartbeats, the fullness of the bladder, hunger or nausea (Cameron, 2001). Internal bodily states can drive cognition and behaviour, with or without awareness (Critchley and Harrison, 2013; Garfinkel et al., 2015), and profoundly influence various dimensions of emotional experience, such as pain perception, emotional reactivity and social decision-making (e.g. Pollatos et al., 2012, 2014; Herbert et al,. 2007; Garfinkel et al., 2014; Gray et al., 2012; Lenggenhager et al., 2013; Dunn et al., 2012; Durlik et al., 2014).

Interoceptive signals are a central feature in the subjective experience of selfhood (James, 1890; Damasio, 1993, 2010; Craig, 2009a; Seth, 2013; Park et al., 2014a). Importantly, experimental studies have recently shown that interoceptive sensations constitute an additional relevant sensory channel in the multisensory integration processes that mediates the experience of body ownership (Tsakiris et al., 2011; Tajadura-Jimenez et al., 2014; Aspell et al., 2013; Suzuki et al., 2013). For example, Aspell and colleagues (2013) projected a flashing silhouette that mimicked the participant's own heartbeats into the image of a virtual body. The authors found that flashing the silhouette in synchrony with the heartbeats increased participants' self-identification with, and self-location towards, the virtual body. Similarly, Suzuki and colleagues (2013) showed that projecting the visual representation of a participant's real-time heartbeats onto a virtual hand enhanced both objective and subjective measures of ownership of the virtual hand, an effect which was moderated by trait interoceptive accuracy. These studies indicate that internal bodily sensations (heartbeats) are integrated with exteroceptive representations of external stimuli (i.e. vision of the body or body part) such that congruence between the two (i.e. synchrony between flashing and the heartbeats) can induce altered self- and other body perception and even some degree of self-other merging.

These findings accord with Predictive Coding theories (PC) that rely on Bayesian principles and posit that the brain continuously generates probabilistic models of the world to explain the causes of sensory inputs (Apps and Tsakiris, 2013; Friston, 2010; Seth, 2013; Sel, 2014). PC moves away from bottom-up perspectives of perception by proposing that perceptual representations arise from comparison between top-down predictions of sensory events and bottom-up sensory evidence. Discrepancies between predictions (e.g. of one's self-location in space) and incoming sensory inputs (e.g. one's own heartbeats projected into a distant avatar) generate surprise signals (prediction errors) that must be minimized by the brain in order to arrive at a percept. Prediction errors may be minimized either by performing actions to alter incoming sensory events or by generating updated predictions about the causes of sensory events. In the body ownership studies discussed above, conflicting multisensory experiences induce updated representations of the body which then incorporate the virtual body, probably by diminishing the relative influence of proprioceptive cues in own-body awareness (Apps and Tsakiris, 2013; Suzuki et al., 2013).

While the importance of interoceptive signals in the processing of emotional and bodily-related stimuli is now widely acknowledged, their influence on the processing of affectively neutral stimuli is under-researched. There is some evidence that cardiac activity modulates the processing of neutral, self-unrelated stimuli at the cortical level (Park et al., 2014b; van Elk et al., 2014; Walker and Sandman, 1982; Sandman, 1984). For example, the timing of the presentation of a brief auditory (Sandman, 1984) or visual (Walker and Sandman, 1982) stimulus, in relation to the cardiac cycle, modulates sensory-evoked potentials. In a recent EEG study, van Elk and colleagues (2014) presented participants with auditory stimuli that were either synchronous or asynchronous with their own heartbeats and asked them to make judgments about whether they were synchronous. Although participants could not identify synchronous trials above chance, the authors observed reduced cortical responses (the N1 component of the auditory-evoked potential) to auditory stimuli that were presented synchronously with their heartbeats. These studies indicate that the central processing of exteroceptive sensory stimuli is modulated by temporal contingency with cardiac signals. A further important piece of evidence is provided by Park and colleagues (2014b), who found that the magnitude of neural responses to heartbeats (i.e., the heartbeat evoked potential) can predict the conscious detection of incoming, near-threshold visual stimuli. This result implies that spontaneous fluctuations in the processing of interoceptive signals impacts on conscious visual processing

Capitalizing on such evidence, we sought to explore how interoception shapes the subjective evaluation of stimuli that are affectively neutral and do not have any particular body-relevance. Specifically, we investigated whether synchrony between one’s own heartbeats and the visual properties of an external object, such as a simple flashing circular shape, influences the way that we perceive the stimulus. We were interested in understanding if cardio-visual integration can occur even in conditions that have no apparent relevance for the (bodily) self. Importantly, this would expand our understanding of body-to-brain interactions by indicating that, beyond the known role interoceptive signals play in the processing of affectively salient stimuli (Herbert and Pollatos, 2012; Craig, 2009a; Critchley and Harrison, 2013), the brain integrates internal bodily states, even when processing neutral stimuli.

With this aim, we fitted participants with ECG and asked them to detect changes in the rhythmic flashing of a circle that gently pulsed on a computer screen. Unknown to them, in some trials the circle was pulsing synchronously with their own heartbeats, while in other trials it followed the rhythm of another person's heart. In half of the trials the flashing mirrored the continuous pulsing of only one person's heart, which could be either the participant's or another individual's. These were the "no-change" trials. By contrast, in the other half of the trials ("change trials") a change occurred towards the middle of the trial, whereby the initial flashing pattern switched to the rhythm of a different person's heart (i.e. from flashing in synchrony with one's own heart to synchrony with the rhythm of another person's heartbeat, or changing from the other person's heartbeat to that of a third individual). If cardiac and visual information are integrated, then we expected different performance as a function of this synchrony/asynchrony. In line with the studies showing that cardio-visual integration can induce ownership over another's body, we reasoned that the synchrony between the flashing and the participant's heartbeats would induce an altered subjective perception of the flashing rhythm. We hypothesized that the perception of a stimulus that is synchronous with one's own private sensations would elicit an increased sense of "resonance" or "familiarity" with that stimulus and that would be reflected in different patterns of accuracy, depending on trial type. Specifically, we predicted improved accuracy in "no-change" trials in the "self" vs. "other" conditions, as a result of the increased resonance with the stimuli. Predictions regarding "change" trials were non-directional. On the one hand, self-referencing could help the participant to detect changes in the flashing pattern. On the other hand, possible initial synchrony-induced feelings of resonance might prevail and interfere with detection of any change of rhythm.

To test whether the ability to perceive one's own heartbeat has an impact on the integration of cardio and visual signals, we related performance on the above task with individual trait interoceptive accuracy, as measured by the Mental Tracking Method (Schandry, 1981). We interpret the results both within standard accounts of multisensory integration and within a predictive coding framework.

2. Experiment 1

2.1. Methods

2.1.1. Participants

A total of 25 participants (2 males; mean age=20.6; SD=2.1) took part in the study. Data from three participants was excluded from analyses (see below) and thus the final dataset comprised 22 participants (2 males; mean age=20.7; SD=2.3). The study was approved by the local ethics committee. All participants gave written consent.

2.1.2. Stimuli and procedure

Upon arrival, participants were fitted with a three lead ECG (Ag-AgCl electrodes) according to Einthoven's triangle configuration. They were then seated comfortably in an armchair and asked to relax for 5 minutes. During this period cardiac activity was recorded, in order to assess the participant's resting heart rate variability (HRV).

The visual stimulus consisted of a circle that flashed from light grey to red, against a black background. Each pulse had a duration of 100 ms. The rhythm of the flashing, i.e. the time between each pulse, was either exactly synchronised with the participant's own heartbeats ("self conditions") or followed the rhythm of another person's (previously recorded) heartbeat ("other conditions").

Thus, in the “self conditions” the circle flashed synchronously with the participant’s ongoing heartbeats, while in the “other conditions” the flashing mimicked someone else’s heartbeat. Importantly, participants were completely unaware of what the flashing represented and were simply instructed to pay close attention to the flashing circle and to try to detect changes in the pattern of its flashing. Specifically, they were told that on each trial the circle would start pulsing with a rhythmic pattern and that at some point the rhythm might change. They were also told that on each trial there would be only one change (“change trials”), or there might be no change (“no-change trials”). There were thus four trial types (see Figure 1): if the initial flashing pattern mirrored the participant’s heart it could either (i) switch to another person’s heart rhythm (“self-to-other-change”) or (ii) remain synchronous with the participant’s own heartbeat throughout the trial (“self-without-change”). If the initial flashing followed another person’s heartbeat it could either (iii) remain the same (“other-without-change”) or (iv) switch to the rhythm of a third individual’s heart (“other-to-other-change”). Changes in the flashing rhythm included both a phase shift, which reflected different patterns of heart rate variability between the first and second hearts, and also changes in flashing frequency, i.e. the second heartbeat was always chosen to differ by approximately +/- 5% bpm from the initial heartbeat (see below further details and limitations). Asynchronous stimuli randomization was performed within participants such that each participant was exposed to both 5% faster and slower rhythms.

To synchronize the flashing of the circle with the participant’s heart, a hardware-based function (Fast output response) in Powerlab (AD Instruments, www.adinstruments.com) was used for online detection of the R-waves from the ECG trace, with minimal delays. Customised software was then used in Matlab (The Mathworks, Natick, MA) to time the onset of each pulse to occur 200 ms after the R-wave peak. Because each pulse had a fixed duration of 100 ms, the flashing occurred between 200-300 ms after the R-wave, thus coinciding with peak systolic pressure and the period of maximum subjective perception of heartbeats (Brener et al., 1993; Suzuki et al., 2013). By contrast, the asynchronous stimuli, i.e. other persons’ heartbeats, differed from the participant’s heartbeat both in terms of phase (due to differences in heart rate variability) and frequency - as they were faster or slower than the participant’s heart. As a result, asynchronous flashes occurred at random phases across the participant’s own cardiac cycle.

The experimental task was organized in 3 blocks of 16 trials, presented in fully randomized order. Before each block we included a short rest period during which the participant’s heart rate data was calculated, based on the timing of 30 consecutive heartbeats. This information was used to select the appropriate control stimulus, i.e. for the “other” heartbeat samples in the subsequent block. Each trial consisted of a sequence of 15, 17, 20, 23 or 25 pulses. On “change trials” the switching occurred after 7, 9, 11, 13 or 14 pulses, so that there were always at least 7 pulses before and after the change. On each trial, the exact timing sequence of the “other" heart was randomly selected from 5 minute sequences of heartbeat recordings, allowing the sequences to vary from trial to trial. Participants’ responses were recorded at the end of each trial with a button-press, using the “up-arrow” computer key for “change” answers and the “down-arrow” for “no-change” responses.

----------insert Figure 1 here---------

After task completion, trait interoceptive accuracy was measured with the heartbeat tracking task (Schandry, 1981). In this task, participants are 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 calculate an index of interoceptive accuracy (IAcc; Garfinkel et al., 2015).

2.1.3. Debriefing

To understand if participants suspected that the flashes were synchronized with their heartbeats we asked them to provide written responses to the following questions: “What do you think was the purpose of this experiment?” and “Did anything about the experiment seem strange to you, or was there anything you were wondering about?” If participants mentioned a possible relationship between heartbeats and flashes, we asked further questions in order to understand whether they had thought that the pulses could be synchronous with their heartbeat, or if they were instead referring to the possible influence that the flashing stimulus might have on their own heart rate.

2.1.4. Data analyses

Movement during task performance can sometimes generate artifacts in the ECG trace and lead to inaccurate R-wave detection. The ECG trace was therefore visually inspected to detect and exclude trials where such artifacts interfered with stimuli presentation. If artifacts during the rest period led to inaccurate heart rate calculation, data from the subsequent experimental block was excluded from analyses. One participant had such artifacts in two experimental blocks (representing over 50 % of trials) and therefore data from this participant was excluded. Data from two other participants was also excluded due to the lack of availability of appropriate control stimuli, i.e. there were no samples with appropriately 5% faster or slower heart rates.

Performance was analysed by comparing accuracy rates in “change” and “no-change” trials in conditions of initial synchrony, “self”, or asynchrony, “other”. With that purpose, accuracy rates were entered into a Synchrony (Self/Other) x Trial (Change, No-change) ANOVA. When appropriate, post-hoc pairwise comparisons were carried out to identify conditions in which performance differed as a function of Synchrony.

Resting heart rate variability (HRV) was estimated using Labchart’s HRV toolbox (ADInstruments; http://www.adinstruments.com/), based on the 5 minutes of ECG recording at rest. Our analyses focused on the time domain, calculating the RMSSD (square root of the mean squared differences of successive inter-beat intervals) as an index of HRV. Participants with higher HRV might be more likely to observe greater variability in the time interval between consecutive flashes than participants with less HRV, so to control for this we included individual HRV indices as covariate in all our analyses.

2.2. Results

Analyses of accuracy rates revealed a significant main effect of Synchrony (F(1,20)= 8.47, p= 0.009, η^2= 0.3) but neither the interaction (F(1,20)= 0.42, p= 0.53, η^2= 0.020) nor the main effect of Trial (F(1,20)= 3.92, p= 0.062, η^2= 0.16) were found to be significant, suggesting better performance in the "self" conditions independently of trial type. However, the methodological concerns (see the limitations section below) raised by the methods used to estimate heart rate limit the interpretation of performance in "change" trials but not the interpretation of behaviour in "no-change" trials. Thus, although the interaction of Synchrony x Trial was not significant, planned comparisons were carried out to identify Synchrony effects in "no-change" trials, independently of possible confounds on "change" trials. Results revealed better performance in the "self" compared to "other" conditions in "no-change" (F(1,20)= 4.87 , p= 0.039, η^2= 0.2) trials but not in "change" trials (F(1,20)= 2.0 , p= 0.17, η^2= 0.090) (Figure 2; Table 1). There was no significant interaction of the covariate HRV with any measure, *F*(1, 20) < 2.1, *ps*> 0.16, η^2< 0.095.

To explore the effect of the ability to monitor one's own cardiac activity on cardio-visual integration, we tested for correlations between accuracy rates in the "self" conditions and IAcc, i.e. scores on the heartbeat tracking task (mean = 0.73, SD = 0.13). A significant positive correlation was found with performance in the "no-change" trials (*r* = -0.5, *p* = 0.02) but not with that in the "change" trials (*r* = -

0.23, *p* = 0.23) (Figure 2), suggesting that those who are better able to detect their heartbeats were also better at judging "no-change" when the flashing was synchronous with their heartbeat.

----------- Insert Table 1 here ---------------------

------------ Insert Figure 2 here -------------

2.2.1. Debriefing

Three participants suspected that the flashes might have been synchronous with their heartbeats (one of these 3 participants had already been excluded from analyses due to inaccurate heart rate calculation). To understand whether this knowledge confounded our results, we re-ran the analyses excluding data for these two further individuals. With the exception of the main effect of Trial, *F*(1,36)= 5.75, p= 0.028, η^2= 0.24, that was now significant, the results were similar to those obtained in the original analyses: Synchrony x Trial interaction, *F*(1,36)= 0.31, p= 0.58, η^2= 0.02; main effect of Synchrony, *F*(1,36)= 9.18, p= 0.007, η^2= 0.34; "change" trials (mean "self"= 0.54 , SD = 0.17; mean "other"= 0.44, SD =0.19), *F*(1, 18) = 1.96, *p* = 0.18, η^2= 0.1; "no-change" trials (mean "self"= 0.64 , SD = 0.21; mean "other"= 0.50, SD = 0.18), *F*(1, 18) = 4.89, *p* = 0.04, η^2= 0.21; correlation between IAcc and performance on "no-change" trials in the self-condition, *r* = -0.57, *p* = 0.01.

2.3. Discussion – Experiment 1

We asked participants to look at a pulsing circle, which flashed either in synchrony with their own heartbeats or asynchronously. They were required to judge whether the flashing rhythm did, or did not, change within each trial. We found that participants were better at discriminating changes when the flashing was synchronous with their heartbeat, a result that is accounted for principally by improved performance in the “self-no-change” condition. Moreover, individual scores on a standard measure of interoceptive accuracy predicted the correct identification of no-change in the “self” condition, suggesting that individuals who are better at detecting their own heartbeats might have been relying to a greater extent on cardiac signals to perform the task. However, the effect of synchrony seems to be implicit, as most participants did not suspect there had been any relationship between the flashes and their own heartbeats.

2.3.1. Limitations

The methods used to estimate heart rate were not optimal, which could have resulted in inappropriate selection of control stimuli. Specifically, in the experiment above, the participant’s heart rate was only calculated before each block and during rest conditions, which does not take account of possible changes in heart rate over time, as well as heart rate changes that might be contingent on performance of the task. Moreover, the heart rate calculation for the control stimuli was based on a period of 5 minutes, in contrast to the few seconds of each trial. Again, this takes no account of the natural fluctuations in heart rate that are likely to occur over time. As a consequence, during “change trials” the difference in flashing rates before and after the change might have differed inconsistently across trials and may not have always fallen within the desired +/- 5% beats per minute. There is therefore some difficulty in interpreting the results relating to “change trials”. The second study was designed to address these issues.

It should be noted that “no-change trials” were not influenced by the limitations above because the flashing rhythm followed the pattern of one unique heart (the “self” heart or “other” heart). Thus findings that are related to correct rejections of change in the “self condition” (i.e. improved performance and the correlation with trait IAcc) remain valid because they are independent of the accuracy of heart rate calculations.

3. Experiment 2

3.1. Methods

3.1.1. Participants

A total of 45 participants (15 males, mean age = 25.9, SD = 8.7) took part in the second study. Data from 4 participants was excluded from analyses due to: failure to focus on the task (n = 2); misinterpretation of task instructions (n = 1); no appropriate control stimuli available from the database (n = 1). Thus, the final dataset comprised data from 41 participants (14 males, mean age = 25.8, SD= 8.8). The study was approved by the local ethics committee. All participants gave written consent.

3.1.2. Procedure

Procedures were similar to those of study 1. Differences relate only to the control stimuli that were used and to the methods of assessing heart rates. The database of “other” heart rhythms now consisted of recordings of 30 heartbeats duration, taken from participants in Experiment 1 while they were performing the task. Thus the pattern of flashing in the “other conditions” now mimicked the real dynamics of a heartbeat while the person was performing the task. In each such sample the mean heart rate was estimated by averaging the inter-beat interval for the first 15 beats. A second alteration to the method of Experiment 1 was that the participant’s heart rate was now calculated online, as the average inter-beat interval during the ongoing trial, i.e. up to the moment of switching (on “change trials”). These improvements in estimating “self” and “other” heart rates allowed better control in each trial of the relationship between flashing rates for each condition. Particularly, on "change trials", the sample for "other" was now chosen from the database to provide an increase or decrease of 10 % in the average inter-beat interval, with respect to the initial rhythm. This procedure was used both for "self-to-other-change" and "other-to-other-change" trials. By contrast, on "no-change trials", other stimuli differed only by +/- 5% from the participant's heart rate measured on the previous trial.

3.2. Results

Accuracy rates were entered into a Synchrony (Self/Other) x Trial (Change, No-change) ANOVA with the participant's individual HRV as covariate. The interaction was significant, $F(1,39)= 5.24$, $p= 0.028$, $\eta^2= 0.12$, but the main effects of Synchrony, $F(1,39)= 1.8$, $p= 0.19$, $\eta^2= 0.04$, and Trial, $F(1,39)= 0.25$, $p= 0.62$, $\eta^2= 0.006$, were not. Post-hoc comparisons revealed better performance on the "self" (vs. "other") condition on "no-change", $F(1, 39) = 5.93$, $p = 0.02$, $\eta^2= 0.13$) trials but equivalent accuracy on "change" trials, $F(1, 39) = 1.29$, $p = 0.26$, $\eta^2= 0.027$ (Figure 3; Table 2). HRV did not significantly interact with any measure,, $Fs(1, 39) < 2.19$; $ps > 0.19$, $\eta^2< 0.053$. In line with the procedure in study 1, correlation analyses were performed between IAcc, (mean = 0.65, SD = 0.15) and the performance on "change" and "no-change" trials in the "self" condition". No correlation was significant, $rs < 0.06$, $ps > 0.71$.

--------------- Insert Table 2 here ---------------

----------Insert Figure 3 here -------------

3.2.1. <u>Debriefing</u>

Four participants suspected that the flashes might have been synchronous with their heartbeats (one of these 4 participants had already been excluded from analyses due to the lack of availability of appropriate control stimuli). We re-ran the analyses excluding the data of the other 3. The results were equivalent to those obtained in the main analyses: for the Synchrony x Trial interaction, *F*(1,36)= 4.72, p= 0.037, η^2= 0.12; for the main effect of Synchrony, *F*(1,36)= 2.17, p= 0.15, η^2= 0.06; main effect of Trial, *F*(1,36)= 2.47, p= 0.125, η^2= 0.06; for "change" trials (mean "self"= 0.58, SD = 0.16; mean "other"= 0.64, SD = 0.17), *F*(1, 36) = 0.74, *p* = 0.39, η^2= 0.02; for "no-change" trials (mean "self"= 0.61 , SD = 0.19; mean "other"=0.53, SD = 0.17), *F*(1, 36) = 5.73, *p* = 0.02, η^2= 0.14. .

3.3. Discussion - Experiment 2

Using better controlled stimuli we were able to address limitations of Experiment 1. In the second Experiment, changes in the flashing pattern consistently corresponded to a 10% increase or decrease in the initial flashing rate, independently of whether this was the "self" or "other" condition. Moreover, heartbeat stimuli used to represent the "other" now consisted of the rhythm of another person's heart while that person had actually been performing the same task and should therefore, in principle, have exhibited similar patterns of behaviour. "Self" and "other" conditions were thus better matched in Experiment 2.

In contrast to Experiment 1, we found no overall advantage in task performance in the "self" condition. However, the pattern of behavioural responses in "change" and "no-change" trials was similar in both studies. That is, while in "change" trials participants showed equivalent accuracy in the "self" and "other" conditions, they performed better on "no-change" trials when the visual stimulus flashed in synchrony with their heartbeats. Together these results suggest that the participants experienced an increased feeling of resonance with the flashing stimuli in the "self" conditions and confirm the proposal that current interoceptive information influences the subjective perception of external stimuli.

4. General discussion

Interoceptive sensations, defined as the perception of the body from within, are profoundly connected to our sense of self and our body-awareness. Although these sensations are inherently private, they influence the way in which we interact with the external world (Damasio, 2010). Recent research has been exploring how internal bodily signals, such as the heartbeats, shape the subjective experience of emotionally-arousing stimuli, as well as the awareness of the bodily self (Barrett and Bar, 2009). In a departure from these previous paradigms, in the two experiments presented here we sought to understand how cardiac afferent signals modulate the processing of stimuli that are affectively neutral and have no apparent relationship to the participant's body. We asked participants to detect changes in the rhythm of a flashing light that, unbeknownst to them, could be pulsing either synchronously or asynchronously with their own heartbeat. Across two experiments, we observed that participants were better at identifying trials in which there was no change in the flashing rhythm, when the flashing was synchronous with their own heartbeats, compared to when it followed the rhythm of another individual's heart. It appeared that participants implicitly used the rhythm of their own heart to judge the rhythm of this external stimulus. These results indicate that synchrony between exteroceptive and interoceptive sensory modalities modulates the subjective perception of visual stimuli that have no relationship to the participant's own body. Importantly, this was true after controlling for individual HRV, suggesting that irregularities in flashing rhythms were likely to be ignored, provided that they mimicked the participant's own natural variations in heartbeat timings. Such evidence extends previous research on brain-body interactions by showing, for the first time, that interoceptive signals influence the subjective appraisal of affectively neutral and body-unrelated stimuli.

A growing body of literature has investigated the influence of interoception, and of cardiac activity in particular, on emotional experience. A related line of research has focused on the role of internal bodily sensations in the subjective experience of the bodily self (e.g. Tsakiris, 2011; Tajadura-Jimenez et al., 2014; Ainley et al., 2012, 2013). Of particular interest for the experiments we conducted are two recent studies, both inspired by classical bodily illusion paradigms, which have demonstrated the integration of interoceptive and exteroceptive signals in generating the experience of body ownership (Aspell et al., 2013; Suzuki et al., 2013). In those studies, temporal congruency between internal, private (heartbeats) and external stimuli (the flashing of a virtual body) induced a subjective feeling of ownership over a virtual body. This indicates that perceiving one's own private sensations mirrored by a visual stimulus that is projected onto an external body can implicitly result in the incorporation of that body into our own body representation. Our two studies add to this literature by demonstrating that perceiving private interoceptive sensations mirrored by an affectively neutral and body-unrelated object (a circle) modulates the subjective appraisal of that object. We argue that the synchrony between interoceptive and exteroceptive sensory modalities (the heartbeat and the flashing) produced a multisensory percept, such that the temporal properties of the visual stimuli became integrated with the temporal dynamics of the participant's own cardiac activity. As a result, the processing of the flashing rhythm was biased by having the participant's own heartbeat as a reference.

Detection of rhythm changes (on "change trials") was no better in the "self" than in "other" conditions. This seems initially surprising as one could predict that synchrony would facilitate the detection of shifts in the rhythm. A possible explanation is that the initial synchrony with the heartbeat induced a subjective feeling of resonance with the flashing circle, which then persisted throughout the trial and increased the likelihood that participants would judge the stimulus as unchanging. Indeed, this is in line with the improved recognition of "no-changes" in flashing rhythm, that we had predicted and subsequently observed when the flashing was synchronous with the heart. Under such conditions, the emergence of a multisensory percept that included interoceptive information may have induced an altered sensory experience that biased stimulus perception. This raises interesting questions for future research about how stimuli associated with the self are processed, suggesting that once such associations have been formed they may persist even in the face of contrary evidence.

Altogether our results further the understanding of brain and body interactions by demonstrating that interoceptive states shape the subjective perception of stimuli that are apparently irrelevant for the self or for homeostatic balance. They provide important empirical evidence in support of theoretical accounts that propose that internal bodily states are the basis of subjective experience and self-awareness (Park et al., 2014a; Craig, 2009a; Damasio, 1993). According to such frameworks, awareness of an external stimulus requires not only a mental representation of the stimulus but also a mental representation of oneself as a feeling entity as well as a representation of the interrelationship between oneself and the stimulus in that given moment (Craig, 2009a; Damasio, 1993). By using our own bodies as reference, subjectivity is grounded in the integration of representations of the external stimulus with our own interoceptive states. At the neural level, the structure most likely to underpin the integration of interoceptive and exteroceptive phenomenon is the insular cortex. The insula is a hub for the integration of bodily signals, particularly those arising from within the body (Craig, 2009a; Critchley, 2004). The continuous mapping of interoceptive states in the insula is believed to underlie the subjective awareness of the “material me” and of the self in the present moment (Craig, 2009a). Moreover, research on bodily illusions has shown the involvement of this region in the merging of the exteroceptive visual and somatosensory information that it the basis of the subjective experience of body ownership (Tsakiris et al., 2007; Apps et al., 2015). Importantly, the insula is involved in the integration of exteroceptive stimuli arising from different sensory modalities (Bushara et al., 2001; Menon and Uddin, 2010; Craig, 2009a). For example, Bushara and colleagues (2001) found that this cortical region plays a crucial role in detecting synchrony/asynchrony between visual and auditory stimuli. Thus all evidence points to the insula as the probable neural substrate of altered subjective awareness arising from the cardio-visual merging that we investigated.

We note that our results should not be interpreted as directly related to time estimation *per se*, for two reasons. Firstly, “other" heart stimuli were closely matched in terms of heart rate and are therefore within the same time dimension as the participant’s own heart. Thus, differences between these conditions could not be related to individual’s time estimation skills. Secondly, while our results might suggest that participants intuitively used the rhythm of their own heart as a pacemaker in order to judge the regularity of the stimulus, we do not believe that they provide direct support for any account of the cognitive processes involved in time estimation (Muller and Nobre, 2014; Wittmann, 2009). Our interpretation of our results thus does not regard the heart as an endogenous clock-type system for time estimation (but see Craig, 2009b; Meissner and Wittman, 2011; Pollatos et al., 2014) and such considerations are beyond the scope of this study (for a discussion of this issue see Wittmann, 2009). Instead, what we propose is that the statistical correlation between the visual flashes and the internal heartbeat pulses had an impact in the subjective experience of the perception of the flashing rhythm.

Previous studies have shown that the modulation of own-body experience by cardio-visual integration can take place even if participants are unaware of such contingency (Aspell et al., 2013), although the effect is enhanced in people who are good heartbeat perceivers and thus have superior access to representations of their interoceptive states (Suzuki et al., 2013). We found a correlation between accuracy on “no-change trials” and trait IAcc, as measured by the heartbeat tracking task, suggesting that those participants who were better able to detect their own heartbeats might be relying to a greater extent on cardiac timings to perform this task. However, this relationship was only found in Experiment 1, not in Experiment 2. The reason for this inconsistency is not clear, particularly as comparable interoceptive scores were observed between the two experiments. One possibility is that the effect of cardio-visual integration on task performance is moderated by other variables that we have not measured, such as cognitive strategies or selective attention to visual vs. cardiac stimuli (David et al, 2014). Individual differences in these variables may have increased the variability in the mechanisms used to perform the task. It is likely that some participants, even among those scoring high on the IAcc task, used predominantly cognitive strategies that minimized their reliance on heartbeat timings.

Within a PC framework (Friston, 2005; Apps and Tsakiris, 2013; Seth, 2013; Ondobaka et al., 2015), a potential interpretation of our findings is that the individual's cardiac activity was used to generate predictive models of the timing of flashes. Relying on Bayesian principals, PC proposes that sensory information is processed probabilistically and therefore associated with some level of uncertainty (which is its 'precision'). Perceptual experience arises from the comparison between top-down predictions (priors) about sensory events and bottom-up sensory evidence. Inconsistencies between priors and the sensory evidence give rise to prediction errors that are passed up to higher hierarchical cortical levels for resolution. A percept is formed when prediction error is minimised. The relative influence on the final percept of the prior and the prediction errors depends on their reliability i.e. their relative precision. Over time the brain learns to optimise these precisions and thus adjusts the relative influence of prediction and prediction errors, depending on the context.

We assume in our experiments that, when the stimuli are a stream of flashes, the brain must predict the timing of each flash, whilst also predicting in the background, as it always does, the occurrence of each heartbeat. We propose that the temporal synchrony between heartbeats and the visual flashes (during "self" trials) would lead to the generation of a predictive model that contains the (implicit) high probability that future flashes will occur in synchrony with each heartbeat. In other words, there is relatively high precision weighting for the prior. By contrast, when such synchrony was not present, i.e. on "other trials", prediction errors would have a greater influence (precision) and therefore changes in flashing rhythms would be more easily detected. This would explain why there was improved performance in the "self no-change trials".

It is not, however, clear why synchrony between the flashing stimulus and the participant's heartbeats did not lead to enhanced detection of changes. A possibility is that each heartbeat that occurred before the change of heartbeat in mid trial had the effect of reinforcing the existing prior (i.e. that the flash would be synchronous with the heartbeat) and thus diminished the relative weight of subsequent prediction errors (i.e. the influence of any change in rhythm). As in "no-change trials", the lower precision weighting that would then be given to subsequent prediction error signals would diminish the probability of detecting changes in flashing rhythm.

In conclusion, this study demonstrates that people implicitly combine interoceptive with exteroceptive information when interacting with the world. It adds to the existing literature on mind-body interaction by showing, for the first time, that private sensations arising from interoception may be integrated with affectively neutral and self-unrelated external event, such as simple flashing circle, to form a multisensory percept of an external stimulus.

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Figure 1. Schematic representation of the experimental design.

Figure 2. In experiment 1 we observed A) improved performance in “self-no-change” vs “other-no-change” trials B) and a positive relationship between heartbeat tracking scores and correct judgments of “no-change” in the “self” condition.

Figure 3. In experiment 2, and line with the results of experiment 1, we observed greater accuracy in "self-no-change" trials compared to "other-no-change" trials.

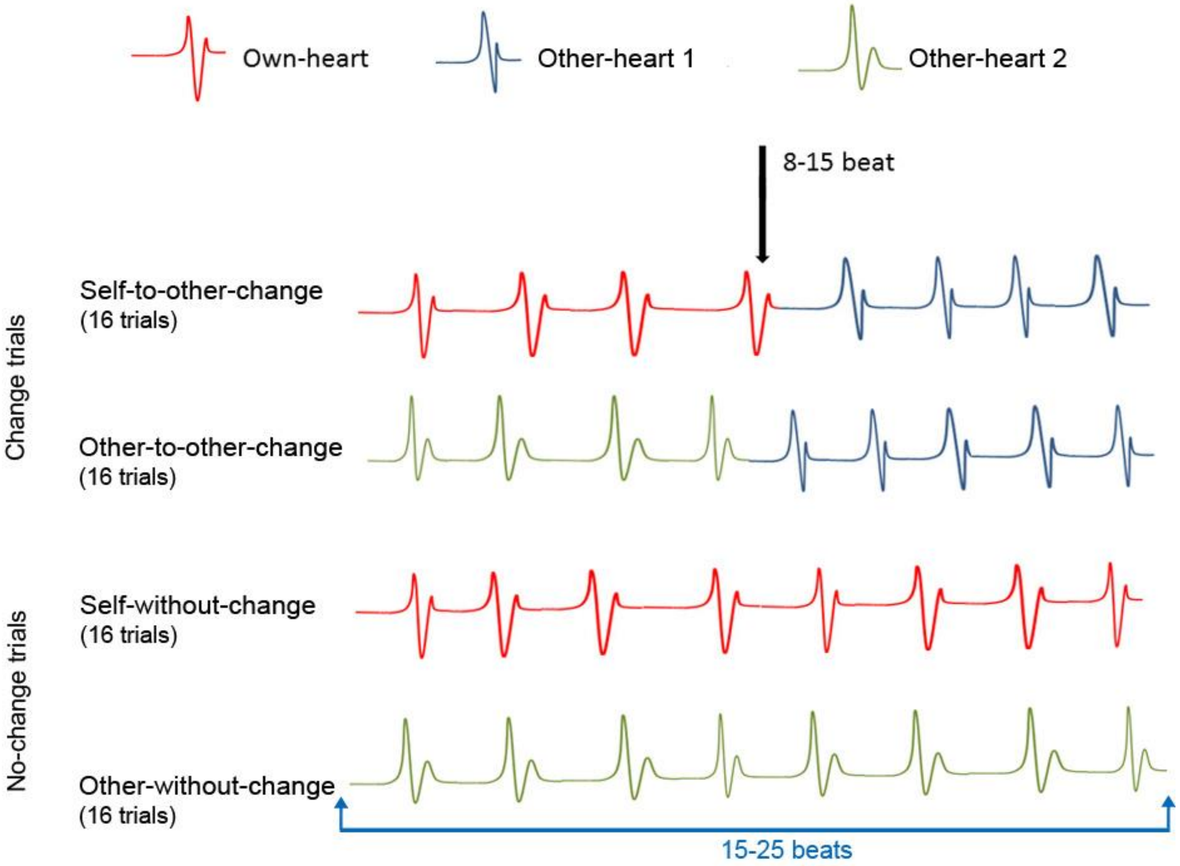
Own-heart
Other-heart 1
Other-heart 2
8-15 beat
Change trials
Self-to-other-change
(16 trials)
Other-to-other-change
(16 trials)
No-change trials
Self-without-change
(16 trials)
Other-without-change
(16 trials)
15-25 beats

Figure 1

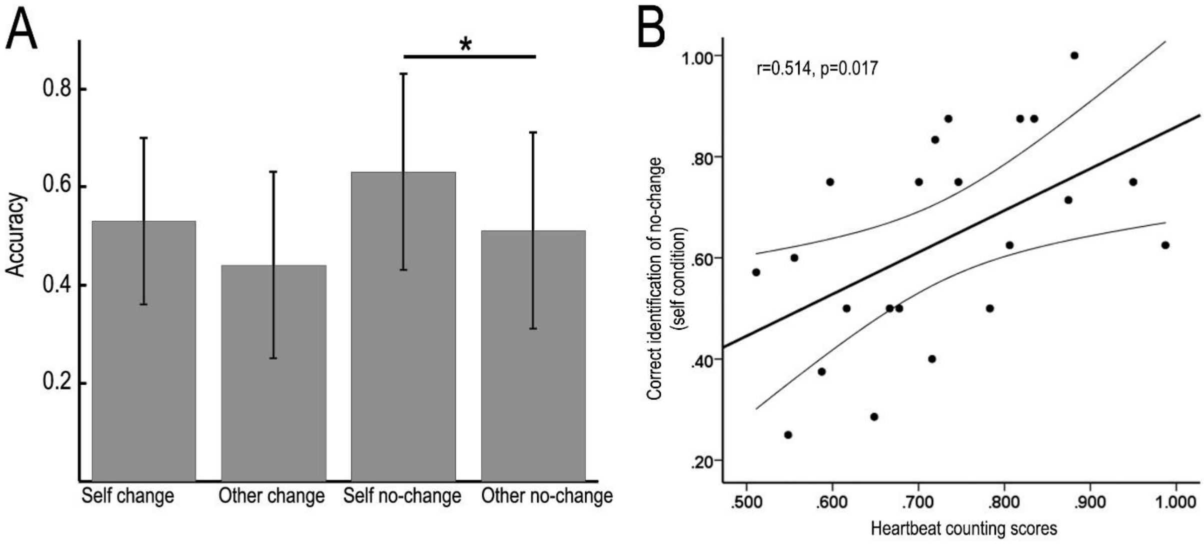
A
*
Accuracy
0.8
0.6
0.4
0.2
Self change
Other change
Self no-change
Other no-change
B
r=0.514, p=0.017
Correct identification of no-change
(self condition)
1.00
.80
.60
.40
.20
.500
.600
.700
.800
.900
1.000
Heartbeat counting scores

Figure 2

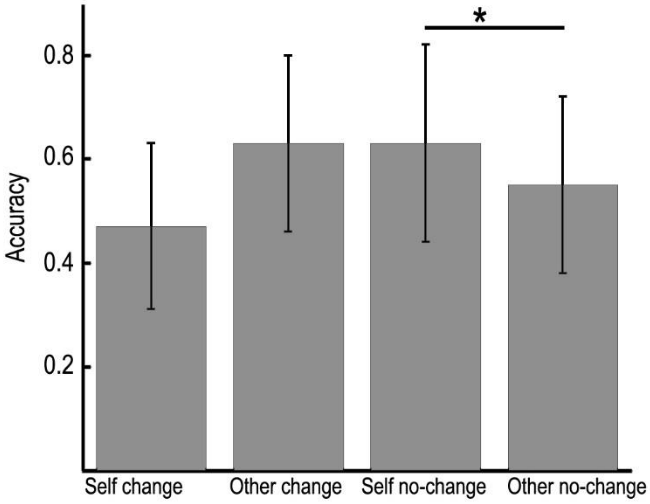
Accuracy
0.2
0.4
0.6
0.8
*
Self change
Other change
Self no-change
Other no-change

Figure 3