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RESEARCH ARTICLE

Affective interoceptive inference: Evidence from heart-beat evoked brain potentials

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Abstract

The perception of internal bodily signals (interoception) is central to many theories of emotion and embodied cognition. According to recent theoretical views, the sensory processing of visceral signals such as one's own heartbeat is determined by top-down predictions about the expected interoceptive state of the body (interoceptive inference). In this EEG study we examined neural responses to heartbeats following expected and unexpected emotional stimuli. We used a modified stimulus repetition task in which pairs of facial expressions were presented with repeating or alternating emotional content, and we manipulated the emotional valence and the likelihood of stimulus repetition. We found that affective predictions of external socially relevant information modulated the heartbeat-evoked potential, a marker of cardiac interoception. Crucially, the HEP changes highly relied on the expected emotional content of the facial expression. Thus, expected negative faces led to a decreased HEP amplitude, whereas such an effect was not observed after an expected neutral face. These results suggest that valence-specific affective predictions, and their uniquely associated predicted bodily sensory state, can reduce or amplify cardiac interoceptive responses. In addition, the affective repetition effects were dependent on repetition probability, highlighting the influence of top-down exteroceptive predictions on interoception. Our results are in line with recent models of interoception supporting the idea that predicted bodily states influence sensory processing of salient external information.

KEYWORDS

emotion, heartbeat-evoked potential, HEP, interoception, prediction

1 | INTRODUCTION

The ability to perceive internal bodily states, such as hunger, thirst, pain, muscular, and visceral sensations, known as interoception, is regarded as a fundamental basis for emotional processing, motivational control, and (embodied) selfhood (Craig, 2002, 2009; Damasio, 1994, 1999; Damasio, 2010; Garfinkel et al., 2013). High interoceptive accuracy has been linked to the intensity of emotional awareness (Herbert, Pollatos, & Schandry, 2007; Schandry, 1981; Wiens, 2005). Deficits in interoceptive processing have been associated with psychiatric conditions such as depersonalization symptoms (Seth, Suzuki, & Critchley, 2011; Sedeño et al., 2014), panic disorders (Yoris et al., 2015), obsessive compulsive disorder (Yoris et al., 2017), and depression (e.g., Avery et al., 2014; Pollatos, Traut-Mattausch, & Schandry, 2009; Terhaar, Viola, Bar, & Debener, 2012).

For many years, interoception was understood as a purely bottom-up, sensory-driven phenomenon, based on the representation of afferent sensory input from the body. However, recent accounts view interoception as a strongly top-down, prediction-driven phenomenon that, as with other sensory modalities, enables the inference of the causes of bodily sensations on the basis of past experiences (Ainley, Apps, Fotopoulou, & Tsakiris, 2016; Allen et al., 2016; Barrett & Simmons, 2015; Garfinkel et al., 2013; Pezzulo, Rigoli, & Friston, 2015; Sel, 2014; Seth et al., 2011). Thus, studies on self-perception and bodily illusions have shown that models of interoceptive self-representations and emotional feeling states can influence top-down perception of visual self-related information (Sel, Azevedo, & Tsakiris, 2017; Suzuki, Garfinkel, Critchley, & Seth, 2013). Moreover, studies have discussed processes of predictive multisensory integration of bodily signals from interoceptive and auditory sources (Canales-Johnson et al., 2015; van Elk, Lenggenhager, Heydrich, & Blanke, 2014). According to the view of top-down

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interoceptive models, visceral predictions are generated to adjust how the bodily systems organize internal resources to deal with the sensory world, not in its current state, but as the brain anticipates it will be in the immediate future. This way, the bodily sensations are in large part a reflection of what the brain predicts is happening within your body based on previous experiences (e.g., Barrett & Simmons, 2015). The idea of interoceptive inference has been mechanistically explained within the context of body homeostasis (Barrett & Simmons, 2015; Strigo & Craig, 2016). Visceral predictions are thought to contribute the maintenance of an optimal use of energy in the body by triggering allostasis, that is, changes in physiological responses to return the body to homeostasis. Animal research has suggested that these visceral predictions, and their associated allostasis, are accompanied by a modulation of attentional, sensory, and visceromotor responses to upcoming stimuli that are homeostatically relevant (Barbas, Zikopoulos, & Timbie, 2011; Gu & FitzGerald, 2014; Paulus & Stein, 2006). This way, the internal bodily states determine the stimulus salience according to its homeostatic value (e.g., as it happens in positive alliesthesia, Cabanac, 1992; Paulus, Tapert, & Schulteis, 2009; van Elk et al., 2014). These ideas highlight the strong link between multisensory integration of external and internal information and attentional and motor responses as determined by the predicted bodily state.

The neural implementation of the interoceptive inference model posits a central role for the anterior insular cortex (AIC; Seth et al., 2011; Garfinkel et al., 2013), which constitutes a site for multimodal integration of interoceptive and exteroceptive signals through interoceptive predictions (Allen et al., 2016; Klein, Ullsperger, & Danielmeier, 2013; Salomon et al., 2018). It has been argued that interoceptive predictions allow the integration of somatic states with external sensory information via suppression of the sensory consequences of cardiac activity (Craig, 2009; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Preuschoff, Quartz, & Bossaerts, 2008). Furthermore, the AIC has been related to awareness of subjective feelings. Specifically, the AIC has been suggested as a locus for responding to prediction error signals (e.g., Paulus & Stein, 2006; Preuschoff et al., 2008; Singer, Critchley, & Preuschoff, 2009) and for instantiating rerepresentations of interoceptive signals, thereby providing the basis for conscious access to emotional states and self-representations (Craig, 2009; Critchley et al., 2004). In this line, structural brain models have highlighted the key role of the AIC as a rich multimodal component of the interoceptive system (Barbas et al., 2011; Evrard, Logothetis, & Craig, 2014). Interoceptive information resulting from visceral changes ascends via the lamina I pathway and vagal nerve through the thalamus, arriving at the AIC, which serves as the primary interoceptive cortex (Saleem, Kondo, & Price, 2008). At the same time, visceromotor areas in frontal and prefrontal areas send afferent projections of the predictive bodily states. The AIC then computes the difference between the predicted interoceptive state and actual interoceptive signals (Barrett & Simmons, 2015). This idea is supported by studies observing abnormal insula activation in depersonalization disorder patients suffering from emotional detachment and a disrupted sense of self (Phillips et al., 2001; Sierra & David, 2011). However, direct empirical investigation of interoceptive predictions and their neural implementation is still lacking.

The majority of investigations in the literature on interoception have focused on cardiac signals, that is, cardiac interoception, mainly because heartbeats are discrete signals, which can be easily measured. As a consequence, heartbeat accuracy performance can be easily quantified (Garfinkel et al., 2016). Thus, cardiac interoceptive awareness (i.e., the ability to perceive one's own heartbeat) has been a key modality for investigating interoception and its neural correlates (Schandry, 1981). By using electroencephalography (EEG) it is possible to acquire neural responses to cardiac interoceptive signals. The so-called heartbeat-evoked potential (HEP; Montoya, Schandry, & Muller, 1993; Pollatos & Schandry, 2004; Pollatos, Kirsch, & Schandry, 2005; Gray et al., 2007; Couto et al., 2014) is an EEG response time-locked to the electrocardiogram (ECG) R-peak of the heartbeat and it is regarded as a marker of interoceptive cortical responses to cardiac signals. The size of HEP amplitude has been found to correlate with heartbeat detection accuracy, and therefore has been quantified as an electrophysiological marker of cardiac interoceptive awareness (Pollatos et al., 2005; Pollatos & Schandry, 2004; Schandry & Weitkunat, 1990; Terhaar et al., 2012). Moreover, the performance of cognitive tasks such as visual perception and self-processing modulate the HEP amplitude (Pollatos & Schandry, 2004; Park et al., 2017; Kim et al., 2018). The HEP latency ranges from 100 to 600 ms after the R-peak onset. The component is generally observed over fronto-central regions as well as in parietal regions (Canales-Johnson et al., 2015; Couto et al., 2014; Gray et al., 2007; Montoya et al., 1993; Schandry & Montoya, 1996; Schandry, Sparrer, & Weitkunat, 1986). In regards to the neural source of the HEP component, intracranial recordings and source analyses on EEG cortical activity have identified a number of sources comprising the right insula, anterior cingulate cortex and the amygdala, as well cortical areas such as the primary somatosensory cortex and the fronto-temporal cortex (Kern, Aertsen, Schulze-Bonhage, & Ball, 2013; Park et al., 2017). In the present study, we used EEG to measure HEP amplitude changes as a marker of interoception.

Using cardiac cues, recent studies have asked how predictions based on interoceptive signals may affect neural processing of sensory information from the world (e.g., Suzuki et al., 2013; van Elk et al., 2014). For example, van Elk et al. (2014) found suppressed processing of sounds in the auditory cortex if they were heartbeat-related, and therefore more predictable, as compared to externally generated sounds. In the same line, at the behavioral level, Allen and Friston (2016) demonstrated that perceptual confidence varies with unexpected prestimulus arousal and increased cardiac responses. Conversely, the reverse question has been largely unexplored. Hence, it remains unclear to which extent (cardiac) interoception itself can be modulated by predictive processes, in particular, by affective predictions of upcoming environmentally relevant cues (Barrett & Bar, 2009). Therefore, the aim of the current study was to explore whether exposure to expected or unexpected emotionally salient and neutral stimuli induces changes in neural responses in the interoceptive system.

To this end, a repetition suppression paradigm was adopted in which predictions are generated by repetitive exposure to the same stimulus (cf., Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Experimental studies using this paradigm have demonstrated that deceased cortical responses to repeated stimuli (repetition

suppression) depend on the local-likelihood of repetitions and are therefore a reflection of top-down predictions rather than neuronal adaptation (Summerfield et al., 2008; den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; e.g., Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Todorovic, van Ede, Maris, & de Lange, 2011). For example, the repetition of a face stimulus has been found to activate face-sensitive visual areas less when the probability of a face repetition is high as compared to when stimulus repetition is less probable (Summerfield et al., 2008; Summerfield, Wyart, Johnen, & de Gardelle, 2011). This finding has been replicated by a growing number of studies (Grotheer & Kovacs, 2014; Larsson & Smith, 2012; Mayrhauser, Bergmann, Crone, & Kronbichler, 2014). Notably, in the exteroceptive domain affective information has been found to influence repetition suppression, with larger effects for negative valence (e.g., fearful faces, Ishai, Pessoa, Bikle, & Ungerleider, 2004; angry prosody, Ethofer et al., 2009) than neutral stimulus material. Furthermore, in two recent studies we were able to show that predicted facial expressions modulated both visual and interoceptive cortical processing in a highly correlated manner (Marshall, Gentsch, Jelinčić, & Schütz-Bosbach, 2017; Marshall, Gentsch, Schröder, & Schütz-Bosbach, 2018). In these studies, the facial identity was kept constant within a given trial, and the repetition manipulation regarded the facial emotion. Therefore, it still remains open to what extent the effects of predictive visual information on interoception is a byproduct of earlier prediction effects in visual regions (i.e., repetition of low-level visual features), or if interoception itself can be modulated by predictive processes independently from processing of features inherent to a visual stimulus.

In analogy with these studies, we explored whether interoceptive responses evoked by cardiac signals are reduced or enhanced at the cortical level when affective expectations are fulfilled or violated, respectively, and if such an effect is independent from the perception of low-level facial features (i.e., facial identity). To this aim, the repetition suppression paradigm was modified to include not only neutral but also affective stimuli, and stimulus repetition was varied with respect to this valence dimension, as opposed to repetition of low-level features (i.e., identity repetition). In addition, we manipulated the likelihood of repetition, so that trials were presented in two probability contexts: repetition blocks, where the probability of stimulus repetition was high; alternation blocks, where the probability of stimulus repetition was low. Our hypotheses are in line with the main idea that sensory processing of external cues is influenced by internal bodily states (Barrett & Simmons, 2015; Salomon et al., 2016). We predict that manipulating the expectation of homeostatically relevant cues associated with internal bodily representations would lead to changes in the cortical processing of cardiac signals. Specifically, we expect that highly predictive affective signals due to stimulus repetition (fulfilled expectations), as compared to stimulus alternations (violated expectations), would modulate the HEP component, and that these HEP changes will be most likely present when the local frequency of repetition is high (i.e., more repetition than alternation trials; e.g., Summerfield et al., 2008). Moreover, previous evidence on the exteroceptive and interoceptive domain has demonstrated increased valence-specific repetition effects to salient, negative information (Ethofer et al., 2009; Ishai et al., 2004). In this line, we hypothesize that the expectation of a negative facial expression would lead to a greater repetition suppression effect on the HEP component that would be characteristically different to the repetition effects when expecting a neutral expression.

2 | MATERIAL AND METHODS

2.1 | Participants

A total of 19 right-handed students (10 females, mean age = 23 ± 3.1 years) with normal or corrected-to-normal vision participated in this study. Consent was obtained from all subjects prior to participation according to the Declaration of Helsinki (BMJ 1991; 302:1194). The study was approved by the Ethical Committee of the Department of Psychology, Royal Holloway University of London, where the data were acquired. Depressive symptoms were assessed using the Beck Depression Inventory (BDI-II; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961). In addition, participants indicated their level of anxiety by completing the State–Trait Anxiety Inventory (STAI; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983). Two participants had to be excluded from analysis, one was because of the report of severe depressive symptoms as indicated by a BDI score above 28 and another one was because of technical problems during EEG recording.

2.2 | Stimuli

The critical visual stimuli for the main experiment were taken from a validated set of face stimuli (NIMSTIM; Tottenham et al., 2009). Specifically, we included a set of 80 colored photographs showing full front faces of 40 young actors (20 females, 20 males) each modeling two facial expressions, neutral, and angry. The faces with the highest validation ratings were selected. In each image, only the face and hair was visible, any background was removed. The original images were resized to occupy 22.4 × 17.8 cm (height × width) on a computer screen at a viewing distance of 100 cm (subtending 12.8 × 10.2° visual angle). All images were centrally presented with a fixation dot at the point of the nose and on a uniform gray background using Presentation software (Neurobehavioral Systems, Inc.).

2.3 | Task and procedure

At the beginning of the experiment participants were fitted with electrodes for electrocardiogram (ECG) and electroencephalogram (EEG) and were seated in front of a computer screen, at an average viewing distance of 90 cm, in a dimly lit and sound-attenuated chamber. Before the main experiment, cardiac awareness was assessed using the Mental Tracking Method by Schandry (Schandry, 1981), a frequently used heartbeat counting procedure to measure trait interoceptive sensitivity (e.g., Herbert et al., 2007; Terhaar et al., 2012). Participants were asked to concentrate on their heart activity and to silently count their own heartbeats during three intervals of varying length, 25, 35, and 45 s, presented in random order. We used a rather strict instruction by emphasizing that participants should not make any guesses but should only count heartbeats that they had really felt. Before the presentation of the first interval, each participant was told to relax, to minimize eye and body movements and to try focusing on

the heartbeat during a brief practice phase. During the counting and ECG recording, participants were instructed to fixate on a cross displayed continuously on the center of the computer monitor. Visual instruction cues (the word "start" and "stop") signaled the beginning and the end of each counting phase, and individuals verbally reported the number of heartbeats they counted after each interval. All participants were able to perform the task.

After the heartbeat detection task, participants performed the main experimental task. In each trial, a cue face and a target face were presented in successive pairs, with each face presented for 500 ms, separated by a fixation screen for 500 ms. A jittered intertrial interval of 1.5–2.5 s was presented between pairs (see Figure 1). The two faces of each pair were either both showing neutral or angry expressions (repetition trials) or differed in valence, such that, a neutral expression was followed by an angry expression or vice versa (alternation trials). That is, stimulus repetition of the cue and target face varied with respect to facial affect as opposed to facial identity. This allowed us to directly manipulate the expectation of the facial emotional content independently from putative neural attenuation effects observed in visual processing when low-level visual features are presented in repetition (e.g., Marshall et al., 2017; Marshall et al., 2018; Summerfield et al., 2008). Moreover, we manipulated the likelihood of stimulus repetition by presenting the emotional expressions in two stimulus contexts (blocks). These stimulus contexts differed in the probability of repetition and alternation trials (see also, Summerfield et al., 2008). In repetition blocks, there were 75% of repetition trials and 25% of alternation trials (i.e., high probability of repetition trials). In the alternation block, there were 25% of repetition trials and 75% of alternation trials (i.e., low probability of repetition trials). Within each block, repetition and alternation trials were presented in random order.

Participants' task was to maintain central fixation throughout each block of trials and to monitor the stimulus stream for occasional arrows pointing left or right (target trials). The arrows were superimposed on the first or second face stimulus, and participants were instructed to signal their occurrence by pressing a left or right response button for which they received immediate feedback. These targets served as catch trials, they occurred on 20% of all trials (equally often for repetition or alternation trials and for the first or second stimulus) and were discarded from later analyses. Within blocks of 40 stimulus pairs (trials) each face stimulus was presented only once. The same face stimuli were used for repetition and alternation blocks. After a short initial training phase, participants performed 16 alternating repetition and alternation blocks resulting in 320 trials for each block condition overall, with a total number of 160 repetition trials and 160 alternation trials (50% neutral or angry facial expression). Each experimental session took about 2 hr with short breaks.

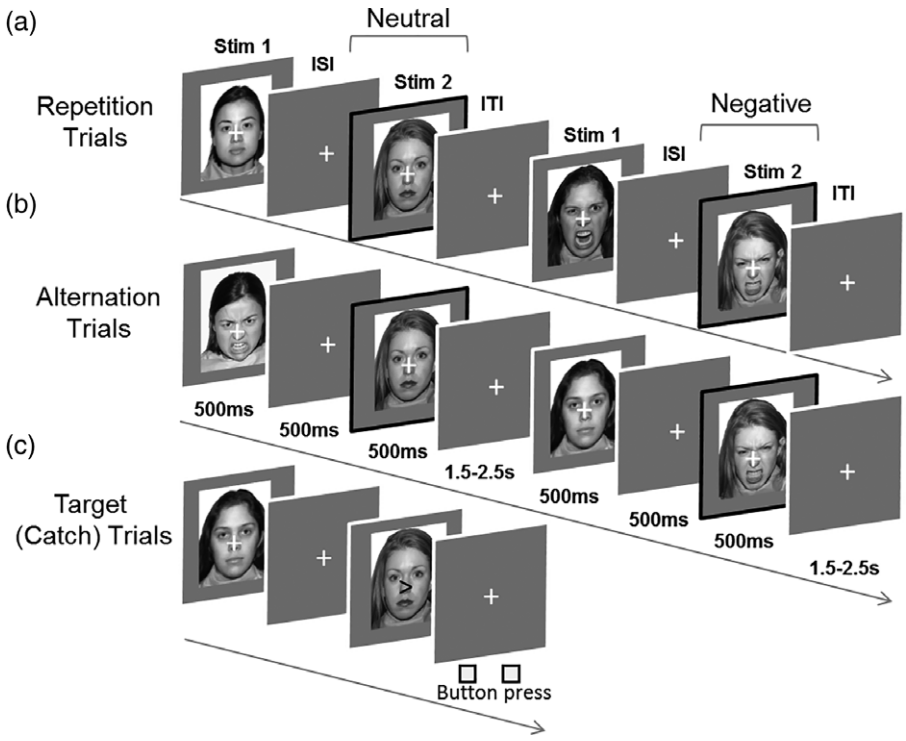

FIGURE 1 Trial structure and conditions. Face stimuli were presented in successive pairs (Stim 1, first face stimulus; Stim 2, second face stimulus) separate by a blank screen. A further blank screen of ~ 2 s was interposed between trials. (a) Two examples of repetition trials. Pairs consisting of two neutral faces or two negative faces were presented. (b) Two examples of alternation trials. Pairs consisted of one negative and one neutral face presented in counterbalanced order. Black frames indicate the main stimulus event (i.e., the onset of the second face stimulus, Stim 2) around which EEG analyses were centered. (c) Example catch trial. Participants screened stimuli for arrows (target trials), occurring on 20% of trials (equally often as first or second stimulus), and indicated the arrow direction with a right or left button press. Target trials were excluded from analyses

2.4 | EEG data recording and analysis

2.4.1 | Data acquisition

EEG data were recorded from 63 active scalp electrodes mounted in a standard electrode head cap (10–20 system) of the Biosemi Active Two system (Biosemi, Amsterdam, The Netherlands) with additional EOG electrodes applied at the outer canthus of each eye and below and above the right eye. Electrodes were referenced to a common mode sense (CMS) active electrode. Two additional ECG electrodes were placed below the left clavicle and below the left pectoral muscle, which produced a large R wave for automatic peak detection. All signals were amplified and digitized online at a sampling rate of 512 Hz, and the data were band-pass filtered during recording with low and high cutoffs of 0.16 and 100 Hz, respectively.

2.4.2 | Preprocessing

Offline EEG data were preprocessed using EEGLAB (EEGLAB 9.0.3, University of San Diego, San Diego, CA). Data were referenced to common average and band-pass filtered from 1–40 Hz. To identify heartbeat events, the EEGLAB plugin FMRIB 1.21 (Niazy, Beckmann, Iannetti, Brady, & Smith, 2005) was used for reliable R-peak detection. Muscular and other large nonstereotyped artifacts were also identified and rejected by visual inspection. The data were then submitted to the extended infomax independent component analysis (ICA) (Jung et al., 2000; Makeig, Debener, Onton, & Delorme, 2004) as implemented in EEGLAB, and was further down-sampled to 128 Hz for subsequent computations. The ICA decomposes the complex multichannel scalp data into a sum of temporally independent and spatially fixed components allowing semi-automatic identification and rejection of stereotyped artifacts, such as, eye movement and the volume-conducted cardiac-field artifact (CFA). The CFA represents a challenge to the analysis of the HEP because the averaging of the data around the R-peak amplifies the CFA becoming time-locked to the heartbeat (Brittain & Brown, 2014; Luft & Bhattacharya, 2015). However, ICA has been shown to be of high efficiency in the removal of the independent components representing CFAs from the EEG signal (e.g., Molinaro, Barber, & Carreiras, 2011; Terhaar et al., 2012). ECG channels were excluded from the analysis and a total number of 40 independent components (ICs) were obtained. The IC identification and selection process were guided by visual inspection of their properties, based on time course, scalp topography, ERP image (i.e., single-trial raster plots) and power spectrum. Specifically, we first inspected the 10 largest ICs contributing to the R wave epoch and identified those that accounted for most of the variance in the data. Subsequently, the ERP image representation was used to confirm the time-course across heartbeat events based on trial-to-trial variation of each IC. Then, the component maps were compared with the topographical distribution of the heartbeat artifact component as reported by Viola et al. (2009). A mean of three components per subject was selected and labeled as representing the heartbeat artifact (similar to the number reported in Viola et al., 2009). The heartbeat artifact-free EEG data were then obtained by back-projecting the remaining nonartifactual ICA components to the original channel signals. Finally, we compared the raw data with the back-projected activities to confirm that the heartbeat artifact was removed from the channel data. Supporting Information Figure S1 shows an example of successful CFA attenuation and HEP recovery following ICA correction.

To further ensure that the HEP changes that we observe are not influenced by CFA artifacts, and they are truly locked to the participants' heartbeat, we created surrogated R-peaks by shifting the onset of the original R-peak (e.g., Babo-Rebelo, Richter, & Tallon-Baudry, 2016; Park et al., 2017). R-peaks were shifted within a time window of −500 to +500 ms and they were shifted by the same amount separately for each subject and each of the eight conditions. We subsequently applied the same criteria for calculating HEP amplitude and submitted these surrogate values to the mass permutation test as described below.

2.4.3 | HEP amplitude

For further segmentation of the data into heartbeat-related epochs and HEP analysis BrainVision Analyzer was used (BrainVision Analyzer 2.0, Brain Products GmbH, Gilching, Germany). Data sets were segmented into 2000 ms periods relative to the presentation of the second face stimulus of each trial, starting 500 ms after stimulus onset to avoid potential overlap with visual stimulus processing from the second face. Within this poststimulus period data epochs were further segmented into periods from −100 to 600 ms relative to the R-peak marker, excluding epochs overlapping with the presentation of the visual stimulus in the next trial. HEPs were calculated by averaging across trials for each experimental condition using the −100 ms interval prior to the R-peak marker for baseline correction.

The topography of the HEP has a frontal-to-parietal distribution over the scalp (Montoya et al., 1993; Pollatos et al., 2005; Pollatos & Schandry, 2004; Schandry & Montoya, 1996), with observations of a right lateralization (Dirlich, Vogl, Plaschke, & Strian, 1997; Pollatos & Schandry, 2004; Schulz et al., 2015). However, across studies, there is considerable variability in HEP polarity, latency, and scalp distribution, which may reflect a functional relation between contextual factors, such as mental states (Gray et al., 2007) and temporo-spatial patterns of the HEP. In view of such variability in the HEP literature, in the current study, we adopted a nonparametric, permutation-based approach to first determine the HEP morphology, and then estimate any HEP modulation by the affective repetition manipulation. We passed the subject-wise activation time courses to the analysis procedure as implemented by ERPlab, the details of which are described in Groppe, Urbach, and Kutas (2011). In brief, data were submitted to a repeated measures, two-tailed cluster mass permutation test (Bullmore et al., 1999) using a family-wise alpha level of 0.05 (i.e., 5,226 total comparisons). Any electrodes within approximately 5 cm of one another were considered spatial neighbors. Repeated measures t tests were performed for each comparison using the original data and 2,500 random within-participant permutations of the data. For each permutation, all t scores corresponding to uncorrected p values of .05 of less were formed into clusters. The sum of the t scores in each cluster is the "mass" of that cluster and the most extreme cluster mass in each of the 2,501 sets of tests was recorded and used to estimate the distribution of the null hypothesis. This procedure provides exact statistics corrected for multiple comparisons and is a common approach used to study large neuroscientific data sets (Groppe et al., 2011; Maris & Oostenveld, 2007). Where appropriate, we calculated Bayesian

statistics for null effects (Babo-Rebelo et al., 2016; Park et al., 2017; Rouder, Speckman, Sun, Morey, & Iverson, 2009; Salomon et al., 2016) using the online Bayes factor calculation tool (http://pcl.missouri.edu/bayesfactor), based on the approach by Liang, Paulo, Molina, and Berger (2008). The BF_{01} allows assessment of the likelihood of the results based on Bayesian prior. As a general rule, a $BF_{01} > 3.2$ provides substantial evidence for the null hypothesis, while a $BF_{01} < 3.2$ does not constitute sufficient evidence to either discount or accept the null hypothesis (Kass & Raftery, 1995).

The topographical distribution of the neural phenomena comprising the HEP was defined by computing mean voltages of the HEPs time-locked to R-wave onset for all trial types at the group level using the nonparametric randomization test including all electrodes sites and across the entire time window where the HEP typically takes place, this is, 100–600 ms (Canales-Johnson et al., 2015; Fukushima, Terasawa, & Umeda, 2011; Pollatos & Schandry, 2004; Schandry & Montoya, 1996; Sel et al., 2017; Yuan, Yan, Xu, Han, & Yan, 2007). For this analysis, no apriori electrode clusters were formed (i.e., all 63 active electrodes were treated as a distinct variable). The topography analysis revealed a number of electrode sites widely spread along the frontal, centro-frontal and posterior areas were the HEP was distributed. These electrodes were then organized in five ROIs according to their spatial distribution (Figure 2) for further processing.

To test if the stimulus repetition effects on cardiac cortical processing differed for negative versus neutral facial affect, and whether these effects rely on the repetition expectation at a given stimulus context (repetition vs. alternation block), we first computed the repetition effect (calculated by subtraction of amplitudes at each time point of the alternation trials from the repetition trials) in both the neutral and the angry faces separately. We then contrasted the repetition effects on neutral versus angry faces by means of nonparametric cluster-based permutation test. According to previous studies (e.g., Summerfield et al., 2008), we expected the repetition effects to be most prominent when the likelihood of repetition is high, that is, repetition block. Therefore, we took a hypothesis-driven approach and tested the influence of facial emotion on repetition suppression effects separately for the repetition block and alternation block. To estimate the repetition effects on neural responses to heartbeats the mean voltages of the HEPs were first divided and averaged in consecutive time windows of 100 ms length starting from 100 to 600 after the R-wave onset. Analyses were restricted to the five ROIS (Figure 2), defined according to the HEP morphology analyses. For each time window, subject-wise activations at electrode sites circumscribed in every ROI were extracted and passed to the analysis procedure. Where appropriate, *p* values were corrected for multiple comparisons using Bonferroni-Holms correction.

2.4.4 | Analysis of heartbeat perception

Each individual's heartbeat perception score was calculated according to the following equation (Schandry, 1981):

$$(1 \div 3) \times \sum_{i=0}^{3} [1 - ((\text{recorded items} - \text{counted items}) \div \text{recorded items})]$$

with high scores (max. 1) indicating more accurate heartbeat perception, that is, increased trait interoceptive sensitivity.

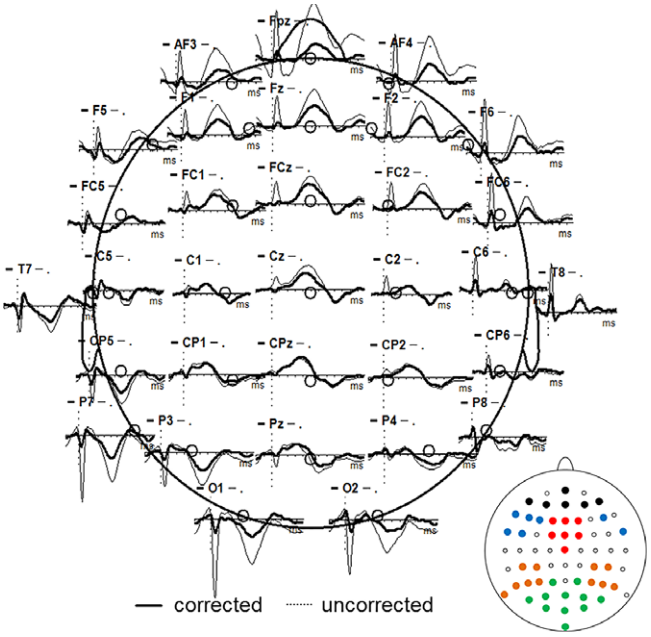

FIGURE 2 HEP morphology. Grand average waveforms across the scalp time locked to the onset of the R-wave (at time 0 ms), contrasting waveforms before (solid line) and after (dashed line) cardiac-field artifact (CFA) correction by means of independent component analysis (ICA). Small topographical map (bottom right) indicates the set of electrodes clustered by ROIs (colour-coded) resulting from the morphology analysis where the repetition effects were tested

2.4.5 | Correlation analysis

To test if the effects of affective repetition on HEP amplitude were associated with individual trait factors, we performed Pearson correlation analyses assessing the relationship between affective repetition effects on HEP and the individuals' interoceptive awareness, symptoms of depression (BDI) and anxiety (STAI). We submitted the resulting r^2 values to the online Bayes calculation tool. Results of this analysis are reported in the Supplementary information.

In light of previous evidence showing that HEP amplitude is modulated by attention to interoceptive signals (Pollatos & Schandry, 2004), we explored the possibility that individual variability on interoceptive attention influences the affective repetition effects on HEP. To this aim, we analyzed the HEP recorded during the heart-beat counting task and calculated the corresponding BF_{01} for the Pearson correlation analysis between HEP amplitude changes during the counting task, and the affective repetition effects on HEP amplitude during the repetition suppression task. The analysis of the HEP data recorded during the heartbeat counting task mirror the main morphology analysis performed for the data collected during the repetition suppression task as described above (see Supporting Information for details).

3 | RESULTS

3.1 | Heartbeat-evoked potential

Figure 2 presents the topographical characteristics of the HEP based on the averaged R wave-locked ERP waveforms across all experimental conditions. The morphology analysis revealed that the HEP was

widely distributed along frontal, fronto-central, and parietal areas including the following spatial regions. Frontal sites: AFz, Fpz, AF4, AF3, AF8, AF7; Fronto-central sites: F1, Fz, F2, FC1, FCz, Cz, FC2; Fronto-lateral sites: FT8, F6, FC5, F5, F7, F3, FT7; Posterior sites: PO7, PO3, P3, P1, O1, POz, Oz, Iz, O2, P2, PO4, PO8; Posterior-lateral sites: CP5, CP3, P9, P7, P5, P3, CP6, CP4, P8, P6, P4 (Figure 2). The results of the cluster-based permutation analysis showed two statistically significant clusters, an anterior negative cluster (that gives statistical support for the sites distributed over anterior and central regions) and a posterior positive cluster (that gives statistical support for the posterior sites) (all p values <.001). Consistent with previous studies (Canales-Johnson et al., 2015; Gray et al., 2007; Pollatos & Schandry, 2004; Sel et al., 2017), in frontal and fronto-central regions the HEP was observed as a negative deflection, whereas the HEP exhibited a positive polarity in parietal regions.

The results of the cluster-based permutation analysis revealed a significant positive cluster in the 200–300 ms time window after the R-wave onset in the fronto-central region at the following electrodes: Fz, F2, FCz, FC2, Cz (p = .006; d = 0.69; BF_{01} = 0.022), when contrasting the repetition effect in negative trials vs. neutral trials in the repetition block, that is, when there was a higher number of repetition trials. This time window and electrode sites are in accordance with the latencies reported in previous HEP studies, where the cortical processing of cardiac signals takes place (Canales-Johnson et al., 2015; Fukushima et al., 2011; Kern et al., 2013; Pollatos & Schandry, 2004; Schandry et al., 1986; Yuan et al., 2007). Contrary, the repetition effect was not significantly different for negative vs. neutral trials in the alternation block at any electrode cluster, or in any other cluster in the repetition block (all ps > 0.05; BFs ranging between 4.01: substantial evidence for the null hypothesis, and 1.12: inconclusive evidence) (see Supporting information, Table S1 for a summary of the BFs).

Overall, these results show that the observed differences between repetition and alternation trials in the repetition block are dependent on the affective content of the face. Figure 3a,b displays the HEP waveforms over fronto-central scalp sites related to repetition and alternation trials separately for neutral and negative stimuli in the repetition block. Specifically, when the angry expression was repeated (i.e., repetition trials) the HEP amplitude recorded after the second angry face was diminished relative to when a target neutral face followed a cue angry face (i.e., alternation trials). In contrast, the HEP amplitude to neutral faces did not differ when contrasting repetition and alternation trials. This pattern of interaction was only observed in the repetition block suggesting that the affective repetition effects found in the cardiac cortical responses heavily relies on the local likelihood of repetitions implicitly driven by the stimulus context (Figure 3c). In addition, the repetition suppression effects on HEP amplitude observed in angry versus neutral faces in the repetition block were independent from individuals' interoceptive attention effects on cortical processing of cardiac signal, that is, HEP amplitude changes during the heart-beat counting task (see Supporting Information results for details).

3.2 | Control analysis of ECG amplitudes

To further reduce potential confounds by the temporally overlapping cardiac-field artifact (CFA), three control analyses were performed. First, we performed the cluster-mass permutation test following the procedure described above on original HEP waveforms prior to ICA transformation. That is, on HEP data uncorrected for the CFA overlap. Unlike the results observed in the ICA-corrected HEP analysis, the contrast between conditions in the uncorrected data did not show any cluster of significant interactions at p < .05. This result indicates that the observed differential ERP amplitudes reflect modulations of the HEP rather than differences because of the artifacts from the overlapping cardiac field.

Moreover, to ensure that the HEP amplitude differences observed in the repetition block cannot be explained by differences in the ECG signal, we analyzed the ECG trace mimicking the analyzing procedure followed in the HEP analysis. We performed the analysis on the average ECG signal where the repetition effects on the HEP were found (i.e., 200–300 ms time window). The results of the cluster-based permutation test on the ECG signal did not reveal any significant cluster of significant interactions at p < .05, corrected for multiple comparisons.

In addition, to determine that the observed HEP changes are not contaminated by CFA artifacts, and they are also truly locked to the participants' heartbeat, we repeated the permutation analysis as explained above using the artificially created surrogate R-peaks. In contrast to what we observed in the topographical analysis of the signal time-locked to the participants' heartbeats, the results of these analyses did not show any cluster of significant interactions at p < .05. Similarly, we submitted the values obtained from surrogate R-peaks over the same time period (200–300 ms) and electrode sites as values obtained with true R-peaks to the cluster-permutation analysis testing for repetition affective repetition effects. The results of the cluster-permutation test did not show any cluster of significant interactions at p < .05.

Altogether, the results of the control analysis demonstrate that HEP expression and its subsequent modulation across stimulus conditions reflects cortical processing of cardiac activity rather than other changes in ongoing EEG activity, such as for example CFA artifacts, or long-lasting effects linked to the visual presentation of the second face.

3.3 | Visual processing

To test whether the affective repetition effects observed in the cardiac neural correlates might be linked to changes in visual cortical responses to the facial stimuli, we analyzed the visual evoked potentials (VEPs) time-locked to the onset of the target face. These analyses mimicked the analysis performed on the HEP component, which are described in the methods section. In brief, we first computed the subject-wise activation time courses for all trial types at the group level using the non-parametric randomization test at all electrodes sites and across the time window ranging from 0 to 600, where early and long-latency VEP components have been reported. The topography analysis revealed a number of electrode sites in the posterior region comprising: P1, P3, P5, PO7, PO3, O1, POz, Pz, P2, P4, PO8, PO4, O2; electrode sites where visual ERPs are typically reported. We then tested the repetition effects (computed by the difference between repetition and alternation trials, in both the neutral, and the angry faces) at the posterior electrode sites on consecutive time windows of 100 ms length (from 0 to 600 ms–time window comprising the latencies reported in previous studies looking at repetition suppression effects on the face visual processing (Engell &

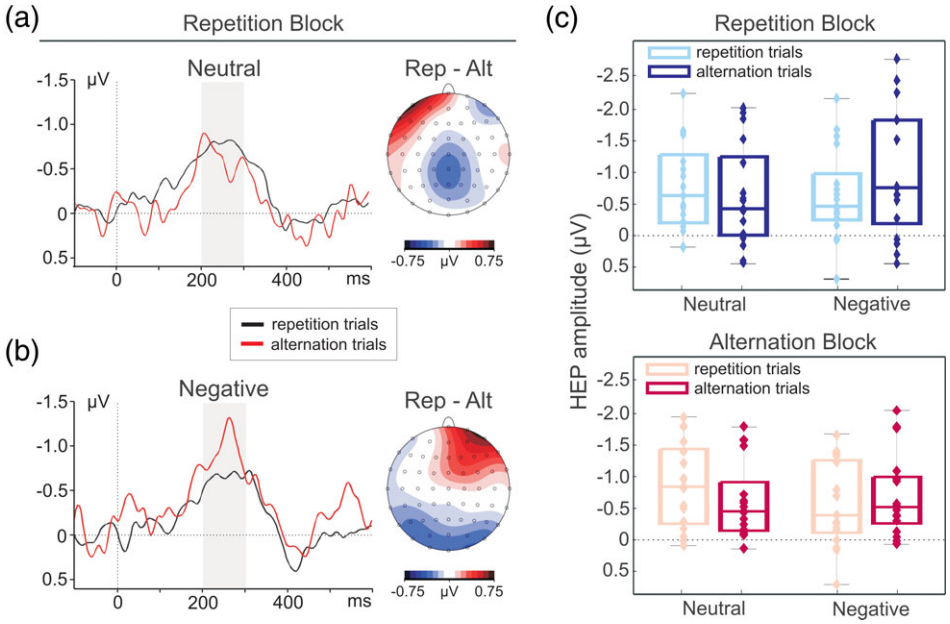

FIGURE 3 HEP waveforms in the repetition block following the onset of the R-wave (at time 0 ms) are shown separately for (a) neutral stimuli and (b) negative stimuli. Repetition trials (black line) are contrasted with alternation trials (red line). Shaded area indicates the time-window (200–300 ms after the R-wave onset) for which a significant positive cluster was revealed by cluster-based permutation analysis. Waveforms represent the average amplitude across the set of electrodes contributing to the positive cluster (Fz, F2, FCz, Cz, FC2; see results). (c) Box plot showing the mean HEP amplitudes (200–300 ms, based on the above electrodes) for neutral and negative stimuli in repetition trials and alternation trials, separately for repetition and alternation blocks

McCarthy, 2014; Nemrodov, Jacques, & Rossion, 2015; Vizioli, Rousselet, & Caldara, 2010). For each time window, subject-wise activations at the posterior electrode sites were extracted and passed to the nonparametric, mass univariate permutation analysis correcting for multiple comparisons. The results of these analyses demonstrated that the repetition suppression effects did not differ when contrasting negative vs. neutral trials neither in the repetition block nor in the alternation block (all ps > 0.05, all BFs_{01} > 3.71). These results show that, in contrast to what we observed in the neural processing of cardiac interoceptive signals, the affective repetition manipulation does not impact neural visual processing of facial expressions. The VEP results suggest that the affective repetition effects observed in HEP amplitude changes are unlikely to represent carry-over effects from repetition effects in the visual domain.

3.4 | Trait interoceptive awareness, BDI, and STAI results

The mean heartbeat perception score in the present sample (N = 17) was M = 0.52 (SD = 0.28, ranging from 0.10 to 0.97). The trait interoceptive awareness (IA) observed here is moderately low with respect to previous studies but on average comparable to the scores reported in the literature (e.g., Ainley & Tsakiris, 2013). The mean depression score on the BDI was 8.2 (SD = 5.9, minimum 0, maximum 19) indicating minimal to mild depression severity in the present sample. The mean STAI state score (M = 35.1, SD = 7.7, minimum 21, maximum 48) and trait score (M = 41.8, SD = 10.1, minimum 26, maximum 64) were comparable to other student samples (e.g., Pollatos et al., 2009). We did not find a significant relationship between these measures and the affective repetition effects on HEP amplitude (See Supporting Information for details).

4 | DISCUSSION

The present study investigated the effects of affective predictions on interoceptive processing by using a repetition suppression paradigm whereby the expectations build on the emotional component of facial expressions. Our results show that affective predictions modulate cortical responses to cardiac interoceptive signals, as measured by HEP amplitude changes. Specifically, we observed a reduction of the HEP amplitude to repetition of angry expressions in comparison to when target neutral expressions followed an angry face. However, this repetition effect on HEP amplitude was not observed in neutral trials, whereby the HEP amplitude did not differ between repetition and alternation trials. Crucially, this emotion specific repetition effects on interoceptive cardiac processing were dependent on the local likelihood of repetitions. Thus, affective predictions influenced cardiac interoception only when the probability of emotion repetition was high, that is, repetition blocks, as compared to when the emotion repetition was less probable. By contrast, we did not find repetition effects in visual cortical processing suggesting that the top-down affective predictive processing occurred only in the cardiac interoceptive domain, over and above processing of low-level visual features.

4.1 | Context-dependent affective prediction effects on cardiac cortical processing

Converging evidence has demonstrated that enhancing the expectations about stimulus occurrence by, for example, increasing stimulus

repetition rate, leads to neural modulations in cortical regions where the expected stimulus is represented, that is, repetition effects (Friston, 2005; Henson, Shallice, & Dolan, 2000; Summerfield et al., 2008; Todorovic et al., 2011; Turk-Browne, Yi, Leber, & Chun, 2007). It has been argued that these repetition effects on neural activity rely on top-down predictive processing, therefore reflecting a suppression of surprise responses elicited by unexpected sensory events, rather than bottom-up neuronal adaptation (Friston, 2005; Summerfield et al., 2008). In the current study, affective repetition effects on cardiac interoceptive processing were only observed in repetition blocks, suggesting that the repetition effects were highly dependent on probability context. Theoretically, top-down prediction signals tend to operate at different timescales, relying on stochastic regularities learned over longer time scales, as well as on local transition probabilities (for review, see Schubotz, 2015). The evidence that affective repetition effects were only present when the likelihood of repetitions was high suggests that the HEP modulation may result from global top-down modulation based on probability context (i.e., high-repetition probability) rather than from lower level sources of local prediction signals from the preceding trial. Our results are in line with previous evidence that highlight the role of expectations in repetition effects (Marshall et al., 2017; Marshall et al., 2018) supporting the idea that repetition suppression is a surprise—context-dependent phenomenon that occurs via probability context.

4.2 | Influence of affective homeostasis on interoceptive processing

The results of our experiment demonstrated repetition suppression effects on interoceptive processing as a function of affective valence. While the repetition of angry faces led to a suppression of HEP amplitude relative to alternated neutral faces, such an effect was not found for repeating neutral faces. Recent theoretical proposals have suggested that interoception can be characterized as an active inference process (Allen & Friston, 2016; Barrett & Simmons, 2015; Garfinkel et al., 2013). According to this view, visceral predictions are generated to adjust how the bodily systems organize internal resources to deal with the sensory world, not in its current state, but as the brain anticipates it will be in the immediate future. It is believed that these visceral predictions allow the body to return to homeostasis, or to enable allostasis, according to how the body will feel in response to upcoming events, that is, bodily predictions (Barrett & Simmons, 2015; Strigo & Craig, 2016). Facial expressions are homeostatically relevant in nature. In comparison to neutral expressions, angry facial expressions trigger a distinctive pattern of homeostatic responses to return the system to equilibrium. For example, during controlled fast breathing unpleasant pictures are associated with increase activation in interoceptive cortical areas, specifically in the right cingulate cortex, whereas in controlled slow breathing pleasant pictures elicit activation in the left insula and left cingulate cortex (Zautra, Fasman, Davis, & Craig, 2010). In the process of allostasis, the somatic state of the body dictates the capacity of an upcoming stimulus to return the body to homeostatic conditions, that is, alliesthesia (Cabanac, 1992). In the current study, it is assumed that future-oriented visceral predictions were made in relation to the presentation of the second facial expression. Given the distinctive nature of homeostatic responses to angry vs. neutral faces, it is possible that in repetition trials both the valence-specific visceral predictions and the associated allostatic process trigger distinctive patterns of physiological responses in preparation for the second "expected" face. This valence-specific interoceptive changes could explain the HEP amplitude suppression observed for repeated angry vs. neutral faces. Similarly, if a neutral expression is presented when the visceral predictions inform the bodily state to expect an angry expression (i.e., angry alternation trials), the unexpected neutral expression would acquire a qualitatively different homeostatic ability than when the neutral face is expected (i.e., neutral repetition trials). These homeostatic mechanisms could underlie the valence-specific HEP amplitude response to angry faces when they are presented in alternation versus repetition trials.

4.3 | Affective inference, bodily predictions, and perceptual bias

Neuronal models of interoception conceptualize interoceptive predictions as afferent signals projecting from agranular visceromotor cortices in frontal and prefrontal areas to the insular cortex, which serves as the primary interoceptive cortex (Evrard et al., 2014; Saleem et al., 2008). These visceromotor regions not only belong to the interoceptive system but are also part of the attention and action control network (Corbetta & Shulman, 2002; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). For example, animal research has demonstrated that areas linked to the visceromotor network, such as the lateral prefrontal cortex and the posterior orbitofrontal cortex send widespread projections to the thalamic reticular nucleus, suggesting a role in channeling sensory information and emotional context for selective attention and action (Barbas et al., 2011). Moreover, the AIC is a key component in multimodal integration of visual, auditory, and somatosensory information, and it is known as the cortical substrate for subjective emotion in humans (Craig, 2002; Craig, 2009; Critchley et al., 2004). This way, the AIC helps to create a multisensory representation of the body in the world, so that information perception is influenced by interoceptive predictions. The proposed source of the HEP has been the AIC (Park et al., 2017; Pollatos et al., 2005), and HEP amplitude increase is commonly viewed as an enhanced interoceptive response to cardiac signals (Park et al., 2017; Terhaar et al., 2012). Thus, one could speculate that the HEP repetition suppression effect found in angry trials can be explained as a consequence of attentional bias to threatening stimuli linked to interoceptive inference. This is, when anticipating angry expressions, it may be more important to direct attention to these homeostatically significant stimuli, rather than prioritizing internal physiological mechanisms. Therefore, the reduced HEP amplitude could be explained as a shift of attentional resources allocated to the exteroceptive facial threat cues as opposed to the internal physiological mechanisms, with the aim to returning to bodily homeostasis.

Accordingly, it seems perhaps counterintuitive that predictive information about negative affective material may not facilitate but interfere with interoceptive processing (see Marshall et al., 2017 for a complementary explanation on the attentional bias hypothesis).

Furthermore, the current findings are in line with evidence demonstrating the influence of affective valence on visceromotor response. For example, ERP evidence has shown that the processing of self-generated actions is selectively reduced for negative but not for positive outcomes (Gentsch, Weiss, Spengler, Synofzik, & Schütz-Bosbach, 2015). Moreover, previous results suggest that motor involvement (for example in a match-to-target task, Ishai et al., 2004) is associated with greater repetition effects for negative versus neutral faces in visual processing, in comparison to when faces are observed passively (Seth et al., 2011). Overall, our results expand on evidence highlighting the relationship between visceromotor and affective processing, supporting the idea of predictive multisensory integration across interoception and exteroception (Babo-Rebelo et al., 2016; Canales-Johnson et al., 2015; Salomon et al., 2016; Sel et al., 2017; Suzuki et al., 2013; van Elk et al., 2014).

It is important to note at this point that caution should be exercised in making direct inferences about the underlying neural mechanisms of cardiac processing, as it is difficult to assert whether the HEP amplitude primarily indicates inhibitory or excitatory neural activity. Thus, it is possible that, within the AIC, both reduced and enhanced responses would be observed for cardiac signals following face repetitions which remains to be tested in future research. Accordingly, the observed HEP suppression to expected versus highly unexpected facial expressions should be interpreted as a change in overall (excitatory and inhibitory) synaptic activity in the underlying region (see also, Canales-Johnson et al., 2015). Moreover, changes in cardiac interoceptive processing as reflected by HEP amplitude changes can take place unconsciously (Canales-Johnson et al., 2015). This is in line with our observation that individual variation in explicit interoceptive ability, as measured by the heartbeat counting task, was not related to the HEP modulation. Altogether, our results suggest a sensitivity of the interoceptive system to global prediction signals due to external stimulus repetition, and an interesting valence-specific homeostatic modulation of this response.

4.4 | Affective inference does not impact visual cortical responses

An interesting finding is the lack of affective repetition suppression in the visual system. These results contrast with previous ERP studies reporting repetition suppression effects on early VEPs (e.g., Engell & McCarthy, 2014; Nemrodov et al., 2015; Vizioli et al., 2010). However, the majority of previous studies have manipulated purely physical perceptual features (i.e., repetition of facial identity), and they have solely focused on exteroceptive measures (Summerfield et al., 2008). By contrast, in our paradigm the repetition manipulation was made in regards to the affective content of the facial expression, that is, emotion component, as opposed to the identity component. The contrast between the affective repetition effects observed in interoceptive processing vs. the exteroceptive visual processing suggests that affective interoceptive predictions (as determined by repetition probability of external homeostatically relevant stimuli) reflect a governing mechanism that is independent from visual processing, operating over and above other sensory modalities. A recently published ERP study has shown that repetition of the same facial identity posing a negative expression leads to repetition suppression of both VEPs and HEP, in comparison to when posing a neutral expression (Marshall et al., 2017, see also Marshall et al., 2018). Interestingly, the amplitude reduction of the visual and the cardiac component were highly correlated suggesting a common process underpinning repetition effects in both the exteroceptive and the interoceptive domain. Despite the multiple control analysis, in Marshall et al.'s (2017) study it was difficult to completely rule out whether the changes observed in the HEP amplitude were a direct effect of the affective repetition manipulation, or whether the amplitude suppression represented carry-over effects of the early affective repetition changes observed in the visual domain. Our results complement these findings demonstrating that the effects of affective interoceptive predictions as reflected by HEP amplitude occur over and above the processing of low-level visual features.

5 | LIMITATIONS AND CONCLUSIONS

Our study has a number of limitations that are worth noting. First, we did not control for other cardio-respiratory parameters that might affect the HEP amplitude changes (Babo-Rebelo et al., 2016; Park, Correia, Ducorps, & Tallon-Baudry, 2014), and therefore, we are unable to account for their potential impact in our findings. Similarly, the short intertrial interval of our experimental setup does not allow the computation of cardiac parameters, such as the interbeat interval and activity in the heart period power spectrum (Rajendra Acharya, Paul Joseph, Kannathal, Lim, & Suri, 2006). Therefore, it was not possible to test for any relationship between HEP amplitude changes and heart-rate variability in the experimental recording. Future studies would benefit from including these measures. Moreover, we did not find a relationship between changes in HEP amplitude linked to the affective repetition manipulation and trait variables of interoceptive accuracy or interoceptive attention effects on HEP amplitude during the heart-beat counting task. Also, the affective repetition effects on HEP amplitude changes were independent from psychopathological symptoms (depression, anxiety). Interoception is a multidimensional construct. Beyond interoceptive accuracy, two other interoceptive dimensions have become relevant in recent years. Interoceptive sensibility, this is the subjective belief of feeling signals from within the body, and interoceptive awareness that refers to metacognitive accuracy or confidence-accuracy correspondence (Garfinkel et al., 2013; Garfinkel et al., 2016). Although, we failed to show a relationship between interoceptive accuracy and changes in HEP amplitude, it might be possible that the affective repetition effects could be related to individual differences in the other interoceptive dimensions, interoceptive sensibility, and awareness. Besides, we did not find a relationship between affective prediction effects on HEP changes and self-reported measures of anxiety and depression. However, the BDI scores in the sample were unexpectedly high, and therefore, might have influenced the observed results. Although, we cannot rule out the influence of depression on the observed results, the lack of correlation between BDI scores and HEP amplitude changes challenges this possibility. Given the relatively small sample size, future studies

examining all interoceptive dimensions and involving distinct clinical populations are needed to further explore these questions.

In conclusion, our study suggests that affective predictions of external relevant information influence interoceptive processing as reflected by amplitude changes in HEP, a cortical index of cardiac signals. Importantly, the changes in HEP amplitude were highly dependent on the expected emotional content of the upcoming information. While expected angry faces lead to a reduction in the HEP amplitude, that is, repetition suppression, such a modulation was not present to expected neutral expressions. This valence-specific pattern of results in interoceptive processing could be interpreted as the result of predicted bodily states to external emotional information that trigger distinctive homeostatic changes that lead to an attentional shift from internal information to environmentally relevant threating cues. This idea is supported by the findings showing that affective repetition effects were dependent on probability context, that is, they were only present when the likelihood of repetition was high. Overall, our findings indicate that expectations toward upcoming emotional information modulate the neural processing of visceral signals from within the body.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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