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Attending to the heart is associated with posterior alpha band increase and a reduction in sensitivity to concurrent visual stimuli

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Abstract

Attentional mechanisms have been studied mostly in specific sensory domains, such as auditory, visuospatial, or tactile modalities. In contrast, attention to internal interoceptive visceral targets has only recently begun to be studied, despite its potential importance in emotion, empathy, and self-awareness. Here, we studied the effects of shifting attention to the heart using a cue-target detection paradigm during continuous EEG recordings. Subjects were instructed to count either a series of visual stimuli (visual condition) or their own heartbeats (heart condition). Visual checkerboard stimuli were used as attentional probes throughout the task. Consistent with previous findings, attention modulated the amplitude of the heartbeat-evoked potentials. Directing attention to the heart significantly reduced the visual P1/N1 amplitude evoked by the attentional probe. ERPs locked to the attention-directing cue revealed a novel frontal positivity around 300 ms postcue. Finally, spectral power in the alpha band over parieto-occipital regions was higher while attending to the heart—when compared to the visual task—and correlated with subject's performance in the interoceptive task. These results are consistent with a shared, resource-based attentional mechanism whereby allocating attention to bodily signals can affect early responses to visual stimuli.

KEYWORDS
attention, EEG, ERPs, HEP, interoception

1 | INTRODUCTION

Most studies regarding the brain's attentional mechanisms have been performed in specific sensory modalities, with a prevalence of visuospatial and auditory paradigms (Corbetta,

Patel, & Shulman, 2008; Hillyard & Anllo-Vento, 1998; Luck, Hillyard, Mouloua, & Hawkins, 1996; Petersen & Posner, 2012). As a consequence, a great deal is known about both the mechanisms and effects of attentional orienting and selection in such situations. Only recently, work on attentional orienting has begun to describe the functioning of attention to internal processes such as mental imagery (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Villena-González, López, & Rodríguez, 2016), working memory representations (Astle, Summerfield, Griffin, & Nobre, 2012), temporal estimation (Babiloni et al., 2004; Morillon & Barbot, 2013), respiratory interoceptive accuracy (Daubenmier, Sze, Kerr, Kemeny, & Mehling, 2013), and mind wandering (Handy & Kam, 2015). Yet, how attention to bodily, internal referents such as respiration, heartbeat, and other visceral targets works, and whether it relies on similar brain networks as sensory-based attention, remains poorly understood. Such targets are increasingly relevant given that recent work has highlighted the importance that interoceptive awareness can have in emotion, empathy, and as the basis of feeling and subjectivity (Bechara & Naqvi, 2004; Pollatos, Gramann, & Schandry, 2007; Terasawa, Moriguchi, Tochizawa, & Umeda, 2014; Werner, Mannhart, Reyes Del Paso, & Duschek, 2014)

Among visceral interoceptive targets, the heartbeat has received the most attention. Early work in the 80s already showed that important individual differences exist in terms of ability and accuracy to detect and track one's heartbeat (Schandry, 1981). Interestingly, such individual differences correlate with differences in empathy and decision making (Pollatos, Kirsch, & Schandry, 2005; Terhaar, Viola, Bar, & Debener, 2012), strengthening the idea that interoceptive awareness can impact behaviors and processes traditionally considered to be purely cognitive or representational. Additionally, several studies have shown that paying attention to one's heartbeat results in changes in cortical activity evoked by it (Montoya, Schandry, & Muller, 1993; Pollatos & Schandry, 2004). Specifically, the so-called heartbeat evoked potential (HEP) shows changes over central and frontocentral electrodes when participants are attending to their heart. Such modulation seems to depend on the individual's capacity to perceive their heartbeat (Yuan, Yan, Xu, Han, & Yan, 2007). HEP has also been correlated with empathy and emotional states (Couto et al., 2015; Fukushima, Terasawa, & Umeda, 2011).

However, while there have been studies addressing the effects of attending to visceral targets, very little is known about the mechanisms by which such attentional orienting and selection takes place. Being able to understand how attention can be directed to interoceptive referents could have important theoretical and clinical implications. On the one hand, it could extend our understanding of whether shared attentional mechanisms exist for interoceptive as well as for exteroceptive sensory targets, thus constraining eventual models of attention. On the other, a better knowledge of the mechanisms by which such orienting and selection takes place, and whether individual differences exist in this process, could be relevant for the treatment of mood disorders where heartbeat perception appears to be altered, such as depression and anxiety disorders (Pollatos, Traut-Mattausch, & Schandry, 2009; Wiebking & Northoff, 2015).

Here, we study what happens when participants shift attention toward their heartbeat and contrast it with an equally demanding visual task that involves minimal change in the locus of attention within the visual modality. Using EEG, we reproduce previous results showing that attending to one's heartbeat modulates the HEP. Additionally, our results show that shifting attention to the heartbeat involves both a reduction of the early visual response (P1/N1) elicited by a checkerboard probe presented foveally, and a concomitant increase in posterior alpha band activity. Moreover, we show that performance in the heartbeat task is positively correlated with the amount of posterior alpha band activity. Together, these results are consistent with models that propose the existence of supramodal attentional shifting brain mechanisms (Eimer & Van Velzen, 2002; Farah, Wong, Monheit, & Morrow, 1989) and suggest that similar processes might be at play during interoceptive attention.

2 | METHOD

2.1 | Participants

Twenty paid volunteers initially participated in this study. Ten subjects were not used for further analysis since they were not capable of consistently detecting their heartbeats during a pretask selection procedure. This pretask selection procedure consisted of two steps: First, participants were required to count a given number of heartbeats (ranging from 2 to 8) as instructed verbally by the experimenter and to press a response button once the required number was detected. This was done 10 times for each subject. Second, participants had to press the response button after every heartbeat they perceived during a 1-min interval. The latter has been used as a protocol to select good perceivers, although it can involve prior training with auditory feedback and a motor control (Couto et al., 2014), which was not used in the present study. In both steps, the electrocardiogram (EKG) was recorded to test for counting accuracy, and only subjects displaying 70% or more for both tasks proceeded to the actual experiment. The results from 10 subjects (2 women) meeting this criteria are therefore reported here (mean age = 22.2, range = 19–28). It is worth noting that this proportion of good versus bad heartbeat perceivers in a
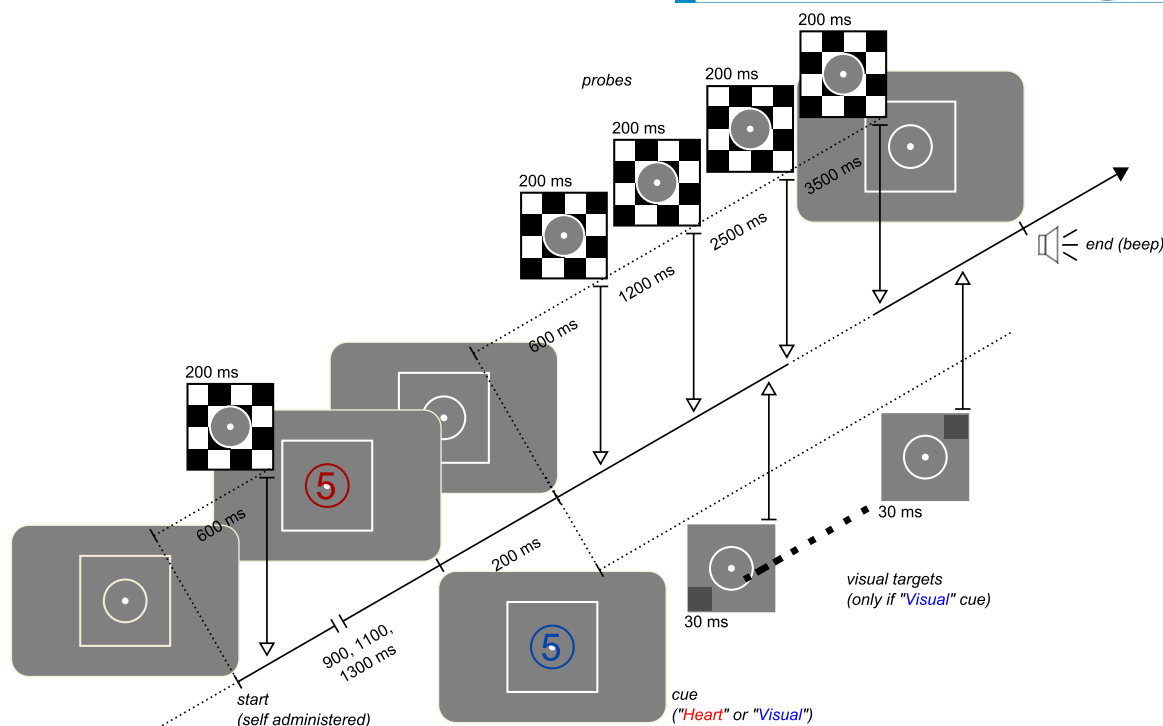
FIGURE 1 Experimental paradigm. Each self-administered trial began with a button press. Next, a colored numerical stimulus (cue) appeared. The color indicated whether the participant had to count their heartbeats (heart condition) or a series of visual targets (visual condition). The cue's number indicated the amount of heartbeats or visual targets the participant had to count. Attentional probes appeared during both conditions and before the cue onset. Color cues were counterbalanced between blocks

sample is consistent with previous reports. Schandry, Sparrer, and Weitkunat (1986) used 22 participants that were divided according to median performance into good/bad perceiver using a similar heartbeat detection task. Pollatos and Schandry (2004) studied a larger group and separated them into 19 good and 26 bad perceivers. In the same line, Lenggenhager, Azevedo, Mancini, and Aglioti (2013) found a median value of 0.7 in an interoceptive sensitivity index (ranging from 0 to 1, with 1 being high sensitivity), which means that half of the group had below 70% performance in their measure. All participants that proceeded to the main task had normal or corrected-to-normal vision, and reported no color vision deficiency. Participants gave informed consent and had no history of drug abuse or neurological or psychiatric conditions. The Ethics Committee of Pontificia Universidad Católica de Chile approved the study, and all experiments were performed at the Psychophysiology Lab of the School of Psychology of the same university.

2.2 | Task

Participants sat in a dimly lit, noise-attenuated, electrically shielded experimental chamber. All stimuli were presented on a black background on a computer screen situated 57 cm away from the subject using Presentation software (Neurobehavioral Systems, Albany, CA). Participants had two controls with one button each, which were used to begin each

trial and to respond according to the instructions given by the experimenter.

The experiment consisted of four blocks composed of 76 self-administered trials each. Participants were instructed to keep their gaze on a fixation point and avoid blinking during each trial. Self-administered trials were chosen to increase the subject's involvement with each instance of the task, while minimizing the chance of eye movements. The task was organized around the appearance of a colored numerical stimulus, which could be red or blue (Figure 1). This would randomly happen after either a 900-, 1,100-, or 1,300-ms interval after the beginning of each trial. The color of the numerical stimulus (cue) indicated whether the participant had to count their heartbeats (heart condition) or a series of short, visual targets (visual condition) that appeared around the fixation symbol. Visual targets consisted of brief, 30-ms changes in luminance of a small square. They were presented starting from 330 ms after the cue appearance until the end of the trial. The interstimulus interval for visual targets varied randomly between 350 and 1,850 ms, with a mean of 998.74 and a standard deviation of 352 ms. The cue's number (varying between 2 and 8) indicated the amount of heartbeats or visual targets the participant had to count. The mapping between color and condition, as well as the button used to respond, was counterbalanced across blocks. Participants signaled their response by pressing the assigned button as soon as they counted the requested number of heartbeat/visual

stimuli. Throughout the trial, behaviorally irrelevant attentional probes were presented as 200-ms checkerboard patterns around the fixation symbol. Probes appeared 600 ms after the trial started (but prior to the numerical cue) with a 33.3% chance in each trial. This specific probe instance was used as a baseline control in order to contrast with the visual and heart attentional conditions. Attentional probes also appeared with a 25% chance at 600 ms, 1,200 ms, 2,500 ms, and 3,500 ms after the numerical cue, and had a 25% chance of appearing every second thereafter. Trials ended once the participant answered with the button press or after a maximum amount of time postcue (1,000 ms × number of requested visual/heartbeat targets + 1,550 ms). Participants performed a short training block prior to the actual experiment in order to ensure that they had understood the instructions and were able to perform the task comfortably.

2.3 | Recordings

EEG data were obtained using 64 electrodes (Biosemi Active-Two) arranged according to the International 10/20 extended system. Horizontal and vertical eye movements were monitored using four external electrodes. Horizontal electrooculography (EOG) was recorded bipolarly from the outer canthi of both eyes, and vertical EOG was recorded from above and below the participant's right eye. Heartbeats were monitored using two electrodes; one placed below the left clavicle and a second one placed below the heart on top of one of the subject's left intercostal muscles. The position of the electrodes was adjusted for each participant so the QRS wave amplitude was substantially greater than the T wave, in order to facilitate reading and analysis of the corresponding EKG.

2.4 | Behavioral data analysis

Trials with correct responses were considered as those where participants pressed the response button after the amount of elapsed heartbeats or visual targets instructed by the preceding numerical cue. Counting one additional heartbeat or visual target was also considered correct in order to compensate for targets or heartbeats that could occur too near the numerical cue, therefore remaining undetected by the participant. Each condition's task accuracy was calculated as the number of correct trials in relation to the total number of trials for each subject independently.

2.5 | Electrophysiological data analysis

2.5.1 | EEG pretreatment

The signal was downsampled offline at 512 Hz. Due to hardware constraints of the setup, all electrodes were referenced to CMS (common mode sense) and DRL (driven right leg) during acquisition, but offline rereferenced to averaged mastoids. A second-order infinite impulse response (IIR) Butterworth filter was used for band-pass filtering of continuous data, with a half amplitude cutoff frequency of 0.5 Hz and 30 Hz, using the EEGLAB toolbox (Delorme & Makeig, 2004). For the analysis of ERPs associated with the attentional checkerboard probes, EEG was epoched into 800-ms periods, starting 200 ms prior to probe onset and ending 600 ms after, to avoid contamination by successive probes. A similar epoching was also carried out around the numerical cue stimuli, starting 200 ms prior to stimulus onset and ending 600 ms after. Artifact detection was performed on segmented data using a moving window peak-to-peak threshold algorithm, with a voltage threshold of 100 microvolts. All epochs containing detected artifacts were rejected, as well as postnumerical cue epochs containing a visual target. The same number of epochs for checkerboard probes was selected across participants and conditions according to the minimal common value after artifact rejection, leaving 70 epochs per subject (700 epochs per condition). A similar approach was carried out for the numerical cue stimuli, arriving at a total of 400 epochs per condition (i.e., 400 epochs for the heart condition and 400 epochs for the visual condition).

Vertical and horizontal EOGs were epoched into 800-ms periods, starting 200 ms prior to the cue onset and ending 600 ms after. Additionally, epochs were extracted around the attentional probe (-200 ms to 200 ms) for each condition.

Finally, continuous EEG was epoched around the EKG's R peak in order to determine the HEP. Epochs had a duration of 800 ms, starting 200 ms before the R peak and ending 600 ms later. The cardiac field artifact, which is very prominent when averages are time-locked to the QRS wave of EKG, was removed using independent component analysis (ICA), identifying the independent components (IC) related with the cardiac field following previous research (Terhaar et al., 2012; Viola et al., 2009). This IC was not identified on two subjects, thus further analyses of HEP were done with eight subjects' data.

2.5.2 | ERP and HEP analysis

Three main ERP analyses were undertaken based on averaging the previously mentioned EEG epochs: ERP waveforms evoked by the attentional probe stimulus, by the numerical cue stimulus, and by the heartbeats. All ERPs were baseline-corrected using a 200-ms time window before the onset of the respective stimulus.

Peak-to-peak amplitude of early P1/N1 ERP's component was calculated according to Luck (2005) using the classical time window and topography (Di Russo, Martinez,

Sereno, Pitzalis, & Hillyard, 2002). In brief, P1/N1 amplitude was calculated as the difference between 10 ms averaged around P1 peak (local peak amplitude) minus 10 ms averaged around N1 peak, for each participant. Latency of P1/N1 components was calculated as the time point at which the respective peak appears, for each subject.

HEP amplitude was analyzed in the 350–550 ms interval after the EKG R wave. Earlier studies have shown that the main electrical brain activity in response to the heartbeat can be observed over central electrodes, mainly C3, C4, and Cz, around a 250–450 ms latency (Pollatos & Schandry, 2004) and 350–550 ms after the QRS wave (Montoya et al., 1993). In the present study, mean amplitudes of HEP were computed in two time windows (350–450 ms and 450–550 ms after the QRS wave) for both conditions. Additionally, heart rate was calculated for each subject using EKG signal for both conditions as beats per second in the time window following the numerical cue.

2.5.3 | Fourier analysis

EEG signal was segmented into 1-s stimulus-free epochs for each condition, and Fourier transforms were calculated for each of them using an in-house script written in MATLAB (MathWorks, Inc.). The script used the MATLAB fft function with a default frequency range between 1–256 Hz and a frequency resolution of 0.25 Hz. Spectrogram data were averaged across epochs for each subject for the baseline epochs and both experimental conditions. Alpha range was defined as a window of 2 Hz above and 2 Hz below to the individual maximum power value in the classical alpha range (8–12 Hz), for each subject separately (Klimesch, 1999). Area under the curve (AUC) of alpha power was calculated in the alpha range for each subject as an average across trials. Alpha power AUC was normalized by the total AUC for each subject. Electrodes for further analyses were chosen using the methodology described by Keil et al. (2014) in order to follow an unbiased approach to the spectral analysis. Specifically, we averaged across all conditions and participants in order to reveal the topographical distribution of alpha band activity in the selected frequency range. This resulted in a set of four contiguous electrodes over the parieto-occipital region lateralized toward the right hemisphere (POz, PO4, O2, Oz). Percentage of change for alpha power's AUC was obtained by calculating the difference between heart/visual and baseline alpha AUC, dividing it by the baseline alpha AUC, and then multiplying it by 100.

2.6 | Statistical analysis

Wilcoxon matched pairs test was performed to compare accuracy rate between conditions. HEP amplitude was ana-

lyzed using repeated measures analysis of variance (ANOVA) with electrode (four levels: C3, Cz, FCz, C4), time (two levels: 350–450 ms, 450–550 ms), and condition (two levels: visual, heart) as factors. Time in the HEP analysis refers to the time window after the R component of the EKG. Two-sided Wilcoxon matched pairs test was performed to compare heart rate between conditions. In order to assess possible differences in the amplitude of P1/N1 components evoked by attentional probes, repeated measures ANOVA was carried out using hemisphere (two levels: left, right), electrode (two levels: PO3/7, PO4/8), and condition (three levels: visual, heart, baseline) as factors. A further univariate test of significance was carried out for planned comparisons following our hypotheses (see Results).

For the analyses of the ERP evoked by cue stimulus, we conducted paired comparisons (Wilcoxon signed-rank tests, two-tailed) across the means of trials of each subject per condition (visual and heart cue). Continuous clusters of significant areas were identified using a cluster-based permutation test (Maris & Oostenveld, 2007). Here, clusters of significant areas were defined by pooling neighboring sites that showed the same effect ($p < .05$). The cluster-level statistic was computed as the sum of the statistics of all sites within the corresponding cluster. We evaluated the cluster-level significance under the permutation distribution of the cluster that had the largest cluster-level statistics. The permutation distribution was obtained by randomly permuting the original data. After each permutation, the original statistical test was computed (e.g., Wilcoxon), and the cluster-level statistics of the largest cluster resulting was used for the permutation distribution. After 200 permutations, the cluster-level significance for each observed cluster was estimated as the proportion of elements of the permutation distribution greater than the cluster-level statistics of the corresponding cluster.

The percentage of change of alpha power between visual and heart conditions was compared using repeated measures ANOVA with electrode (four levels: POz, PO4, O2, Oz) and condition (two levels: visual, heart) as factors. Correlation analyses between alpha power's percentage of change and behavioral performance were made using Pearson correlation test.

In order to control for possible changes in eye position, EOG amplitude after the numerical cue stimulus was compared with the same approach using time (three levels: 0–200, 200–400, 400–600 ms after stimulus onset), axis (two levels: horizontal, vertical), and condition (two levels: visual, heart) as factors. Wilcoxon matched pairs test was performed to compare bipolar EOG amplitude (horizontal and vertical) during the presentation of attentional checkerboard probes between conditions.

We performed a Mauchley sphericity test to each repeated measures ANOVA and applied a Greenhouse–

Geisser correction to cases in which sphericity assumption was violated.

All analyses were done using the STATISTICA software 7 (StatSoft, Inc.).

3 | RESULTS

3.1 | Behavioral

Participants performed the task with an accuracy of 72.6 ± 11.7% for heart condition and 74.6 ± 7% for visual condition. Accuracy did not differ between both conditions ($Z = 0.3$, $p = .759$). The percentage of trials with missing response was 7.3 ± 7% and 8.7 ± 5.9% for heart and visual conditions, respectively, showing no significant differences ($Z = 0.65$, $p = .514$).

3.2 | Heart rate and HEPs

Average heart rate during visual and heart conditions was 1.08 ± 0.13 and 1.07 ± 0.13 (mean ± SD) beats per second, respectively, corresponding to an average period of approximately 926 and 935 ms for each case. No significant differences were observed between conditions (Wilcoxon paired test, two-sided, $p = .1712$).

We compared the amplitude of HEP in both conditions as an index of effective interoceptive awareness during the heart attention task. Statistical analysis of HEP amplitudes revealed a main effect for condition factor, $F(1, 7) = 13.83$, $p = .007$. Figure 2 shows HEP over the central regions during both experimental conditions. In agreement with previous studies, an increase in the HEP amplitude can be seen for the heart condition in the 150 - 550 ms window after the QRS complex.

3.3 | ERP evoked by attentional probe

We compared P1/N1 amplitude evoked by the probe stimulus during the precue baseline and both experimental conditions. As visual condition did not involve shifting attention from the fixation point, we did not expect modulation of early ERP components. In contrast, we hypothesized that, if attentional shifts to the heart recruit resources from a common, supramodal attentional network, they would involve an attenuation of the early visual response to the attentional probes, despite their being presented parafoveally. Figure 3a shows the ERP waveform elicited by checkerboard probes on the parietal-occipital region (average of PO7 and PO8 electrodes) for the precue baseline and the visual and heart conditions. Statistical analysis of P1/N1 amplitude revealed a main effect for the condition factor, $F(2, 18) = 7.09$, $p = .005$. Planned comparisons showed a reduction in the P1/N1 amplitude during the heart condition when contrasted with baseline condition, $F(1, 9) = 6.78$, $p = .02$. Differences can also be observed between both attentional conditions, where attending to the heart showed a smaller P1/N1 amplitude when contrasted with the visual condition, $F(1, 9) = 13.84$, $p = .005$. No differences were observed between the visual condition and the baseline period, $F(1, 9) = 0.03$, $p = .85$ (see Figure 3). We also found a main effect for hemisphere, $F(1, 9) = 14.35$, $p = .004$, with higher voltage amplitudes on the right hemisphere. There was also a main effect of electrode, $F(1, 9) = 7.4$, $p = .023$, with higher values for the more lateralized electrodes (PO7/PO8) than for those nearer to the midline (PO3/PO4). Interaction effects were found between hemisphere and electrode factors, $F(1, 9) = 12.05$, $p = .007$, showing that voltage values were higher on the right hemisphere than on the left hemisphere for the more lateralized PO8 electrode (see Figure 3c). The average
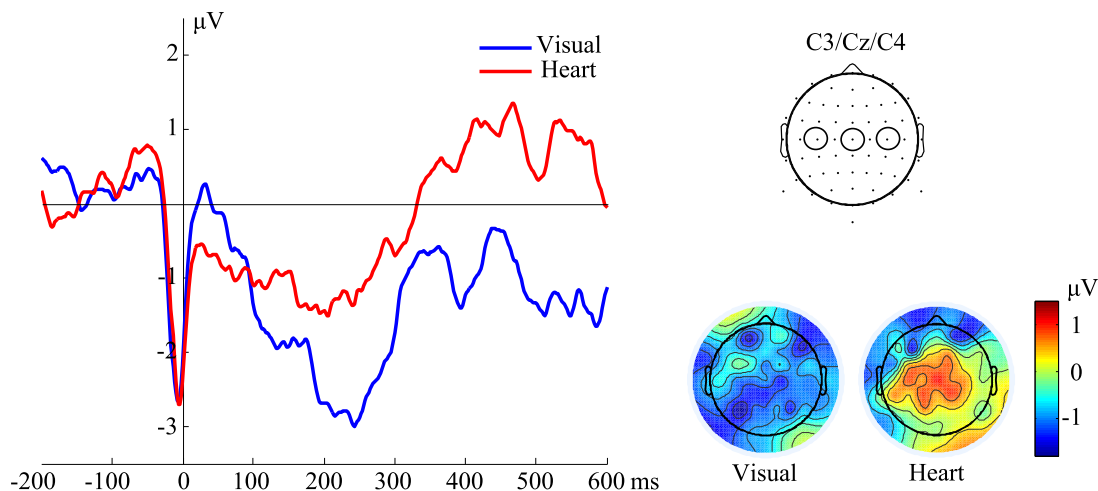
FIGURE 2 Waveform and scalp topography of heartbeat evoked potential. Left: HEP waveform at central regions (average of C3/Cz/C4 electrodes) for the heart and visual conditions (the slight shift toward negative values of the R peak is due to the sampling frequency and the linear interpolation values of the time vector used to plot the HEP figure). Right: Voltage scalp topography for the two conditions from 350 ms to 550 ms after R peak of EKG
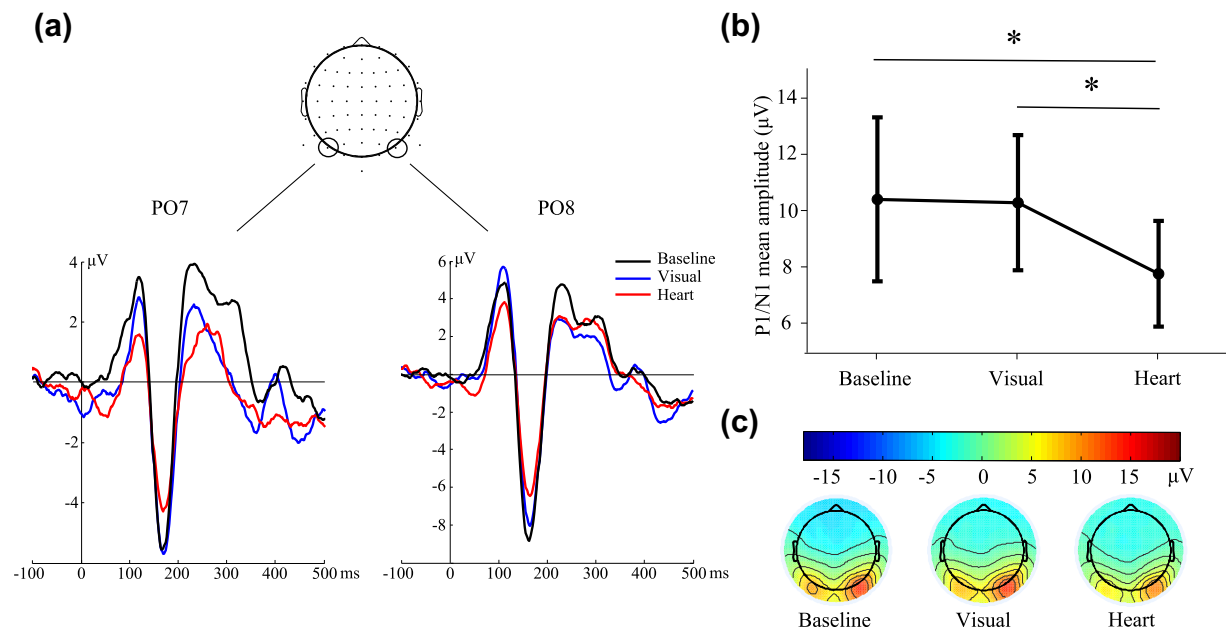
FIGURE 3 ERP evoked by probe stimulus. a) ERP waveform at PO7/PO8 electrodes for the three conditions. b) Mean and standard error of P1/N1 peak-to-peak amplitude for the three conditions (*$p < .05$). c) Voltage scalp topography for the three conditions during the P1/N1 time window

latency for P1 and N1 peaks across subjects and conditions was 127.05 ms and 172.74 ms, respectively.

In order to rule out that differences in P1/N1 could be due to changes in eye position during attentional shifts to the heart, we analyzed the EOG traces between conditions both immediately after the cue and during the presentation of the attentional checkerboard probes. No significant differences were observed for horizontal EOG amplitudes after cue stimulus for condition, $F(1, 9) = 0.04$, $p = .84$, nor time, $F(1, 9) = 2.7$, $p = .094$. We did not find interactions between condition and time factor either, $F(1, 9) = 0.85$, $p = .44$. We did not find differences in the vertical EOG for condition, $F(1, 9) = 0.452$, $p = .518$, or time factors, $F(1, 9) = 3.47$, $p = .053$, and no interactions between factors were observed, $F(1, 9) = 2.61$, $p = .101$ (see online supporting information, Figure S1). Likewise, no differences for either horizontal EOG (Wilcoxon test, $p = .44$) or vertical EOG (Wilcoxon test, $p = .16$) were observed between conditions at the moment when the attentional checkerboard probe was presented (see Figure S2).
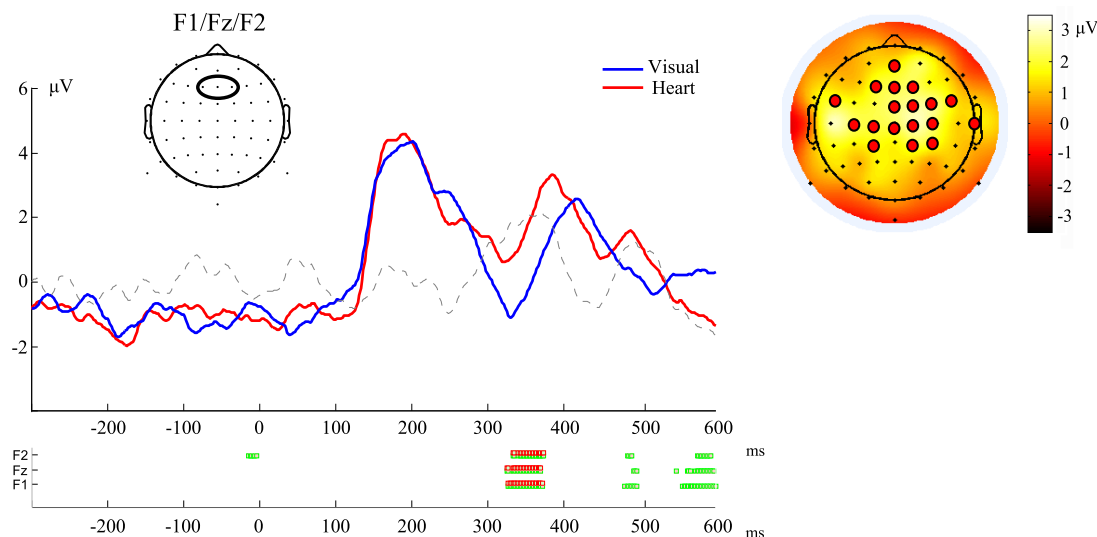
3.4 | ERP evoked by cue stimulus

Given the lack of previous studies on specific shifts of attention toward interoceptive targets, we explored differences between ERPs evoked by the visual and heart cues using a statistical analysis without prior assumptions regarding components or timing of possible voltage changes (*see Statistical Analysis for* details). The visual condition presented a more negative deflection 350 ms after the cue stimulus, leading to

a significant difference between conditions ($p < .005$, cluster permutation test) between 320 to 380 ms after the cue stimulus (Figure 4, left). The topographical distribution of these differences involved frontal and frontocentral electrodes (Figure 4, right) where F1, Fz, and F2 electrodes showed the strongest differences ($p < .001$).

3.5 | Spectral alpha power

We studied the modulation of oscillatory activity when directing attention to the heartbeat by measuring alpha power's AUC for heart and visual conditions and contrasted it with the precue baseline period. As shown in Figure 5a, differences can be seen only in the heart condition at parieto-occipital and occipital regions with a slight right-hemisphere lateralization. We found significant differences for condition factor, with main effect, $F(1, 9) = 12.11$, $p = .0009$. We did not find differences either for electrode factor, $F(1, 9) = 0.57$, $p = .63$, or interaction between factors, $F(1, 9) = 0.09$, $p = .95$. This difference corresponds to an increase in the alpha power's AUC for the heart condition that is not present for the visual condition (Figure 5b). If there is a relation between alpha power and shifting attention to the heartbeat beyond inhibiting the processing of visual stimuli, performance in the heartbeat perception condition should depend on the capacity to modulate posterior alpha activity as seen in the percentage of change in the AUC. In line with this hypothesis, results showed these two variables to be correlated positively only for the heart condition at POz ($r^2 = .33$,

FIGURE 4 ERP evoked by cue stimulus. Left: ERP waveform at frontal regions (average of F1/Fz/F2 electrodes) for the heart and visual conditions. Dotted line represents the subtraction of the two curves. Under the ERP waveform, green lines represent time windows showing uncorrected statistical differences ($p < .05$), red lines are corrected by cluster ($p < .005$). Right: Voltage scalp topography presents the average amplitude difference between the two conditions from 330 ms to 370 ms after the cue stimulus onset. Red dots indicate electrodes showing significant differences between conditions
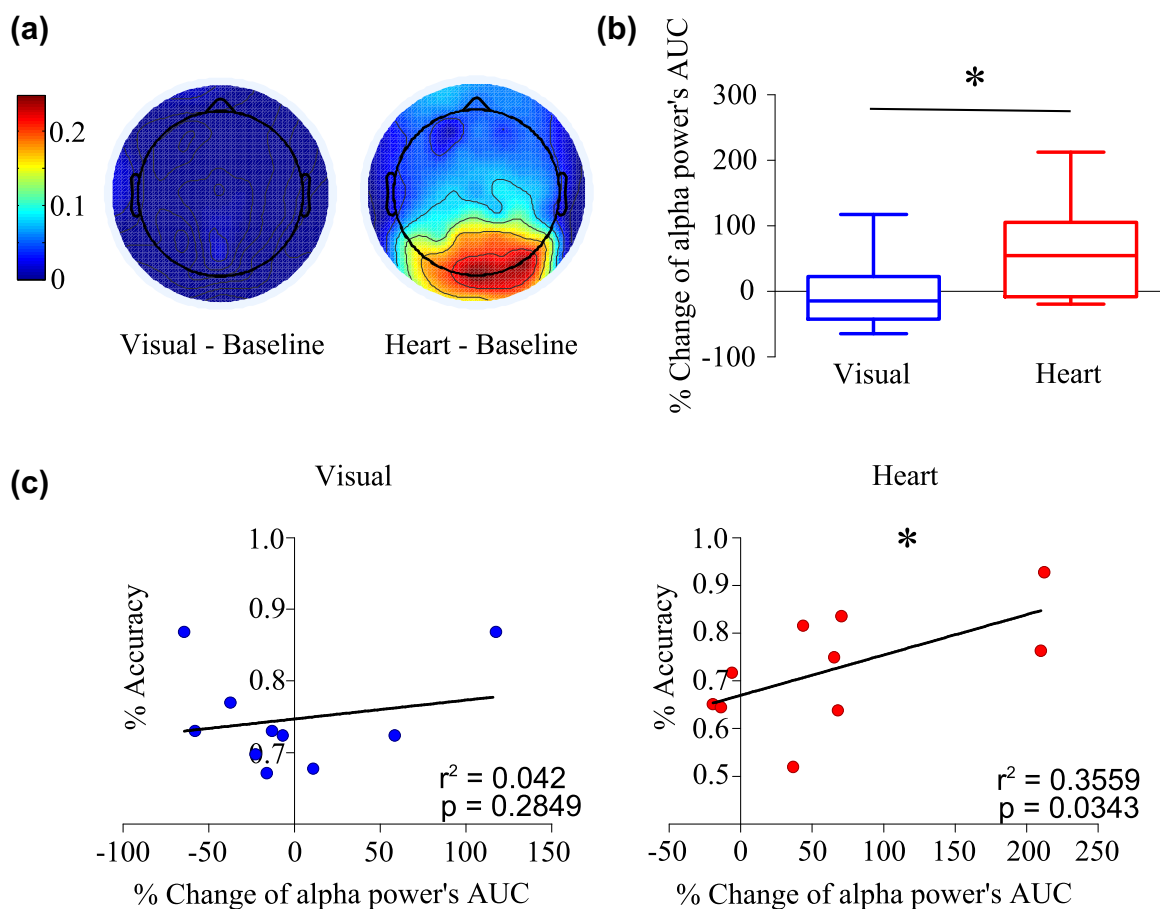
FIGURE 5 Spectral alpha power results. a) Scalp topography of normalized alpha power's AUC for the visual and heart condition contrasted with the precue baseline period. b) Percentage of change of alpha power's AUC with respect to baseline for the visual and heart condition at PO4 electrode. c) Correlation between the percentage of change of alpha power's AUC and performance for the visual and heart condition at PO4 electrode

$p = .04$), PO4 ($r^2 = .35$, $p = .03$), and Oz ($r^2 = .31$, $p = .04$) electrodes (Figure 5c).

4 | DISCUSSION

4.1 | Interoception and HEP modulation by attention

A classical measure to assess heartbeat perception in psychophysiological research has been the HEP. This potential corresponds to electrical brain activity evoked by the heartbeat with a central topographical distribution, mostly observed at C3, C4, and Cz electrodes 250 to 550 ms after the R peak of EKG signal (Montoya et al., 1993). Since the first report of HEP by Schandry et al. (1986), it was recognized that not all subjects are equally good at counting their heartbeats. Importantly, differences in terms of the stability of the HEP signal could be observed depending on whether the subject had been classified as a good or poor perceiver in a previous heartbeat perception test. Recent research has supported this finding, showing a positive correlation between heartbeat perception score and the mean of HEP amplitude (Pollatos & Schandry, 2004).

In the present study, we did not observe such correlation between performance and HEP amplitude. However, we did find a consistent modulation of HEP amplitude when subjects attended to their hearts. This is in line with a number of previous studies that show that when attention is oriented to the heartbeats a larger HEP amplitude is observed, contrasted to when it is oriented to external tones or during a resting state (Montoya et al., 1993; Yuan et al., 2007).

A growing interest about interoceptive awareness has given rise to studies showing correlations between participants' accuracy to detect/track their heartbeats and differences in cognitive and emotional processes such as empathy, feelings, and decision making (Bechara & Naqvi, 2004; Fukushima et al., 2011; Kleint, Wittchen, & Lueken, 2015; Pollatos, Gramann, & Schandry, 2007; Pollatos et al., 2005; Terhaar et al., 2012). This has strengthened the idea that interoceptive awareness can impact behaviors and processes traditionally considered to be purely cognitive or representational. Furthermore, altered perception of bodily signals has been associated with psychological disorders such as depression, panic disorder, and stress (Limmer, Kornhuber, & Martin, 2015; Schulz & Vögele, 2015; Terhaar et al., 2012). It is therefore relevant to understand attentional processes potentially underlying individual differences in interoception. A recent study has shown increased HEP amplitudes during high arousal induction (contrasted with low arousal) in a mood induction protocol (Luft & Bhattacharya, 2015). The capacity for interoception has been correlated positively with more elaborate information processing in general (Pollatos et al., 2005;

Pollatos, Matthias, & Schandry, 2007), as well as with better performance in tasks assessing selective and divided attention (Matthias, Schandry, Duschek, & Pollatos, 2009). It could be that good perceivers are therefore better at heartbeat tracking tasks due to enhanced attentional abilities in general. Increased HEP amplitude in these participants (or during attentional tasks requiring heartbeat perception) could be a neural correlate of attentionally enhanced processing of somatosensory information.

4.2 | Evidence of shared attentional resources for interoceptive awareness

The issue of whether attentional control rests on common, supramodal brain processes or depends on modality-specific mechanisms remains a matter of debate (Frey, Ruhnau, & Weisz, 2015; Shrem & Deouell, 2017; Spagna, Mackie, & Fan, 2015; Wang, Viswanathan, Lee, & Grafton, 2016; Ward, 1994). In the domain of interoception, this is all the more evident as very few studies have specifically targeted attentional processes underlying this capacity. Shifting attention toward interoceptive targets does not share the same spatial nature of other exteroceptive sensory modalities. Also, interoception is primarily related to regions beyond the primary sensory areas such as the right anterior insular/opercular cortex (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). The mechanisms underlying the corresponding shifts of attention could therefore be different. To our knowledge, whether the attentional facilitation of heartbeat perception comes from a specific interoceptive attentional network or relies on shared attentional mechanisms has not been assessed. If the latter were the case, it should be possible to find interference between modalities as well as evidence of common shared resources.

Several studies have shown that the amplitude of early ERP's components is influenced by attention. Specifically, P1/N1's amplitude attenuation has been classically associated with a reduced sensory processing of stimuli due to ignoring a visual field in which stimuli are more likely to appear (Hillyard & Anllo-Vento, 1998; Hillyard, Vogel, & Luck, 1998; Luck & Hillyard, 1995; Mangun & Hillyard, 1988). Interestingly, a similar effect can also be seen when visual stimuli appear while participants' attention is directed toward their self-generated thoughts. In this case, early ERP components show a reduction when attention is turned toward mental images as contrasted to when it is directed at the external task (Baird, Smallwood, Lutz, & Schooler, 2014; Kam et al., 2011; Villena-González et al., 2016).

Our results are consistent with these findings and extend them to the study of interoceptive attention. While participants counted their heartbeats, checkerboard probes that were presented parafoveally evoked a reduced P1/N1

response. This was true when compared both to the visual task or the preceding baseline, suggesting that attending to the heart can draw significant resources from the visuospatial modality. It is worth noting that P1/N1 amplitude during the visual task did not differ from the precue baseline. This, in addition to the pattern of alpha band activity over occipital cortices (see Figure 5a), suggests that the precue baseline period involved an active visual engagement from the participant and is therefore not a completely neutral baseline. While this can be a limitation of the current design, it is important to consider that the self-administered trial choice is meant to increase participants' engagement with the task and is therefore bound to focus their expectation on each trial and the upcoming cue (Figure S3 presents a comparison of alpha band activity during the precue baseline with a distant, pretrial baseline period that suggests that, as indexed by alpha band activity, expectation was consistently high throughout the execution of the task). On the other hand, however, this has the benefit of reducing eye movements (and related blinks) in a paradigm where gaze stability is critical. As such, we highlight the comparison between the visual and interoceptive task as the main contrast and consider the baseline as an additional control.

While the attenuation of visual responses to irrelevant attentional probes suggests that shared attentional resources exist between the visual and the interoceptive modalities, it cannot shed light on whether such attenuation is due to passive inhibition of the visual stimuli or an active reallocation of shared resources toward the visceral target. In order to better understand this relation, we therefore explored posterior alpha band activity.

Alpha power modulation in attentional processes has been consistently demonstrated in a wide range of tasks (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Klimesch, 2012). Accordingly, it has been considered as part of the brain mechanisms that underlie the effects of attention on sensory processing. Previous research, using variations of the classical cue-target paradigm (Posner, 1980), has shown alpha power decrease in parieto-occipital regions contralateral to cued location (Sauseng et al., 2005). Other studies have also shown alpha power increase in parieto-occipital regions ipsilateral to cued location (Cosmelli et al., 2011; Kelly, Lalor, Reilly, & Foxe, 2006; Worden, Foxe, Wang, & Simpson, 2000). Romei, Gross, and Thut (2010) found that both ipsilateral alpha power increase and contralateral alpha power decrease affect performance in a visual perception task. In line with this, research has been carried out in cross-modal attention with similar results (Fu et al., 2001). Taking this body of evidence into account, alpha power has been proposed as an active mechanism for inhibition of irrelevant external information rather than simple resting state default activity (Foxe & Snyder, 2011).

Here, we observed that, during heart-directed attention, alpha power levels increased over bilateral parieto-occipital regions when compared to both the precue baseline and the visual task. Most importantly, however, we found a significant positive correlation between posterior alpha power increase and behavioral accuracy only during the heart condition, suggesting that changes in parietal alpha band activity could be directly implicated in shifting attention toward a nonvisuospatial, interoceptive target. A recent study reported that participants with higher alpha power over parietal regions showed a higher increase in the HEP in response to a high arousal induction compared to a low arousal condition (Luft & Bhattacharya, 2015). We did not observe such correlation between HEP amplitude and alpha power. This contrast could be due to task differences in terms of manipulating mood versus attention directly. Nevertheless, both results are consistent with the idea that better heartbeat perception is related to a better interoceptive sensitivity, and that stronger posterior alpha band activity facilitates such interoceptive awareness.

The above early ERP and alpha band results therefore support the existence of a shared, resource-based brain mechanism at play during the shift of attention to visceral targets. While our results are consistent with a supramodal, attentional-orienting network (Eimer & Van Velzen, 2002; Farah et al., 1989), a full account of such putative supramodality should consider contrasting interoceptive targets with more than just a visual task (for instance, using an auditory or tactile target). Additionally, because attention was oriented toward a nonvisual modality, reductions in visual processing could happen as a consequence of this fact (see, for instance, the gating for inhibition hypothesis: Jensen & Mazaheri, 2010). According to this alternative explanation, if visual regions are not involved in the current task (in this case, counting heartbeats), they are likely to be inhibited by means of an increase in posterior alpha band activity. However, as stated above, our results show that attention to the heart is not only related to an increase in posterior alpha alpha band activity: parieto-occipital alpha band modulation is also significantly correlated with performance in the interoceptive, heartbeat counting task. In other words, while it is likely that concomitant inhibitory mechanisms are at play in visual regions (Jensen & Mazaheri, 2010), alpha band activity over parieto-occipital cortices seems to be more than just an increase associated with visual disengagement/inhibition, and could be actively involved in the attentional facilitation of visceral sensations.

4.3 | Cue-related ERPs

Several studies have reported an enhanced negativity at frontal electrodes contralateral to the direction of attentional

shifts, known as the anterior directing attention negativity (ADAN), with an onset latency of 300–400 ms after cue onset (Cosmelli et al., 2011; Nobre, Sebestyen, & Miniussi, 2000). This ADAN would reflect the activation of dorsolateral frontal control processes involved in initiating and programming shift of attention (Praamstra, Boutsen, & Humphreys, 2005). Such anterior negativity is followed by a posterior contralateral positivity about 500 ms postcue onset, named late directing attention positivity (LDAP). This last component has been linked to preparatory changes in the excitability of visual areas in anticipation of an expected visual stimulus at a specific location (Harter, Miller, Price, Lalonde, & Keyes, 1989).

Later studies have demonstrated that ADAN and LDAP are also triggered in tasks where attention is directed toward the cued location of auditory or tactile events (Eimer, van Velzen, & Driver, 2002; Green, Teder-Salejarvi, & McDonald, 2005). These results provide strong support for the hypothesis that attentional shifts are dependent on a supramodal system (Farah et al., 1989). However, there is much less evidence about attention oriented toward internal information. Nobre et al. (2004) have assessed the neural system involved in directing attention to locations in arrays held as mental representations (using retrocues; Griffin & Nobre, 2003), and compared it with the system for directing spatial attention to locations in the external world (using precues). Using fMRI, they observed that both spatial-orienting attentional processes are supported by extensively overlapping networks. When these two processes were explored using ERPs, Griffin and Nobre (2003) found lateralized early posterior and later frontal negativities for both pre- and retrocues. Importantly, they found differences between ERPs evoked by pre- and retrocue independent of the direction of attention. There was an increased relative positivity for retrocues over posterior scalp regions. This effect was nonlateralized and was evident from 360 ms. Furthermore, there was a selective effect of spatial orienting for retrocues as a positive potential over frontal electrodes around 200 ms, which was not evident for precues.

Our results from ERP elicited by the cue stimuli showed a more negative deflection 350 ms after the cue only in the visual condition, leading to a significant difference between conditions. Considering the evidence described above, one possible explanation can be that, similarly to retrocue results, the heart attention condition elicits a frontocentral positivity that might be a possible electrophysiological index of internally oriented attention. Another possible explanation could be, for instance, that this negative deflection belongs to the family of frontal negativities that are related to behavioral feedback or performance errors (Cavanagh & Frank, 2014). These regions are involved in a network that senses signals related with the onset of a task or tasks shifts, estimating or

predicting a cognitive control requirement demanded by the situation (Aarts, Roelofs, & van Turennout, 2008; Dosenbach et al., 2006; Shenhav, Botvinick, & Cohen, 2013). Therefore, the visual cue of the present study might be more predictive of cognitive control by predicting the presence of attentional targets at the same sensory modality. However, more evidence is needed to shed light on the exact nature of this frontal positivity.

4.4 | Alpha band and task demands

One of the most important constraints when studying interoceptive awareness is the difference observed in terms of the different participants' ability to perceive and track their own heartbeats. There is an important body of evidence showing this kind of individual differences in interoceptive ability, and these studies often compare good perceivers with bad perceivers (Montoya et al., 1993; Pollatos & Schandry, 2004; Yuan et al., 2007). In this study, two different tests were carried out to select participants. First, participants were asked to silently count a determined amount (between 2 and 8) of heartbeats and press a button when they reached the number. Secondly, they had to press a button after each perceived heartbeat during an interval of 1 min, and their reports were contrasted with the EKG signal. Previous studies usually distinguish between good and bad perceivers in a similar way, by asking subjects to count their heartbeats during time windows of different lengths, generally between 25, 35, and 45 s (Montoya et al., 1993; Pollatos, Matthias, & Schandry, 2007). However, these protocols have a considerably longer duration compared with the time windows of the trials in our task. Our selection method had the advantage of being more adapted to the current experimental setup timing. Furthermore, it allowed us to keep a group of good perceivers, while maintaining a performance range compatible with the correlation analysis.

In this context, it could be the case that maintaining attention around fixation to count visual targets is less demanding than paying attention to and counting one's heartbeats, given that interoceptive awareness can be a difficult task for some people (Pollatos & Schandry, 2004; Yuan et al., 2007). This additional difficulty of the heart task could account for the increase in alpha band, as it has been shown that mental effort can modulate oscillatory activity in this frequency range (Keil, Mussweiler, & Epstude, 2006; Ray & Cole, 1985). However, differences in effort are unlikely to explain the results obtained here, as both the visual and the heart task were performed with comparable accuracy (see Behavioral in Results). Additionally, this represents an additional argument in favor of the choice of contrasting the interoceptive task with a visual task instead of a neutral baseline. As both conditions were equally difficult, it is possible

to contend that the increase in posterior alpha band activity we observe is specifically related to the shift in attention toward the heart.

4.5 | Conclusions

We have investigated brain dynamics during the orienting of attention toward a visceral target using a cue-stimulus paradigm. We reproduced previous results showing that attending to one's heartbeats modulates the HEP, increasing its amplitude. Using checkerboards as visual attentional probes, we observed a change in visual sensitivity (as indexed by a decrease in the amplitude of early P1/N1 components) when subjects shifted their attention to their heart as compared to attending to an equally demanding visual task. Likewise, when contrasted with maintaining attention around fixation, orienting attention to the visceral target induced a more positive deflection over frontal electrodes around 350 ms postcue. Finally, we observed a posterior increase in alpha band activity when subjects shifted attention toward the heart. Importantly, the amplitude of this oscillatory activity correlated with the subjects' performance in the heartbeat counting task. Taken together, these results suggest that shifting attention toward visceral targets could rely on similar mechanisms to those supporting the orienting of visuospatial attention.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1
Figure S1
Figure S2
Figure S3