

Heart-rate modulations reveal attention and consciousness interactions

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Abstract

Our environment is constantly overloaded with information, although we cannot consciously process all the stimulation reaching our senses. Current theoretical models are focused on the cognitive and neural processes underlying conscious perception. However, cognitive processes do not occur in an isolated brain but in a complex interaction between the environment, the brain, and the organism. The brain-body interaction has largely been neglected in the study of conscious perception. The aim of the present study was to explore if heart rate and skin conductance (SC) are modulated by the interaction between phasic alertness and conscious perception. We presented near-threshold visual stimuli that could be preceded by an alerting tone on 50% of the trials. Behaviorally, phasic alerting improved perceptual sensitivity for detecting a near-threshold stimulus (along with changes in response criterion). Following the alerting tone, a cardiac deceleration-acceleration pattern was observed, which was more pronounced when the near-threshold stimulus was consciously perceived in comparison with unconsciously perceived stimuli. SC results further showed some degree of subliminal processing of unseen stimuli. These results reveal that cardiac activity could be a marker of attention and consciousness interactions, emphasizing the need for taking into account brain-body interactions for current theoretical models of consciousness.

KEYWORDS

attention, consciousness, heart rate, phasic alerting, skin conductance

1 | INTRODUCTION

Conscious perception has been a topic of great interest since even before psychology was born as a discipline. Its scientific study has been especially challenging because of the difficulty of disentangling conscious experience from verbal reports. Block's (2011) characterization of “phenomenal” and “access” consciousness captures this distinction between the experience of seeing (phenomenal consciousness) and the ability to report this perception (access consciousness).

Another challenge in the study of conscious perception is the characterization of the mechanisms that allow the selection of information. From all the information reaching our

senses, only a small fraction can be consciously reported. Attention has been postulated as one of the mechanisms allowing this selection. According to S. E. Petersen and Posner (2012), the attentional system can be divided into three anatomically and functionally distinct subsystems: alerting, orienting, and executive control. In this study, we will focus on the alerting system, which maintains an optimal vigilance state (tonic alerting) or increases the activation of the organism for a brief period of time following a salient event (phasic alerting; S. E. Petersen & Posner, 2012). Phasic alerting has been demonstrated to improve perceptual sensitivity for detecting targets presented near the threshold of consciousness (Botta, Ródenas, & Chica, 2017; Kusnir, Chica, Mitsumasa, &

Bartolomeo, 2011; A. Petersen, Hilkjaer-Petersen, Bundesen, Vangkilde, & Habekost, 2017), producing its effects through a frontostriatal network (Chica, Bayle, Botta, Bartolomeo, & Paz-Alonso, 2016).

Until now, current theoretical models of conscious perception have mainly focused on cognitive and neural processing (Dehaene & Changeux, 2011; Lamme & Roelfsema, 2000; Tononi, 2012; Zeman, 2001). However, cognitive processes do not happen in an isolated brain, and thus it is important to understand the interaction between the brain and the environment, and between the brain and the organism (Craig, 2009; Critchley & Harrison, 2013; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Park & Tallon-Baudry, 2014). Even though brain-body interactions have received some attention in the study of self-awareness (Tsuchiya & Adolphs, 2007) and emotions (Seth, 2013), only recently have Tallon-Baudry and colleagues started to explore the relationship between body signals and consciousness (Park & Tallon-Baudry, 2014; Park, Correia, Ducorps, & Tallon-Baudry, 2014). The central nervous system monitors the state of the internal organs (e.g., the heart) to regulate the homeostatic state of multiple biological parameters. The heart has a group of mechanosensory neurons that send information reflecting fast events (Amour & Ardell, 2004; Park et al., 2014) through ascending afferent pathways to the central nervous system. According to Park and Tallon-Baudry (2014), the continuous updating of these neural maps about the internal state of the body gives rise to the so-called “neural subjective frame”, a first-person experience of conscious perception.

Physiological studies have associated cardiac changes with several cognitive processes. For example, following an alerting tone, there is a cardiac deceleration followed by an acceleration (Lacey & Lacey, 1978). While the cardiac deceleration has been associated with preparatory processes, cardiac acceleration has instead been associated with stimulus identification and response preparation (Vila et al., 2007). Moreover, the amplitude of the decelerating cardiac pattern has been demonstrated to depend on stimulus relevance (Somsen, Jennings, & Molen, 2004). In the field of consciousness, Park et al. (2014) demonstrated a cardiac deceleration before a to-be-detected target was presented and acceleration after response delivery. Moreover, conscious perception increased the observed cardiac deceleration as compared to nonconsciously perceived stimuli, especially after participants delivered the motor response to signal their decision.

The objective of the present study is to explore cardiac modulations associated with the interaction between attention and consciousness. We manipulated phasic alertness and measured its impact on the conscious perception of a near-threshold Gabor stimulus (titrated to be consciously perceived on ~50% of the trials). Behaviorally, the alerting tone should increase perceptual sensitivity to detect the near-threshold

stimulus (Botta et al., 2017; Kusnir et al., 2011). We expected to observe an increase in the deceleration-acceleration cardiac pattern following the alerting tone. If an interaction between phasic alerting and consciousness were observed, the deceleration-acceleration pattern should be greater for consciously perceived as compared to nonconsciously perceived stimuli, especially following the alerting tone. These data may be important for understanding brain-body interactions in the study of attention and conscious perception.

2 | METHOD

2.1 | Participants

Twenty-six healthy volunteers (16 female, mean age of 23 years, $SD = 3.5$, all right-handed) participated in the experiment in exchange for course credit. All participants were undergraduate students from the Faculty of Psychology (University of Granada), who had not previously participated in similar experiments. One participant was excluded from the sample because his behavioral data were not properly recorded, and a further participant was excluded because she never responded to the objective task (see Procedure). All participants reported having normal or corrected-to-normal vision and audition and had no clinical history of neurological or psychiatric disorders. Signed informed consent was collected before the study, and participants were informed about their right to withdraw from the experiment at any time. The local research ethics committee from the University of Granada approved the experiment, which was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

2.2 | Apparatus and stimuli

E-prime software was used to control stimuli presentation, timing operations, and behavioral data collection (Schneider, Eschman, & Zuccolotto, 2002). Participants were seated at an approximate distance of 57 cm from the computer screen. At this distance, 1 cm corresponds to 1° of visual angle. All stimuli were presented on a gamma-corrected LCD monitor (17", Benq FP731, $1,024 \times 768$ pixels) with a refresh rate of 60 Hz. The experimental display consisted of three markers (6° width \times 5.5° height) presented on a gray background (luminance = 64.6 cd/m^2). A fixation point (a black plus sign, $0.5^\circ \times 0.5^\circ$) was presented within the central marker. The other two markers were presented 11.5° to the right and to the left of the fixation point (distance measured from the center of fixation point to the center of the marker). The target could appear inside one of two lateral boxes, and consisted of a Gabor with a spatial frequency of 4 cycles/degree spatial frequency, a diameter of 3° , and with its inner lines tilted 10° to either the left or the right.

A MATLAB script was used to create 100 Gabor stimuli, with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively.

Two arrowlike stimuli (<<< or >>>) were presented above and below the fixation point to collect the subjective response (see Procedure).

The alerting tone consisted of a beep burst presented at 97.5 dB. It was presented through headphones (Philips adjustable SHP2000; frequency range of 15–22,000 Hz; maximum sensitivity 100 dB; impedance 32 ohm; maximum input power of 500 mW).

2.2.1 | Psychophysiological variables and apparatus

Psychophysiological recording was accomplished by means of a Biopac System, model MP150, and a PC running AcqKnowledge acquisition software (v. 3.9.1.6). The electrocardiogram (ECG) was obtained by placing three disposable electrodes, filled with hypertonic gel, at Lead II. Frequencies below 0.5 and above 35 Hz were filtered out by means of a Biopac amplifier, model MEC110C. Although our main hypotheses referred to heart rate measures, we also recorded skin conductance (SC), using a

Biopac EDA100C amplifier. All signals were acquired at a sampling rate of 2,000 Hz.

2.3 | Procedure

Figure 1 shows the sequence and timing of the stimuli in a given trial. Each trial started with a fixation display (493–986 ms). This fixation display was followed by an alerting tone (17 ms) in 50% of the trials. After an interstimulus interval (ISI) varying randomly between 204–306 ms, the Gabor could be presented. On 50% of the trials, no Gabor was presented (catch trials). On the remaining 50% of the trials, the Gabor was equally likely to appear at either the left or the right marker for 34 ms. Therefore, the Gabor could be presented between 714–1,309 ms after the onset of the fixation point. Participants were asked to discriminate the orientation of the lines composing the Gabor as fast and as accurately as possible (objective response). Participants used the mouse to respond with their right hand, clicking the left button with their index finger if the lines were oriented to the left, or clicking the right button with their middle finger if the lines were oriented to the right. No response was required when no Gabor was perceived. In previous work (Botta et al., 2017), we asked

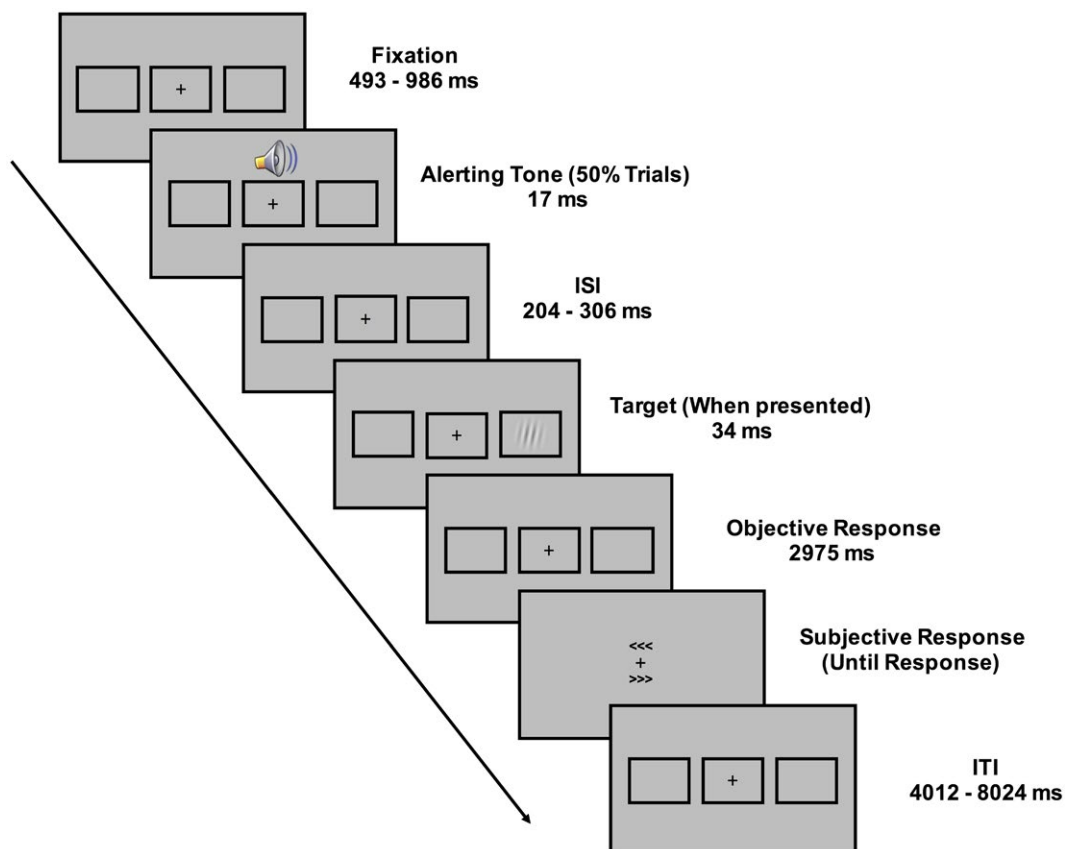


FIGURE 1 Sequence of events in a given trial. In the trial presented as an example the alerting tone and the Gabor were presented (although in the experiment, there were 50% of the trials without alerting tone, and 50% of the trials without Gabor)

participants to respond to the objective task even if no Gabor was perceived in order to equate motor preparation requirements for seen and unseen stimuli. However, it was very difficult to ask for an objective response when no tone was presented and no Gabor was perceived given the long jitter interval between trials (the intertrial interval, ITI, varied randomly between 4,012–8,024 ms to allow heart rate, HR, to reach the baseline). The random duration of the ITI and the fixation period made it difficult to estimate the moment in which a response was required.

After the objective response, we presented participants with two arrowlike stimuli, one below and the other one above the fixation point (>>> or <<<). We provided participants with three keys (to be pressed with the left hand): an upper key (*d*, pressed with the middle finger), a lower key (*c*, pressed with the index finger), and the space bar (pressed with the thumb). The upper key always corresponded to the arrow presented in the upper part of the fixation point, while the lower key was associated with the arrow presented in the lower part of the fixation point. Participants were asked to report, as accurately as possible, whether they had seen the target or not. If they had not, they were required to press the space bar. If they had seen the target, they were asked to indicate its location on the screen, left or right, when the arrows were presented. This procedure prevented lateralized response preparation until the arrow display appeared. This response is considered subjective because there is no correct response. Instead, participants indicated their conscious perception of the Gabor (seen or unseen). Participants were required to respond as accurately as possible, with no time pressure.

The experiment consisted of five blocks of 48 trials each, separated by a 2-min pause after each block.

Before the experimental trials, Gabor contrast was manipulated in a separate titration block until participants perceived ~50% of the Gabors presented. During titration, trials were similar to the experimental task except that no tone was presented (fixation point = 493–986 ms; ISI = 204–306 ms; Gabor = 34 ms; objective response = 2,975 ms; subjective response = until response). Titration began with a suprathreshold stimulus (Michelson contrast = 0.184), of which the contrast was manipulated in successive blocks depending on the mean percentage of seen Gabors every 16 trials. After each block, if participants reported seeing 63% or more targets, Gabors of the subsequent lower contrast level (Michelson contrast minus 0.009) were presented during the next block of trials; on the contrary, if the percentage of seen targets was equal to or lower than 38%, the next block of trials used Gabors at the subsequent higher contrast level (Michelson contrast plus 0.009). The titration procedure stopped when Gabor contrast yielded a percentage of seen targets ranging between $\geq 38\%$ and $\leq 63\%$ for two consecutive blocks of trials. This contrast value

was used in the experimental task. During titration, participants were required to keep the percentage of false alarms below 20%.

After titration, participants were informed about the procedure used to record the psychophysiological data, including the place of electrode location, the need to clean the skin, and to use electrolytic gel. For HR recording, three disposable electrodes were placed following the Lead II configuration: the negative pole on the right wrist, the positive pole on the left ankle, and ground sensor on the right ankle. This configuration was chosen to optimize the R wave of the ECG. Lead III configuration was used with one male participant (negative pole: left wrist; positive pole: left ankle; ground: right ankle) because he had a bandage on his right arm. For SC, two electrodes were placed in the hypothenar eminence of the left hand.

2.4 | Data reduction and statistical analyses

ECGLAB RR software (Vicente, Johannesen, Galeotti, & Strauss, 2013) was used to calculate the HR from the ECG. We measured each cardiac period (i.e., the R-R interval) in milliseconds and transformed it into HR in beats per minute. Then, the Kardia software (Perakakis, Joffily, Taylor, Guerra, & Vila, 2010) was used to obtain, for each trial, the weighted average of the HR every 100 ms, for an interval of 5 s (starting with the onset of the fixation point). These HR values were finally transformed into differential scores by subtracting the weighted average of the HR during the 400 ms prior to the presentation of the fixation point. Due to artifacts in the ECG, five participants were excluded from the HR analysis.

SC in microSiemens was first averaged every 500 ms, for an interval of 5 s (starting with the onset of the fixation point) and then transformed into differential scores by subtracting the average SC during 1 s prior to presentation of the fixation point. Due to artifacts, three participants were excluded from the SC analyses.

3 | RESULTS

3.1 | Behavioral data analysis and results

Data from the objective and the subjective tasks were analyzed using *t* tests to compare trials in which the alerting tone was absent or present. In the objective task, we analyzed response accuracy, the percentage of no responses, and reaction time (RT) for seen Gabors (only of trials with correct responses in the objective task; see Table 1). No anticipations or responses shorter than 150 ms were observed. For the subjective task, we analyzed the percentage of seen targets and the percentage of false alarms (FA), as well as perceptual sensitivity and response criterion according to signal

TABLE 1 Results of the objective and subjective tasks as a function of the alerting tone presence

	Objective task			Subjective task	
	RT	Accuracy	No responses	Seen Gabors	False alarms
No tone	1,083 (44)	0.86 (0.052)	0.29 (0.059)	0.42 (0.033)	0.01 (0.003)
Tone	963 (47)	0.85 (0.052)	0.16 (0.045)	0.85 (0.019)	0.04 (0.011)

Note. Mean (*SE*) are presented. RTs are expressed in milliseconds; all other measures are rates (0–1). RT = reaction time; SE = standard error.

detection theory (MacMillan, 2002). We computed a non-parametric index of perceptual sensitivity (A')¹, and response criterion (β'') to detect the Gabor.

$$A' = 0.5 + \frac{(\text{Hits} - \text{FAs}) \times (1 + \text{Hits} - \text{FAs})}{4 \times \text{Hits} \times (1 - \text{FAs})}; \beta'' = \frac{\text{Hits} \times (1 - \text{Hits}) - \text{FAs} \times (1 - \text{FAs})}{\text{Hits} \times (1 - \text{Hits}) + \text{FAs} \times (1 - \text{FAs})}$$

A' values usually range between 0.5 (the signal cannot be distinguished from noise) to 1 (perfect performance). For β'' , values close to 1 indicate a conservative criterion while values close to -1 indicate a nonconservative criterion (Stanislaw & Todorov, 1999).

3.2 | Objective task analysis

When the Gabor was consciously perceived, response accuracy for the objective task was 0.70. This value was significantly greater than chance (0.50; $t(25) = -3.58$, $p < 0.001$, Cohen's $d = 0.70$). No responses were given in most trials when the Gabor was not consciously perceived (only 0.01 responses were recorded). No alerting effect was observed in the accuracy analysis for correct responses, $t(23) = 0.875$, $p = 0.391$, Cohen's $d = 0.179$. However, the percentage of no responses to the target decreased when the alerting tone was presented as compared to conditions with no alerting tone, $t(25) = 3.366$, $p = 0.002$, Cohen's $d = 0.660$ (see Table 1). RT results demonstrated a main effect of alerting, with shorter responses when the alerting tone was presented as compared to conditions with no alerting tone, $t(22) = 6.406$, $p = 0.001$, Cohen's $d = 1.336$.

3.3 | Subjective task analysis

Participants consciously perceived more targets, $t(25) = -14.55$, $p = 0.001$, Cohen's $d = -2.854$, but also produced more false alarms, $t(25) = -2.533$, $p = 0.018$, Cohen's $d = 0.497$, when the alerting tone was presented as compared to conditions with no alerting tone (see Table 1). Signal detection theory analyses demonstrated that perceptual sensitivity increased, $t(25) = -7.625$, $p = 0.001$, Cohen's $d = -1.495$, and response criterion was less conservative, $t(25) =$

2.423, $p = 0.023$, Cohen's $d = 0.475$, when the alerting tone was presented as compared to conditions with no alerting tone (see Figure 2).

3.4 | HR analysis

HR data were analyzed using a repeated measures analysis of variance (ANOVA) with three independent variables manipulated within participant: alerting tone (absent or present), consciousness of Gabor (seen or unseen), and time (50 time points from the presentation of the fixation point—each 100 ms long). The analysis demonstrated a main effect of time, $F(49, 980) = 27.48$, $MSE = 4.19$, $p < 0.001$, $\eta_p^2 = 0.58$, showing the traditional cardiac deceleration-acceleration pattern along the trial. Four significant interactions were found: an interaction between alerting tone and consciousness of Gabor, $F(1, 20) = 5.74$, $MSE = 127$, $p = 0.027$, $\eta_p^2 = 0.22$; between alerting tone and time, $F(49, 980) = 9.13$, $MSE = 1.79$, $p < 0.001$, $\eta_p^2 = 0.31$; between consciousness of Gabor and time, $F(49, 980) = 5.25$, $MSE = 13.01$, $p < 0.001$, $\eta_p^2 = 0.21$; and between alerting tone, consciousness of Gabor, and time, $F(49, 980) = 4.83$, $MSE = 1.43$, $p < 0.001$, $\eta_p^2 = 0.19$ (see Figure 3). We used Fisher post hoc comparisons to explore the latter interaction, comparing the HR when the Gabor was seen and unseen at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, HR significantly differed for seen and unseen trials between 3,200 and 5,000 ms after fixation onset (all $ps < 0.05$). However, when the alerting tone was present, HR significantly differed for seen and unseen trials between 1,100 and 3,600 ms after fixation onset (all $ps < 0.05$; see Figure 3).

The above-described analysis, locked to the appearance of the fixation point, demonstrated that HR on seen and unseen conditions differed at earlier time points when the alerting tone was presented as compared to conditions with no alerting tone. Target onset time was variable (714 to 1,309 ms from the onset of the fixation point), and the subjective response occurred on average 2,975 ms after the fixation display was presented. Therefore, data indicate that in the no tone condition, HR differentiated between seen and unseen conditions only after the subjective response was given, while in the tone condition differences in HR between seen and unseen trials occurred approximately at the time of Gabor onset. To

¹[Correction added on 20 November 2018, after first online publication: The formula for A' has been amended.]

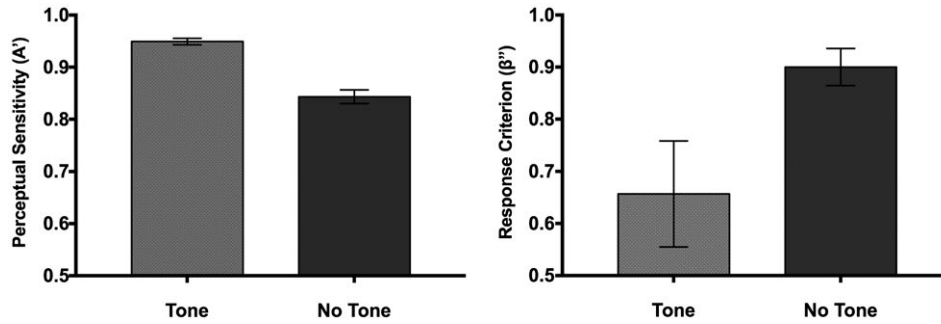


FIGURE 2 Perceptual sensitivity (A') and response criterion (β'') for detecting the Gabor when the alerting tone was present versus absent. Bars represent the standard error of the mean

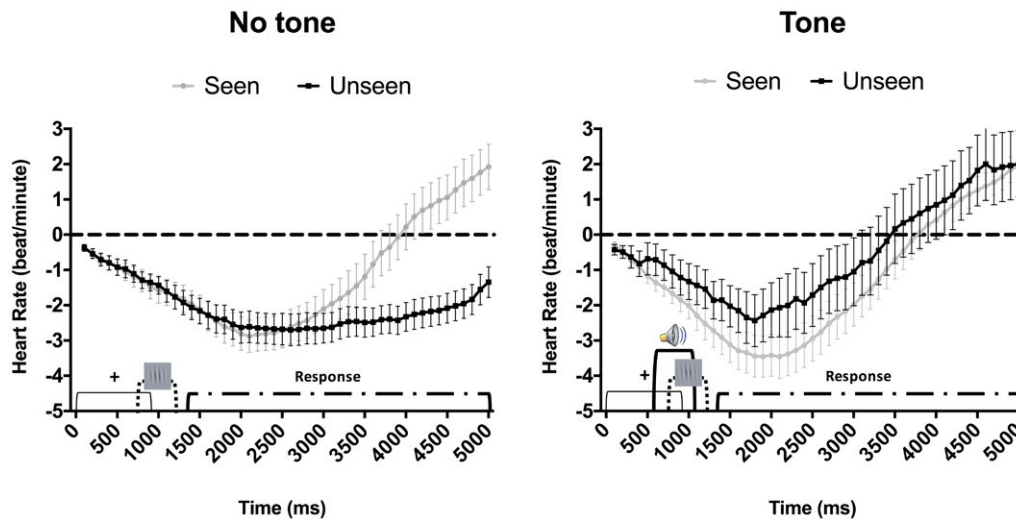


FIGURE 3 Changes in HR (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the x axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. In both tone and no tone conditions, the deceleration-acceleration HR pattern is observed. A significant interaction between phasic alerting, consciousness, and time is also observed (see Results). Bars represent the standard error of the mean

better understand the timing of the interaction between phasic alertness and conscious perception, the above-described ANOVA was repeated but locked to the appearance of the target (instead of the fixation display). This analysis demonstrated an interaction between alerting tone, consciousness of Gabor, and time, $F(39, 780) = 4.56$, $MSE = 1.13$, $p < 0.001$, $\eta_p^2 = 0.18$. Fisher post hoc comparisons demonstrated that, when the alerting tone was absent, HR significantly differed in the tone and no tone conditions from 2,200 ms after target onset until the end of the interval (all $ps < 0.05$), coinciding on average with the moment of the subjective response time window. However, when the alerting tone was present, HR significantly differed from the onset of the target until 2,600 ms later (all $ps < 0.05$).

We also wondered whether HR would differentiate between unseen trials when the target was actually present but it was reported as unseen, and when the target was absent and it was reported as unseen. Data from the HR were analyzed using a repeated measures ANOVA with three independent

variables manipulated within participant: alerting tone (absent or present), condition (unseen absent vs. unseen present), and time (50 time points from presentation of the fixation point—each 100 ms long). This analysis demonstrated a main effect of alerting tone, $F(1, 20) = 8.50$, $MSE = 136$, $p = 0.008$, $\eta_p^2 = 0.30$, and a main effect of time, $F(49, 980) = 15.74$, $MSE = 3.23$, $p < 0.001$, $\eta_p^2 = 0.44$. The interaction between alerting tone and time was also significant, $F(49, 980) = 18.62$, $MSE = 1.78$, $p < 0.001$, $\eta_p^2 = 0.48$; however, neither the main effect of condition nor any of its interactions with the other variables were significant (all $ps > 0.221$).

3.5 | SC analysis

SC data were analyzed using a repeated measures ANOVA with three independent variables manipulated within participant: alerting tone (absent or present), consciousness of Gabor (seen or unseen), and time (10 time points from presentation of the fixation point—each 500 ms long).

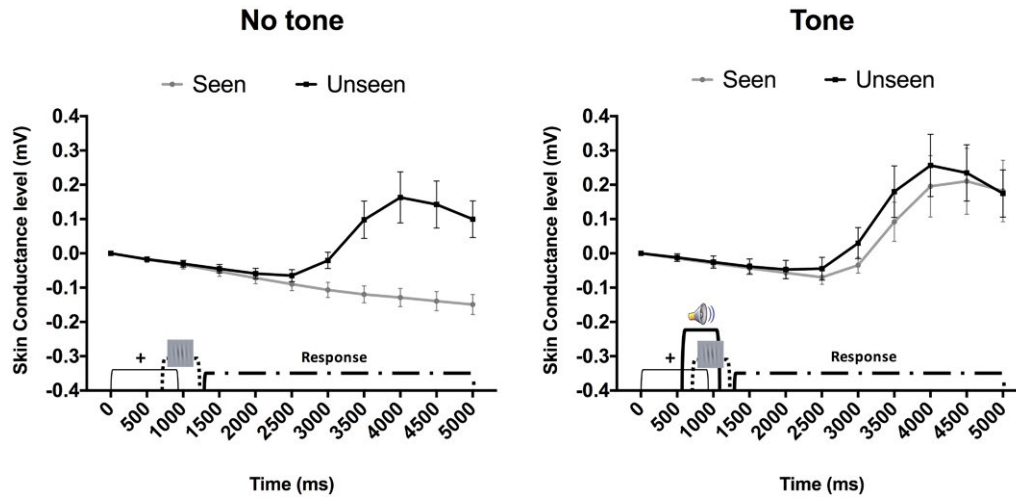


FIGURE 4 Changes in SC (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the x axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. A significant interaction between phasic alerting, consciousness, and time is observed (see Results). Bars represent the standard error of the mean

A main effect of tone was observed, $F(1, 22) = 14.28$, $MSE = 0.24$, $p < 0.001$, $\eta_p^2 = 0.39$, showing increased SC when the alerting tone was presented as compared to conditions with no alerting tone. A main effect of time was found, $F(9, 198) = 6.53$, $MSE = 0.04$, $p < 0.001$, $\eta_p^2 = 0.23$, with increased SC as time passed within the trial. Three significant interactions were found: between alerting tone and time, $F(9, 198) = 12.47$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = 0.36$; between consciousness of Gabor and time, $F(9, 198) = 2.08$, $MSE = 0.01$, $p = 0.032$, $\eta_p^2 = 0.09$; and between alerting tone, consciousness of Gabor, and time, $F(9, 198) = 4.38$, $MSE = 0.01$, $p < 0.001$, $\eta_p^2 = 0.16$ (see Figure 4). We used Fisher post hoc comparisons to explore the latter interaction, comparing the SC when the Gabor was seen and unseen at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, SC for seen and unseen Gabors significantly differed from 4,000 ms from fixation onset until the end of the trial (all $ps < 0.001$). However, when the alerting tone was present, SC differed significantly for seen and unseen Gabors between 3,000 and 4,000 ms (all $ps < 0.05$) (see Figure 4).

We also wondered whether SC would differentiate between unseen trials when the target was actually present and when the target was absent. Data were analyzed using a further repeated measures ANOVA with three independent variables manipulated within participant: alerting tone (absent or present), condition (unseen absent vs. unseen present), and time (10 time points from presentation of the fixation point—each 500 ms long). This analysis demonstrated a main effect of alerting tone, $F(1, 22) = 16.32$, $MSE = 0.25$, $p < 0.001$, $\eta_p^2 = 0.42$, and a main effect of time, $F(9, 198) = 4.95$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = 0.18$.

Three significant interactions were found: between alerting tone and time, $F(9, 198) = 14.39$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = 0.39$; between condition and time, $F(9, 198) = 2.20$, $MSE = 0.003$, $p = 0.023$, $\eta_p^2 = 0.09$; and between alerting tone, condition, and time, $F(9, 198) = 2.94$, $MSE = 0.003$, $p = 0.003$, $\eta_p^2 = 0.12$ (see Figure 5). We used Fisher post hoc comparisons to explore the latter interaction, comparing SC when the Gabor was present but unseen, and when it was absent and unseen, at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, there were no significant results (all $ps > 0.05$). However, when the alerting tone was present, SC significantly increased for present but unseen Gabors as compared to absent Gabors. This effect was observed from 3,000 ms after fixation onset until the end of the trial (all $ps < 0.002$).

4 | DISCUSSION

The present study was designed to examine brain-body interactions in the relation between attention and consciousness. Brain-body interactions have been demonstrated to be important in many cognitive processes such as self-consciousness (Canales-Johnson et al., 2015; Critchley & Harrison, 2013) and emotions (Craig, 2009; Critchley & Harrison, 2013; Lang, Bradley, & Cuthbert, 1990; Reizenstein, Meyer, & Schützwohl, 1995). Consistent with previous observations, HR results demonstrated the traditional deceleration-acceleration pattern (main effect of time; Lacey & Lacey, 1978). As expected, cardiac deceleration was more pronounced when the alerting tone was presented than when it was absent (Vila et al., 2007), confirming previous observations of heart rate modulations by phasic alerting.

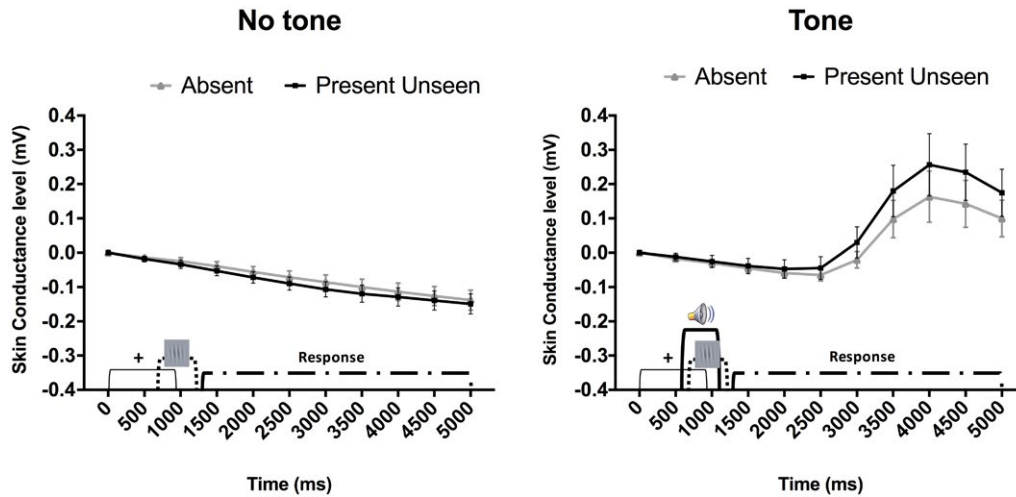


FIGURE 5 Changes in SC (relative to baseline) for absent versus present but unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the x axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. A significant interaction between alerting, consciousness, and time is observed (see Results). Bars represent the standard error of the mean

Importantly, the heart rate deceleration-acceleration pattern demonstrated an interaction between phasic alerting and consciousness. When the alerting tone was absent, HR only differed between seen and unseen Gabors after the subjective response was given, probably reflecting postdecisional, evaluative processes (Andreassi & Filipovic, 2013; Lacey, 1967; Lacey & Lacey, 1978; Vila & Guerra, 2009). However, when the alerting tone was presented, HR deceleration was more pronounced for seen as compared to unseen Gabors before the presentation of the Gabor stimulus and until 3,600 ms later. The alerting modulation was also associated with shorter RTs, as well as changes in both perceptual sensitivity and response criterion (see also Botta et al., 2017; Kusnir et al., 2011).

SC results revealed some kind of subliminal processing of stimuli reported as unseen. Despite participants' inability to perform the objective task when the Gabor was reported as unseen in this and in previous studies (Chica et al., 2011; Kusnir et al., 2011), SC increased for unseen, but present, Gabors as compared to unseen, and absent, Gabors when the alerting tone was presented. Subliminal processing has been demonstrated in multiple experiments (Gaillard et al., 2006; Kentridge, Heywood, & Weiskrantz, 1999, 2004; Sklar et al., 2012; Van Gaal et al., 2014; Van Gaal, Lamme, & Ridderinkhof, 2010). Although near-threshold Gabors in our experiments do not usually demonstrate subliminal effects, a recent investigation using machine learning decoding techniques have demonstrated that present but unseen Gabors can affect magnetoencephalography (MEG) responses for a sustained period of time (King, Pescetelli, & Stanislas, 2016). To our knowledge, SC has never been explored in the context of attention-consciousness interactions. Our results suggest that phasic alerting increases subliminal processing, although

more research is needed to understand the level of processing of these subliminal Gabors that did not affect behavior (the objective response).

The results reported here highlight that attentional processing (phasic alerting) boosts conscious perception of near-threshold stimuli (Botta et al., 2017), as proposed by the Global Neuronal Workspace model (Dehaene & Changeux, 2011). The neural interaction between phasic alerting and consciousness has been associated with the activity of a frontostriatal network, including structures such as the caudate nucleus, the thalamus, the anterior cingulate cortex (ACC), the supplementary motor area (SMA), and the frontal eye fields (Chica et al., 2016). According to Sturm and Willmes (2001), the ACC, midbrain, and thalamus constitute the anterior alerting system, while the pre-SMA is involved in response selection and preparation. An important theoretical question is how the central nervous system (CNS) influences the peripheral nervous system (PNS). Many authors agree with a main role of the insula in this interaction (Craig, 2009; Critchley & Harrison, 2013; Critchley et al., 2004; Park et al., 2014). Critchley and Harrison (2013) described two communication pathways between the CNS and PNS: direct and indirect. Both pathways send information to the thalamus, which projects to the posterior insula (PI; Menon & Uddin, 2010; Park et al., 2014), which is involved in homeostasis and regulation of the body and physiological state (Critchley & Harrison, 2013; Critchley et al., 2004; Menon & Uddin, 2010; Park et al., 2014). PI sends information to the anterior insula (AI), which transmits the information to ACC (Menon & Uddin, 2010; Uddin, 2014), an important region of the frontostriatal network involved in phasic alerting. The communication between the AI and the ACC has also been related to the salience network (Menon & Uddin, 2010; Uddin,

2014). As proposed by Critchley and Harrison (2013), the CNS-PNS systems coordinate and integrate their functioning through dynamic feedback. Although theoretically unlikely, we have no data to disprove that PNS effects might be secondary to the main CNS effects (observed in the frontostriatal network; Chica et al., 2016).

Brain-body interactions have been largely neglected in the consciousness literature. Our study was inspired by Park et al. (2014), who measured the conscious detection of a near-threshold Gabor and observed a similar cardiac deceleration-acceleration pattern to that observed in our study for seen as compared to unseen Gabors. The present study has demonstrated that this brain-body interaction mediates the phasic attentional modulation of conscious perception. In particular, cardiac deceleration was more pronounced at the time of Gabor onset for seen as compared to unseen trials, but only when the alerting tone was presented. Park et al. (2014) complemented ECG data with MEG data, locked to the heartbeat-evoked response. Brain sources were located in the ACC, the right posterior medial insula, inferior parietal regions of the right hemisphere, and somatosensory cortex (Park et al., 2014). These brain structures resemble the visceral projection described in the Introduction, and some of them have also been associated with conscious perception (Kranczoch, Debener, Schwarzbach, Goebel, & Engel, 2005). The insula, in particular, seems to be implicated in conscious perception (Craig, 2009; Tsuchiya & Adolphs, 2007) and has also been proposed as a network hub of the salience network (Menon & Uddin, 2010; Uddin, 2014). It is one of the first regions to receive information from the PNS (Craig, 2009; Critchley & Harrison, 2013; Menon & Uddin, 2010; Uddin, 2014), and it belongs to a circuit—including the ACC and other limbic and subcortical structures—which is associated with the integration of the external sensory information with the internal state of the body (Seeley et al., 2007; Uddin, 2014). We therefore hypothesize that the phasic alerting and consciousness interaction observed in the HR response might be associated with this neural circuit, which is considered important in the integration of signals from the body and the brain. Alerting signals modulate the HR and the saliency network (Corbetta, Patel, & Shulman, 2008; Uddin, 2014), and these peripheral and central signals might be integrated in structures such as the insula. As we have previously demonstrated both with phasic alerting (Botta et al., 2017; Chica et al., 2016; Kusnir et al., 2011) and exogenous attention manipulations (Botta et al., 2017; Chica & Bartolomeo, 2012; Chica et al., 2011; Chica, Lasaponara, Lupiáñez, Doricchi, & Bartolomeo, 2010), the interactions between attention and consciousness occur in frontoparietal and frontostriatal regions, distant from the primary sensory regions in which perceptual information is initially processed. This observation argues

against the so-called “low order theories of consciousness”. (Zeki & Bartels, 1999), postulating that consciousness depends mostly on the activation of primary sensory regions.

In summary, the present study replicates previous behavioral results demonstrating attentional boosting of near-threshold stimuli (Botta et al., 2017; Chica et al., 2016, 2011; Kusnir et al., 2011). In addition, these effects are reflected in the organism (HR and SC), generating the need to take into account brain-body interactions for current theoretical models of consciousness (Park & Tallon-Baudry, 2014).

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