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 allowing 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 (HR) and skin conductance (SC) are affected by the interaction between phasic alertness and conscious perception. We presented near-threshold visual stimuli which could be preceded by an alerting tone on 50% of the trials. Behaviorally, phasic alerting improved perceptual sensitivity to detect the 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 of supplementing current theoretical models with a biological component.

Keywords: attention, phasic alerting, consciousness, heart-rate, skin conductance.

1. Introduction

Conscious perception has been a topic of great interest 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 (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 related to 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 Petersen and Posner’s (2012), the attentional system can be divided into three anatomically and functionally distinct sub-systems: alerting, orienting, and executive control. In this study, we will focus on the alerting system, which allows maintaining 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 to detect targets presented near the threshold of consciousness (Botta, Ródenas, & Chica, 2017; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; A. Petersen, Hilkjaer-Petersen, Bundesen, Vangkilde, & Habekost, 2017), producing its effects through a fronto-striatal network (Chica, Bayle, Botta, Bartolomeo & Paz-Alonso, 2016).

Until now, current theoretical models about conscious perception have mainly focused in cognitive and neural processing (Dehaene & Changeux, 2011; Lamme & Roelfsema, 2000; Tononi, 2012; Zeman, 2001). However, cognitive processes do not happen in an isolated brain, being 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 attention in the study of self-awareness (Tsuchiya & Adolphs, 2007) and emotions (Seth, 2013), only recently, Tallon-Baudry and colleagues have started to explore the relationship between body signals and consciousness (Park, Correia, Ducorps & Tallon-Baudry, 2014; Park & Tallon-baudry, 2014). The central system monitors the state of the internal organs (for example the heart) to regulate the homeostatic state of multiple biological parameters. The heart has a group of mechano-sensory neurons that send information reflecting fast events (Amour & Ardell, 2004; Park et al., 2014). This information is sent through ascending afferences to the central system. According to Tallon-Baudry and colleagues (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 the conscious perception.

Physiological studies have associated cardiac changes to several cognitive processes. For example, following an alerting tone, there is a cardiac deceleration followed by an acceleration (Lacey & Lacey, 1978). While cardiac deceleration has been associated with preparatory processes, cardiac acceleration has 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 an acceleration after response delivery. Moreover, conscious perception increased the observed cardiac deceleration as compared to non-consciously perceived stimuli, especially after participants delivered the motor response to signal their decision.

The objective of the present study is to explore for the first-time cardiac modulations associated to attention and consciousness interactions. In particular, fi 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 a traditional cardiac pattern of deceleration-acceleration, which should be increased when the alerting tone is presented. If an interaction between phasic alerting and consciousness were observed, the deceleration-acceleration pattern should be increased for consciously perceived as compared to non-consciously perceived stimuli, especially when the alerting tone was presented. These data might be important to understand brain-body interactions in the study of attention and conscious perception.

2. Method

2.1 Participants

Twenty-six healthy volunteers (sixteen females, mean age of 23 years, SD=3.5, right-handed) participated in the experiment in exchange of course credit. All participants were undergraduate students from the Faculty of Psychology (University of Granada), which 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 section). All participants reported having normal o corrected-to-normal vision and audition, and had no clinical history of neurological or neuropsychological 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 stimulus presentation, timing operations, and data collection (Pavlopoulos, Soldatos, Barbosa-Silva, & Schneider, 2010). 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 monitor (17 inch, Benq FP731, 1024x768) with a refresh rate of 60 Hz. The experimental display consisted of three markers (6° width x 5.5° height) presented on a gray background (luminance= 64.6 cd/m^2). A fixation point (a black plus sign, 0.5° x 0.5°) 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/°, 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 arrow-like stimuli (<<< or >>>) were presented above and below the fixation point to collect the subjective response (see Procedure section).

The alerting tone consisted of a beep burst presented at 97.5dB. It was presented through headphones (Philips adjustable SHP2000; frequency range of 15-22000Hz; maximum sensitivity 100dB; impedance 32 Ohm; maximum input power of 500mW).

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 (EKG) 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 heat-rate measures, we also recorded skin conductance (SC). SC was recorded using a Biopac EDA100C amplifier. All signals were acquired at a sampling rate of 2000 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 (493-986ms), followed by the alerting tone (17 ms) on 50% of the trials. Subsequently, the Gabor could appear (32 ms) randomly at the left or the right location. On 50% of the trials no Gabor was not presented (catch trials). Participants were asked to discriminate the orientation of the lines composing the Gabor as fast and as accurately as possible (objective response). No response was required when no Gabor was perceived. In previous work (Botta et al., 2017), we asked 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 inter-trial interval, ITI, varied randomly between 2006-4012 ms to allow 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 arrow-like stimuli, one below and the other one above the fixation point (>>> or <<<). We provided participants with three keys (which should be pressed with the left hand): an upper key (“d”), a lower key (“c”), and the space bar. 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 for 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.

[Please, insert here Figure 1]

The experiment consisted of 5 blocks of 48 trials, 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 (fixation point=493-986 ms;

Gabor=32 ms; objective response= 2975 ms; subjective response= until response) except that no tone was presented. Titration began with a supra-threshold stimulus (Michelson contrast = 0.184), which contrast was manipulated in successive blocks depending on the mean percentage of seen Gabors after every 16 trials. After each block, if participants reported seeing 63% or more targets, Gabors at the immediately following lower contrast level (Michelson contrast minus 0.009) were used during the next block of trials; besides, if the percentage of seen targets was equal or lower than 38%, the next block of trials used Gabors at the immediately following higher contrast level (Michelson contrast plus 0.009). The titration procedure stopped when Gabor contrast yielded a percentage of seen targets ranging between ≥38% and ≤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 of the procedure to record the psychophysiological data indicating the place of electrode location as well as the need to clean the skin and use electrolite jelly. 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 right ankle. This configuration was chosen to optimize the R wave of the EKG. Lead III configuration was used with a participant (negative pole: left wrist; positive pole: left ankle; ground: right ankle) because he had 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.

HR was obtained from the EKG measuring each cardiac period –i.e., the R-R interval- in milliseconds (ms) and transforming it into HR in beats per minute using the ECGLabRR software (Vicente, Johannesen, Galeotti, & Strauss, 2013). 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 during 5 s starting with the onset of the fixation point. These HR values were finally transformed into differential scores subtracting the weighted average of the HR during the 400 ms prior to the presentation of the fixation point. Due to artifacts in the EKG, five participants were excluded from the HR analysis.

SC in microSiemens was first averaged every 500 ms during 5 s starting with the onset of the fixation point and then transformed into differential scores 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 with alerting tone (absent or present) as independent variable. In objective task, we analyzed response accuracy, the percentage of no responses, and reaction time for seen Gabors (with correct responses of 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 the signal detection theory (MacMillan, 2002). We computed a non-parametrical index of perceptual sensitivity: A'= 0.5+(((Hits-FA)*(1+Hits-FA))/(4*Hits*(1-FA))); and response criterion: Beta''=

(((Hits*(1-Hits)-FA*(1-FA))/(Hit*(1-Hit)+FA*(1-FA)))). A’ values usually range between 0.5 (the signal cannot be distinguished from the noise) to 1 (perfect performance). For Beta’’, values close to 1 indicate a conservative criterion while values close to -1 indicate a non-conservative criterion (Stanislaw & Todorov, 1999).

[Please, insert here Table 1]

3.2 Objective task analysis.

When the Gabor was consciously perceived, response accuracy to the objective task was 0.70. This value was significantly greater than chance (0.50; $t(25)=-3.58$, $p<0.001$, Cohen’s= 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=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=0.497, when the alerting tone was presented as compared to conditions with no alerting tone (see Table 1).

[Please, insert here Figure 2]

Signal detection theory analyses demonstrated that perceptual sensitivity was 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= 0.475, when the alerting tone was presented as compared to conditions with no alerting tone (see Figure 2).

3.4 Heart Rate analysis.

HR data were analyzed using a repeated measures ANOVA with three independent variables manipulated intra-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, $F(49, 980)= 27.48, MSE=4.19, p<.001,$ $\eta_p^2= .58$, showing the traditional cardiac deceleration-acceleration pattern along the trial. Four significant interactions were found: an interaction between alerting tone and consciousness of Gabor, $F(1, 20)=5.74, MSE=127, p=.027,$ $\eta_p^2=.22$; between alerting tone and time, $F(49, 980)= 9.13, MSE= 1.79, p<.001,$ $\eta_p^2=.31$; between consciousness of Gabor and time, $F(49, 980)=5.25, MSE=13.01, p<.001,$ $\eta_p^2=.21$; and between alerting tone, consciousness of Gabor, and time, $F(49, 980)=4.83, MSE= 1,43, p<.001,$ $\eta_p^2=.19$ (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 3200 and 5000 ms after fixation onset (all p<.05). However, when the alerting tone was present, HR significantly differed for seen and unseen trials between 1100 and 3600 ms after fixation onset (all p<.05) (see Figure 3).

[Please, insert here 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. The time of target presentation was variable (from 610 ms to 1205 ms since the onset of the fixation point) and the subjective response occurred in average 2975 ms after the fixation display was presented. Therefore, data indicate that in the no tone condition, HR only differentiated between seen and unseen conditions 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 better understand the time in which the HR demonstrated an 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, $F(39, 780)=4.56$, $MSE= 1.13$, $p<.001$, $\eta_p^2=.18$. Fisher post-hoc comparisons demonstrated that when the alerting tone was absent, HR differed significantly in the tone and no tone conditions since 2200 ms after target onset until the end of the interval (all $p<.05$), coinciding in average with moment of the subjective response time window. However, when the alerting tone was present, HR differed significantly since the onset of the target until 2600 ms after target onset (all $p<.05$).

We also wondered if HR would differentiate between unseen trials when the target was actually present but unseen and when the target was absent and unseen. Data from the HR was analyzed using a repeated measures ANOVA with three independent variables manipulated intra-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 main effect of alerting tone, *F(1,20)=8.50, MSE=136, p=.008,* η_p^2=.30, and a main effect of time, *F(49, 980)=15.74, MSE=3.23, p<.001,* η_p^2=.44. The interaction between alerting tone and time was also significant, *F(49, 980)=18.62, MSE=1.78, p<.001,* η_p^2=.48; however, neither the main effect of condition, nor any of its interactions with the other variables were significant (all ps>.221) .

3.5 Skin conductance analysis.

SC data were analyzed using a repeated measures ANOVA with three independent variables manipulated intra-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).

A main effect of tone was observed, *F(1, 22)= 14.28, MSE=0.24, p<.001,* η_p^2= .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<.001,* η_p^2= .23, with increased SC as time passed by within the trial. Three significant interactions were found: between alerting tone and time, *F(9,198)=12.47, MSE=0.03, p<.001,* η_p^2=.36; between consciousness of Gabor and time, *F(9,198)=2.08, MSE=0.01, p=.032,* η_p^2=.09; and between alerting tone, consciousness of Gabor, and time, *F(9,198)=4.38, MSE=0.01, p<.001,* η_p^2=.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 since 4000 ms from fixation onset until the end of the trial (all ps<.001). However, when the alerting tone was present, SC differed significantly for seen and unseen Gabors between 3000 and 4000 ms (all ps<.05) (see Figure 4).

We also wondered if SC would differentiate between unseen trials when the target was actually present and when the target was absent. Data from the SC was analyzed using a further repeated measures ANOVA with three independent variables manipulated intra-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<.001,* η_p^2=.42, and a main effect of time, *F(9,198)=4.95, MSE=.03, p<.001,* η_p^2=.18. Three significant interactions were found: between alerting tone and time, *F(9,198)=14.39, MSE=0.03, p<.001,* η_p^2=.39; between consciousness of Gabor and time, *F(9,198)=2.20, MSE=0.003, p=.023,* η_p^2=.09; and between alerting tone, consciousness of Gabor, and time, *F(9,198)=2.94, MSE=0.003, p=.003,* η_p^2=.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>.05). However, when alerting tone was present, SC significantly increased for present but unseen

[Please, insert here Figure 4]

[Please, insert here Figure 5]

Gabors as compared to absent Gabors. This effect was observed since 3000 ms after fixation onset until the end of the trial (all ps<.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; Reisenzein, Meyer, & Schutzwohl, 1995). Consistent with previous observations, HR results demonstrated a traditional pattern of deceleration-acceleration in all conditions (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.

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 post-decisional, evaluative processes (Andreassi & Filipovic, 2013; B. C. Lacey & Lacey, 1978; J. I. Lacey, 1967; 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 and until 2600 ms later. The alerting modulation was also associated to shorter reaction times, and 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 was 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 do not usually demonstrate subliminal effects, a recent investigation using machine learning decodification techniques have demonstrated that present but unseen Gabors can affect magnetoencephalography (MEG) responses for a sustain period of time (King, Jean-Rémi, Pescetelli, & Stanislas, 2016). To our knowledge, SC has never been explored in the context of attention-consciousness interactions. Our results suggest that 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).

These results are important to 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 to the activity of a fronto-striatal network, including structures such as the caudate nucleus, the thalamus, the anterior cingulate cortex, the supplementary motor area, and the frontal eye fields (Chica et al., 2016).

However, consciousness has a clear biological component (Park & Tallon-baudry, 2014) which has been neglected in the 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. In the present study, we have proved for the first time in the literature 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 EKG data with MEG data, locked to the heartbeat-evoked response (HER). Brain sources were located in the anterior cingulate cortex, 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 to conscious perception (Kranczioch, 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. The insula is one of the first regions receiving information from the organism (Uddin, 2014), and it belongs to a circuit including the anterior cingulate cortex and other limbic and subcortical structures, associated to 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 to this neural circuit that is considered important to integrate signals from the body and the brain. Alerting signals modulate the HR, and the saliency network (Corbetta, Patel, & Shulman, 2008; Uddin, 2014), and this 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 (Botta et al., 2017;Chica et al., 2011; Chica, Lasaponara, Lupiáñez, Doricchi, & Bartolomeo, 2010; Chica & Bartolomeo, 2012) manipulations, the interactions between attention and consciousness occur in fronto-parietal and fronto-striatal regions, distant from the primary sensory regions where perceptual information is initially process. This observation argues against the so called "low order theories of consciousness" (Zeki & Bartels, 1999) postulating that consciousness depends mostly of the activation of primary sensory regions.

In summary, the present study replicates previous behavioral results demonstrating attentional boosting of near-threshold (Botta et al., 2017; Chica et al., 2011, 2016; Kusnir et al., 2011). In addition, these effects are reflected in the organism (HR and SC), generating the need to add a biological component to theoretical models of consciousness (Park & Tallon-baudry, 2014).

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Table 1. For the objective task, the table shows the means RTs, accuracy, and the proportion of no responses (with standard errors in parenthesis). For the subjective task, the proportion of seen Gabors and the proportion of false alarms in shown (with standard errors in parenthesis).

	Objective Task			**Subjective Task**	
	RT	Accuracy	No Responses	Seen Gabors	False Alarms
No Tone	1083(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)

CAPTIONS

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 there were 50% of the trials without alerting tone, and 50% of the trials without Gabor).

Figure 2. Perceptual sensitivity (A') and response criterion (B'') to detect the Gabor when the alerting tone was present vs. absent.

Figure 3: Changes in HR (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left panel) and present (right panel). 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 and consciousness is also observed.

Figure 4*:* Changes in SC (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left panel) and present (right panel). 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 and consciousness is observed.

Figure 5: Changes in SC (relative to baseline) for absent vs. present but unseen Gabors when the alerting tone was absent (left panel) and present (right panel). The 0 value on the x axis represents the moment of fixation onset. The moment of presentation of the

alerting tone and the Gabor were variable. A significant interaction between alerting and consciousness is observed.