

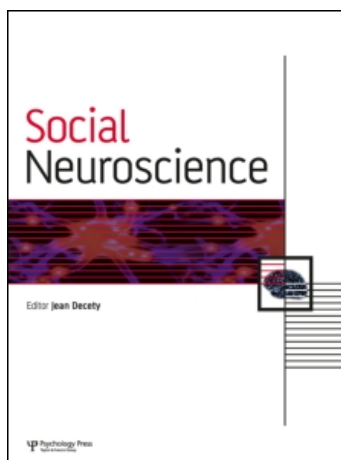
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### Exploring the relationship between vagal tone and event-related potentials in response to an affective picture task

Michele Dufey<sup>a</sup>; Esteban Hurtado; Ana María Fernández<sup>b</sup>; Facundo Manes<sup>c</sup>; Agustín Ibáñez<sup>d</sup>

<sup>a</sup> Universidad Diego Portales, Santiago, Chile <sup>b</sup> Universidad Diego Portales, and Universidad de Santiago de Chile, Santiago, Chile <sup>c</sup> Institute of Cognitive Neurology (INECO) & Institute of Neurosciences, Favaloro University, Buenos Aires, Argentina <sup>d</sup> Universidad Diego Portales, Santiago, Chile, Institute of Cognitive Neurology (INECO) & Institute of Neurosciences, Favaloro University, and National Scientific and Technical Research Council (CONICET), Buenos Aires, Argentina

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# Exploring the relationship between vagal tone and event-related potentials in response to an affective picture task

**Michele Dufey**

*Universidad Diego Portales, Santiago, Chile*

**Esteban Hurtado**

*P. Universidad Católica de Chile, and Universidad de Santiago de Chile, Santiago, Chile*

**Ana María Fernández**

*Universidad Diego Portales, and Universidad de Santiago de Chile, Santiago, Chile*

**Facundo Manes**

*Institute of Cognitive Neurology (INECO) & Institute of Neurosciences, Favaloro University, Buenos Aires, Argentina*

**Agustín Ibáñez**

*Universidad Diego Portales, Santiago, Chile, Institute of Cognitive Neurology (INECO) & Institute of Neurosciences, Favaloro University, and National Scientific and Technical Research Council (CONICET), Buenos Aires, Argentina*

The present study is the first to investigate the relationship between vagal tone level and event-related potentials (ERPs) in adults. Numerous studies have shown a relationship between vagal tone and the individual differences between a variety of psychophysiological, affective, and social outcomes. This suggests that vagal tone can be related to how people process relevant affective social information at the brain level. This study aimed to assess whether the ERP response varies between high and low vagal tone groups, in the face of salient affective information. In the experimental cohort, two groups were separated according to their vagal tone level. ERPs were recorded while individuals performed an affective picture task that included positive, neutral, and negative emotional stimuli. Differences between the high and low vagal tone groups were observed at the early posterior negativity for both positive and negative valences, and at the late positive potential for all the categories. It can be concluded that differences between high and low vagal tone levels are related to differences in the ERPs at early, middle, and late latencies. The results are discussed with respect to the effect of differences between the vagal tone conditions on various stages of information-processing.

**Keywords:** Vagal tone; ERPs; EPN; LPP; P1; IAPS; Affective social information; Peripheral–central relationship.

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Correspondence should be addressed to: Agustín Ibáñez, Laboratory of Experimental Psychology & Neuroscience and Institute of Cognitive Neurology (INECO) & CONICET Castex 3293 (CP 1425) Buenos Aires, Argentina. E-mail: aibanez@neurologiacognitiva.org

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## INTRODUCTION

In order to understand human behavior in its social context, it is important to study how people extract and process relevant information from their environment through complex stimuli in order to make decisions (San Martín et al., in press). Emotional information has been shown to be robust and to have predictable effects on cognition by providing specific cognitive strategies that influence the selection of responses (Forgas, 1995; Frith & Singer, 2008; Levenson, 1999; Riveros et al., 2010) through the activation of bounded brain areas (Eslinger et al., 2008; Harris & Fiske, 2007; Jabbi & Keysers, 2008; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008). Previous studies have identified and characterized both central and peripheral responses to incoming emotional information, with either positive or negative hedonic valence (Bradley, Codispoti, Cuthbert, & Lang, 2001a; Bradley, Codispoti, Sabatinelli, & Lang, 2001b; Lang, Bradley, & Cuthbert, 1998a; Schupp et al., 2000; Schupp, Junghöfer, Weike, & Hamm, 2004a). This suggests that complex emotional information provided by the social environment triggers high-level cognitive processing not only through structures and networks in the brain, but also by means of the participation of peripheral organs in affective self-regulation. This leads to a permanent feedback loop between central and peripheral components (Porges, Doussard-Roosevelt & Maiti, 1994) that is coordinated by a central autonomic network (Thayer & Lane, 2000). The present study represents an inquiry into this kind of peripheral–central relationship that occurs in response to affective social information. More specifically, the purpose of this work is to assess whether high and low vagal tone levels are related to differences in the modulation of event-related potentials (ERPs) evoked by emotional stimuli, categorized with positive, neutral, or negative hedonic valence.

At the peripheral level, and from an affective regulation standpoint, several studies have established individual differences in responses to socially and emotionally challenging situations as a function of vagal tone. Vagal tone is a psychophysiological construct that is often quantified by the amplitude of respiratory sinus arrhythmia (RSA), which is the result of permanent increases and decreases in heart rate (HR) coupled to the phase of inspiration and expiration of the breathing cycle (Eckberg, 1983). There is a considerable body of research that has shown that vagal tone is related to affective, social and cognitive variables, and therefore it has been proposed as an index of emotional regulation (Appelhans & Luecken, 2006; Porges et al., 1994).

Various studies have shown that young children with a high vagal tone level present more positive psychophysiological, behavioral, and social performance in diverse experimental settings (Calkins, 1997; Huffman et al., 1998; Linnemeyer & Porges, 1986; Porter, Porges, & Marshall, 1988) as well as predictive outcomes in mental, motor, and social skills (Doussard-Roosevelt, McLenny, & Porges, 2001; Doussard-Roosevelt, Porges, Scalton, Alemi, & Scalton, 1997), relative to children with lower vagal tone. In fact, some studies have indicated that vagal tone and self-regulation ability are related to children's parental socialization (Calkins, Smith, Gill & Johnson, 1998; Haley & Stansbury, 2003; Hastings et al., 2008; Katz, 2007). Although not entirely consistent, these findings support the idea that vagal tone can be related to differences associated with individuals' perceptions about their own social environments.

Vagal tone in adults has been less extensively studied. It has been reported that high expression of vagal tone predicts a superior level of self-control on self-reports and a lower level of negative emotional arousal towards moderate to high stress (Fabes & Eisenberg, 1997). Similarly, a higher level of RSA is associated with more intense emotional responses on exposure to negative films (Demaree, Robinson, Everhart & Schmeichel, 2004). Furthermore, evidence suggests that individual differences in RSA are predictive of increasing negative reactivity during face-to-face interactions (Butler, Wilhelm, & Gross, 2006; for other results see Frazier, Strauss, & Steinhauer, 2004). The divergent nature of these results could stem from methodological differences in the experimental settings used to evoke emotional responses in these studies. Nonetheless, the bulk of evidence suggests that vagal differences are related to variations in affective and emotional reactions. Reinforcing this idea, poor vagal modulation has been related to affective disorders, such as anxiety and depression (Light, Kothandapani, & Allen, 1998; Lyonfields, Borkovec, & Thayer, 1995; Rechlin, Weis, Spitzer, & Kaschka, 1994; Yeragani et al., 1991), as well as higher levels of social anxiety (Movius & Allen, 2004).

One particular aspect that has received little attention in the literature is the relationship between vagal tone and brain activity. On one hand, a few studies have evaluated variations in brain activity using neuroimaging, as well as variations of cardiac activity in the high frequency (HF) domain, caused essentially by parasympathetic (mainly vagal) influence on the heart. While these studies illustrate the correlation between the activity of specific brain structures and autonomic parasympathetic activity towards cognitive and emotional tasks, the variations according to vagal

tone and their relationship with brain activity concerning emotional information have yet to be established. On the other hand, only one study so far has evaluated vagal tone and brain activity using the electroencephalogram (EEG) in infants by employing a mismatch negativity paradigm (MMN, Leppänen et al., 2004). That study demonstrated that, among other cardiac measures, vagal tone correlates significantly with the ERP amplitude in some positions of the scalp, which indicates a greater maturity of this component.

An experimental strategy frequently used to study the modulation of brain activity in response to emotionally relevant stimuli is the presentation of images with emotional valence that can be positive, negative, or neutral, and with differing levels of arousal within each hedonic category, obtained through the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005). While such studies have not assessed vagal activity, some have been able to characterize the motivational aspects of attention responses, at both the peripheral and brain levels (e.g. ERPs). These studies are particularly relevant to the search for correlates between peripheral and central parameters in relation to how subjects react to psychophysiological, adaptively relevant information.

At the peripheral level, exposure to emotional stimuli is reflected through specific cardiac response patterns, as well as facial muscle activity and electrical conductance of the skin (Bradley et al., 2001a, 2001b; Lang et al., 1998a). At the brain level, it has been reported that emotional stimuli modulate early ERP latency components (e.g., P1), medial ERP latency components (N2; P2; and early posterior negativity, EPN) and late ones (P300; late positive potential, LPP; and slow wave, SW). This modulation depends on the nature of the task and its methodological implementation. Specifically, emotional valence seems to predominantly modulate early components situated between 100 and 350 ms after the presentation of stimuli, while arousal appears to influence a later time window (200–1000 ms after stimulus presentation; Olofsson, Nordin, Sequeira, & Polich, 2008). In relation to the topographic distribution of ERPs on the scalp, a greater positive modulation on the posterior region is seen lateralized to the right hemisphere, albeit inconsistently (Junghöfer, Bradley, Elbert, & Lang, 1995; Schupp, Junghöfer, Weike, & Hamm, 2003; Schupp et al., 2006).

The present research study stems from the fact that little attention has been given to the relationship between vagal tone and brain processing. Given the individual differences in emotional vagal tone across the normal adult population, expanding the knowledge

about this relationship would be instrumental in elucidating the way in which people process relevant, emotionally adaptive information at the central level. To this end, we propose to evaluate the brain activity of subjects who present either high or low vagal tone, by employing an experimental paradigm with emotional images portraying human social situations associated with positive, negative, and neutral valence. This will allow us to test whether vagal tone influences variations in ERPs induced by complex stimuli that are adaptively relevant.

One advantage of using the previously described affective task is that it offers a framework from which to characterize the subject's brain response in a way that is comparable to previous evidence. Another advantage is the fact that ERPs have a high temporal resolution in the processing of the presented stimuli, which ensures a substantial degree of accuracy in the time window within which processing differences by group may occur. If discrepancies in the brain processing between the high and low vagal tone groups are produced at early stages of the information codifying, it is also predictable to find differences in the modulation of the sign in the early components of the ERPs. Otherwise, if differences occur at the later stage of information-processing, then variations in the amplitude of the sign will be reflected in the later components of the ERPs. Alternatively, it is possible that no differences at the early, middle or late components of the ERPs exist between the high and low vagal tone levels.

## MATERIALS AND METHODS

### Participants

A total of 32 undergraduate students were recruited for the study. Data from four of them were discarded due to artifacts in electrophysiological recording. The final sample included 28 students (57% females) ranging between 18 and 27 years of age, with a mean of 21.56 years ( $SD = 2.56$ ). Individuals were screened to exclude any cardiac (e.g., arrhythmia) or respiratory (e.g., asthma alterations) or drug consumption that might affect any of the target variables. Visual acuity and handedness were controlled, including only normal or corrected-to-normal individuals and right-handed participants (selected with the Oldfield Inventory; Oldfield, 1971). All participants read and signed an informed consent approved by the institutional ethical committee and in agreement with the Declaration of Helsinki of 1975 before the study.

## Group selection

Vagal tone was operationalized as RSA. In order to obtain this measure the electrocardiograms (ECGs) of participants were recorded under resting conditions while asking the subjects to remain comfortably seated for 5 min. The ECG was registered continuously and digitized online by the Biopac amplifier MP100 and AcqKnowledge Software, using a Lead II configuration for electrode placement. Sample frequency was set at 250 Hz. Afterwards the heart period (HP) was quantified offline from the ECG recording as the time in milliseconds between consecutive R-wave peaks. Results were analyzed with MxEdit software (Porges, 1985) that computes the HP series for each epoch of 30 s, which is then graphically displayed and manually edited in order to remove artifacts. Then the HP series are sampled in time, to obtain an instant estimation of it on equally spaced intervals of 500 ms, which allows further filtering by means of conventional techniques. Sources of nonstationary tendencies (aperiodicity and slow periodicity) are modeled and removed from the HP by means of a 21-point moving polynomial. Resulting HP stationary series are filtered with a bandpass filter (0.12–0.40 Hz), in order to exclude variance out of the range of respiratory frequency that is typical in adults (e.g., 7–24 respirations/min). Finally, the variance of the filtered data is calculated and RSA is estimated by the natural logarithm of the variance, to normalize its distribution, varying the RSA values between 0 and 10, approximately (Spalding, Jeffers, Porges, & Hatfield, 2000).

According to the method proposed by Porges (1985), RSA was calculated every 30 s for the resting period. RSA scores for each subject (min. = 3.58, max. = 8.88, mdn = 5.93) were considered in order to divide the sample into a high (HVT,  $n = 13$ , 69% females, mean age = 21.46,  $DE = 2.79$ ) and a low vagal tone group (LVT,  $n = 15$ , 47% females, mean age = 21.64,  $DE = 2.44$ ). After the conformation of the HVT and LVT groups, age and gender differences were analyzed in order to control the matching between groups for those variables. No age,  $t(25) = .18$ , *ns*, or gender differences,  $\chi^2(1) = 1.45$ , *ns*, were found. Finally, mean RSA values for the high and low vagal tone groups were  $M = 7.18$  ( $SD = 0.74$ ) and  $M = 5.06$  ( $SD = 0.74$ ), respectively.

## Stimulus validation

The stimuli presented in the affective picture processing task were obtained from the IAPS (Lang et al., 2005) and were initially selected according to their

arousal score (1 = low; 9 = high), and valence (1 = negative; 9 = positive) following the IAPS's norms with a pilot sample of students (see below). The images of the IAPS have been previously standardized on US samples, showing test–retest reliability coefficients and internal consistencies of  $r = .99$ ,  $\alpha = .94$  in valence, and of  $r = .97$  and  $\alpha = .93$  in arousal (Lang et al., 2005). From the standardized scores, a total of 187 images representing people in different social situations were selected. Some examples of the selected images are, for the positive category: children playing, couples in romantic situations; for the neutral category: people walking on the street, inside a house or standing up; and for the negative category: people crying, situations of violence and obfuscation, drugs and alcohol consumption.

Following the original standardization protocol (Lang et al., 2005) a validation sample of 135 volunteers (mean age = 20.13,  $SD = 2.29$ ) rated the stimuli in valence and arousal. Finally, 20 images on each affective category were intentionally obtained from the above described contents (valence scores for positive  $M = 7.37$ ,  $SD = 0.40$ ; negative  $M = 2.66$ ,  $SD = 0.44$ ; neutral  $M = 4.64$ ,  $SD = 0.44$ , and arousal scores for positive  $M = 5.76$ ,  $SD = 0.48$ ; negative  $M = 6.02$ ,  $SD = 0.56$ , neutral  $M = 4.29$ ,  $SD = 0.51$ ).<sup>1</sup>

In order to calibrate valence and arousal values between different categories of stimuli, it was expected that all categories differed significantly from the others, and that positive and negative categories were similar in arousal values but different with respect to the neutral one. Statistical analysis revealed significant differences between all categories in valence,  $F(2, 133) = 168.97$ ;  $p = .001$ , and arousal differences were also found between categories,  $F(2, 133) = 140.818$ ,  $p = .001$ , with both positive and negative categories differing from neutral,  $p$  values = .001, even though both showed similar arousal values with no significant differences between the two of them.

## Experimental design and procedure

EEGs were assessed in both groups (HVT and LVT) while subjects completed a processing task of affective

<sup>1</sup> IAPS picture numbers for the pleasant category: 2070, 2071, 2152, 2208, 2209, 2216, 2311, 2340, 2345, 2530, 2550, 4574, 4599, 4607, 4623, 4660, 4689, 7325, 8490, 8496; neutral category: 2104, 2190, 2200, 2210, 2214, 2280, 2381, 2410, 2440, 2441, 2480, 2493, 2512, 2520, 2570, 2579, 2600, 2749, 2850, 9210; unpleasant category: 2120, 2130, 2141, 2205, 2312, 2399, 2490, 2691, 2700, 2710, 2750, 2753, 2900, 3280, 4621, 6562, 6825, 9041, 9220, 9520.

images. Following the precedent of previous research protocols (e.g., Schupp et al., 2000), the 60 images were presented for 1500 ms, and each trial was preceded by a signaling image with a fixation point at the center of the screen at 200 ms. The interval between stimuli was randomized, ranging from 800 to 1500 ms. Images were presented four times each, with a total of 240 trials, no stimulus being presented more than twice for the same affective valence on each sequence. The total set of 60 images appeared completely prior to the new sequence presenting them in a different order.

Participants were instructed to carefully observe each image, avoiding movements that could interfere with the quality of the assessment (e.g., eye-blinks, and eye or head movements). Then they had to rate the valence of the image (positive, neutral, or negative) once it disappeared from the screen, using three keys on a response keyboard placed in front of the participant. The maximum response time was 2000 ms, during a period in which the screen went black awaiting the participant's response. The affective task was run on a computer monitor situated approximately 80 cm away from the participant.

Once the EEG assessment was finished, participants were shown each image again, in order to evaluate them on a behavioral task according to the valence and arousal dimensions. For this purpose, the paper and pencil version of the Self-Assessment Manikin (SAM; Lang, 1980) was used. This is a language-free scale that evaluates valence and arousal by presenting graphical illustrations that represent nine varying levels for each of these dimensions. The affective scores of the SAM are highly correlated with longer instruments that include language, such as the semantic difference scale by Bradley & Lang (1994).

## EEG acquisition and processing

Signals were recorded online using a GES300, 129-channel system with HydroCel Sensors from Electrical Geodesic, Inc. with a DC coupling amplifier, 24-bit A/D converter, 200 M $\Omega$  input impedance, 0.7  $\mu$ V RMS/1.4  $\mu$ V pp noise, and NetStation<sup>TM</sup> software. Analog filters were 0.1 and 100 Hz. A digital band pass filter between 0.5 and 30 Hz was applied offline to remove unwanted frequency components. Signals were sampled at 500 Hz and later resampled at 250 Hz to reduce the data size. The reference was set by default to vertex, but then was re-referenced offline to average electrodes. Two bipolar derivations were designed to monitor vertical and horizontal ocular movements (electrooculographs).

Stimulus-locked epochs were selected from the continuous data, beginning 200 ms prior to stimulus onset. All epochs with eye movement contamination were removed from further analysis, using an automatic (Gratton, Coles, & Donchin, 1983) method for removing eye-blink artifacts and visual procedures. Artifact-free epochs were averaged to obtain the ERPs. The analysis was done separately based on group (HVT and LVT), category (positive, negative, and neutral) and regions of interest (ROIs). ERP waveforms were averaged separately for each experimental condition. The EEGLAB Matlab toolbox and T-Besp software were used for EEG offline processing and analysis.

## Data analysis

A mixed repeated-measures ANOVA was conducted for the behavioral data from obtained offline recordings, with a between-subjects factor (Group: HVT and LVT) and a within-subject factor (Category: positive, neutral, negative). ROIs were used to represent and analyze the scalp topography of the ERP components as recommended for dense arrays, in order to avoid loss of statistical power (Oken & Chiappa, 1986). The ERP analysis was carried out based on the ROIs chosen by visually checking each component. Each ROI comprised three adjacent electrode sites centered around the maxima: P1 (right: 96, 90, 83; left: 58, 65, 70); EPN (right: 96, 90, 83; left: 58, 65, 70); and LPP (anterior: 11, 16, 15; central: 129, 6, 55; posterior: 81, 72, 75). Although the figures show the ERP grand averages for each group, all statistical calculations were done using each participant's individual data. ERP amplitudes were quantified as the peak negative or positive deflection occurring within a 115–125 ms temporal window (P1); 220–290 ms temporal window (EPN) and 350–500 ms temporal window (LPP). For each component, a mixed repeated-measures ANOVA with one between-subjects factor (Group: HVT and LVT) and two within-subject factors (Category: positive, neutral, negative) and ROI (left and right P1; left and right EPN; and finally, anterior, central and posterior LPP) were performed. Univariate comparisons were done whenever necessary. Results were corrected with the Greenhouse-Geisser and Bonferroni methods to adjust the unvaried output of the repeated-measures ANOVA for violations of the compound symmetry assumption. All post-hoc comparisons for both the behavioral and electrophysiological data were performed with Tukey's HSD tests.

## RESULTS

## ERPs

## Behavioral data

## Valence effects

A main effect for Category was observed,  $F(2, 25) = 505.07, p = .001$ . Post-hoc analysis ( $MS = 0.26, df = 75.26$ ) revealed that positive ratings ( $M = 6.47, SD = 1.00$ ) were significantly higher than neutral ( $M = 4.54, SD = 0.44$ ), and neutral scores were significantly higher than negative ( $M = 2.09, SD = 0.51$ ) scores,  $p$  values = .001. No significant effects for Group,  $F(1, 26) = 1.32, ns$ , or Category  $\times$  Group interaction  $F(2, 75) = 0.48, ns$ , were found.

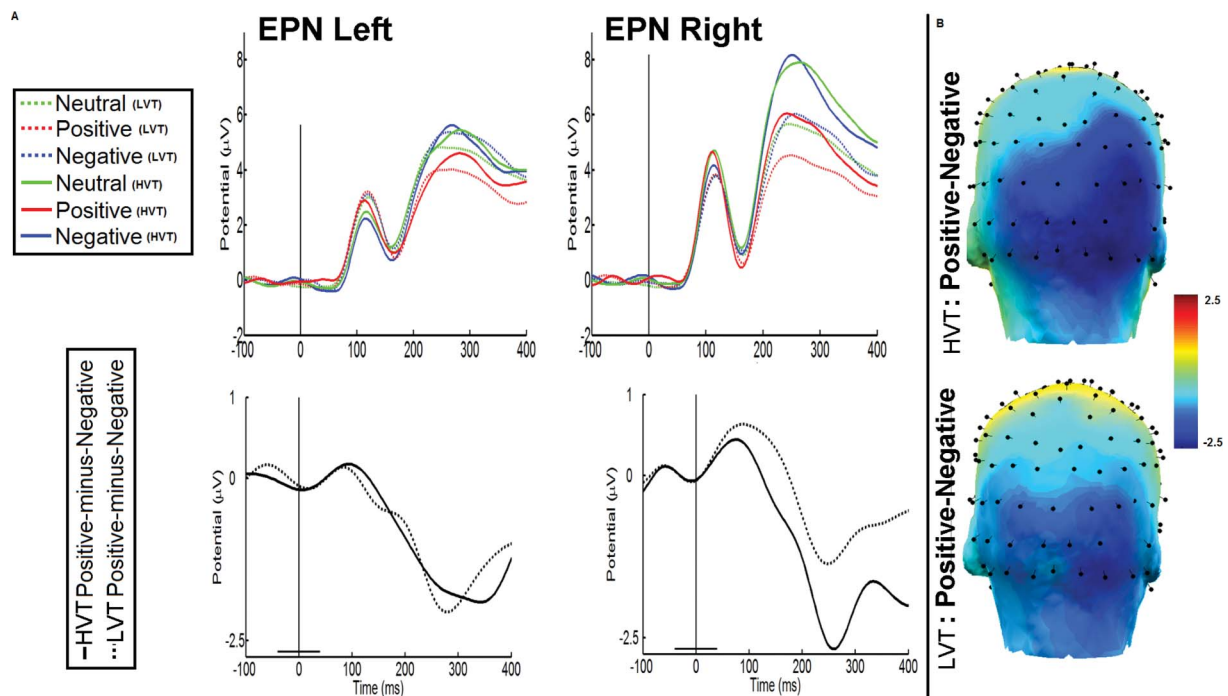
## Arousal effects

Similar to valence results, a significant Category effect was found,  $F(2, 25) = 34.67, p = .001$ . The post-hoc analysis ( $MS = 1.37, df = 77.20$ ) showed that both negative ( $M = 6.47, SD = 1.00$ ) and positive ( $M = 5.18, SD = 1.44$ ) categories significantly differed from neutral ( $M = 4.28, SD = 1.00$ ),  $p$  values = .001 and .01 respectively, but that there was no difference between affective categories,  $ns$ . No main effect for Group,  $F(1, 26) = 0.34, ns$ , or Category  $\times$  Group interaction,  $F(2, 25) = 0.87, ns$ , was observed.

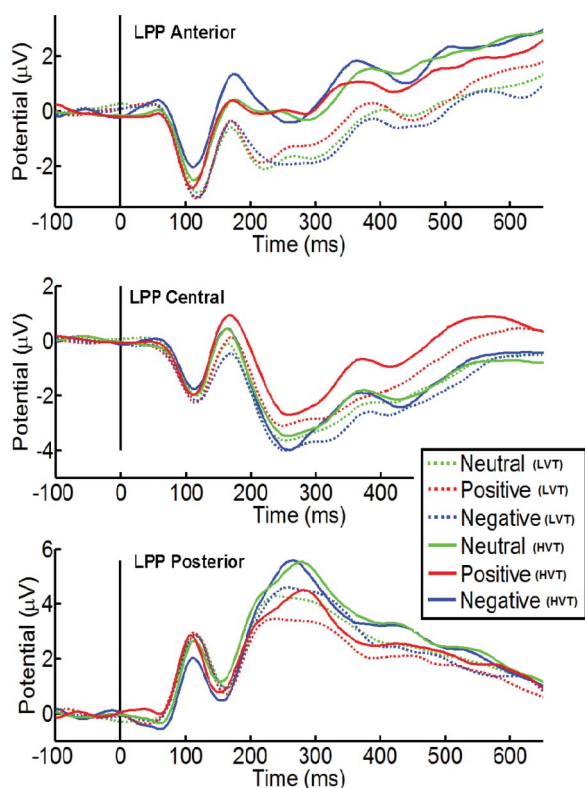
**PI.** A main effect on ROI's variables was observed  $F(1, 26) = 13.69, p = .001$ , in which the right ROI ( $M = 3.02, SD = 0.39$ ), presented higher amplitudes than the left ROI ( $M = 4.46, SD = 0.56$ ; see Figure 1B). There was also a main effect of Category,  $F(2, 52) = 3.49, p = .037$ . Post-hoc comparisons ( $MS = 0.42192, df = 52.00$ ) showed that only the negative category ( $M = 3.56, SD = 0.41$ ) was significantly distinguishable from the positive ( $M = 3.88, SD = 0.49, p = .044$ ). Neither main effect nor interaction of the Group variable was observed.

**EPN.** The analysis of this posterior component showed a main effect of Category,  $F(2, 52) = 34.11, p = .001$ . The negative category presented a greater amplitude ( $M = 5.95, SD = 0.44$ ) followed closely by the neutral ( $M = 5.65, SD = 0.38$ ) and finally by the positive category, with the lowest scores ( $M = 4.52, SD = 0.41$ ). A main effect of ROI was also observed,  $F(1, 26) = 27.26, p = .001$ . Greater amplitude values were obtained on the right scalp ( $M = 6.19, SD = 0.48$ ) compared to the left scalp ( $M = 4.56, SD = 0.37$ ; see Figure 1).

Regarding the interactions, there was a significant interaction between Group  $\times$  ROI,  $F(1, 26) = 5.53, p = .026$ . The HVT group presented greater lateralization difference (right:  $M = 7.01, SD = 0.70$ ; left:  $M = 4.64,$



**Figure 1.** Early posterior negativity (EPN) effects. Left and right ROI waveforms (top) and difference waveforms (bottom, positive – negative subtraction); to the right are topographic maps showing the voltage difference (positive – negative) over the scalp for each group of participants (HVT and LVT Groups).



**Figure 2.** Triple interaction between the Regions of interest, Group of participants and Category. The amplitude graph shows that the greater differences between the groups of participants and category type occurred mostly in the right hemisphere.

$SD = 0.54$ ) than the LVT group (right:  $M = 5.37$ ,  $SD = 0.65$ ; left:  $M = 4.48$ ,  $SD = 0.51$ ). Post-hoc comparisons ( $MS = 5.17$ ,  $df = 33.76$ ) confirmed that only in the HVT group was the lateralization effect significantly different,  $p = .001$ .

There was also a triple ROI  $\times$  Category  $\times$  Group interaction,  $F(2, 52) = 3.86$ ,  $p = .027$ . The greater differences between categories and groups of participants were observed on the right region (see Figure 2).

To compare differences in categories between groups, a restricted ANOVA was conducted on the ROI. Besides a main effect of Category,  $F(2, 52) = 20.93$ ,  $p = .001$ , an interaction of Category  $\times$  Group,  $F(2, 52) = 3.19$ ,  $p = .049$  was observed. Post-hoc comparisons ( $MS = 7.23$ ,  $df = 32.73$ ) showed that only in the HVT group could the positive category ( $M = 5.49$ ,  $SD = 0.79$ ) be distinguished from the negative ( $M = 7.94$ ,  $SD = 0.77$ ,  $p = .001$ ) and neutral categories ( $M = 7.60$ ,  $SD = 0.67$ ,  $p = .001$ ).

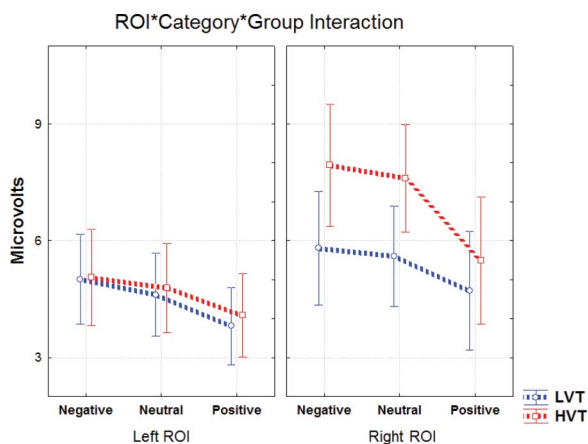
*Difference waveforms analysis (EPN).* Additionally, an analysis of the wave differences was conducted. Given that the above analysis showed that the largest differences occurred between the negative and positive

categories, a subtraction of these (positive – negative) was conducted, in order to compare the discrimination of the emotional content through the wide gap between the opposite valences in the two groups of participants. To compare these results, an ANOVA of the different waveforms (positive – negative) was used on a design with a within-subjects factor (ROI) and a between-subjects factor (Group).

The ROI variable was significant,  $F(1, 26) = 4.95$ ,  $p = .034$ , demonstrating greater amplitudes in the right region ( $M = -1.77$ ,  $SD = 0.28$ ), compared to the left ( $M = -1.09$ ,  $SD = 0.19$ ). Although the Group factor was not significant itself, an interaction of ROI  $\times$  Group,  $F(1, 26) = 6.63$ ,  $p = .016$  was observed, indicating that, in the right region, differences between positive and negative categories were greater in the HVT group.

Because of this last interaction, a one-way ANOVA (difference in waveform  $\times$  Group) was performed, aiming to compare the differences of positive – negative in the right region, where the main differences between groups showed up. This difference was significant,  $F(1, 26) = 6.13$ ,  $p = .020$ , showing that the HVT group had a greater difference between negative and positive categories ( $M = -2.45$ ,  $SD = 0.40$ ) than the LVT group ( $M = -1.10$ ,  $SD = 0.37$ ).

*LPP.* There was a Group effect,  $F(1, 26) = 18.57$ ,  $p = .001$ , with the LTV group ( $M = -0.31$ ,  $SD = 0.30$ ) obtaining lower amplitudes compared to the HVT group ( $M = 0.96$ ,  $SD = 0.22$ ). A main ROI effect was observed,  $F(2, 52) = 17.37$ ,  $p = .001$ , showing different values for the frontal ( $M = 0.61$ ,  $SD = 0.38$ ), central ( $M = -1.71$ ,  $SD = 0.41$ ) and occipital ( $M = 2.08$ ,  $SD = 0.50$ ) LPP (see Figure 3).



**Figure 3.** LPP component distribution on the midline and ERPs corresponding to the LPP for each category and each group of participants.



Also, a Category effect was evident,  $F(2, 52) = 3.40, p = .040$ . Post-hoc comparisons ( $MS = 0.73869, df = 52.00$ ) revealed that only the negative category ( $M = 0.20, SD = 0.23$ ) differed from the positive category ( $M = 0.53, SD = 0.23, p = .040$ ), but not from the neutral category ( $M = 0.25, SD = 0.24$ ).

Finally, there was an ROI  $\times$  Category interaction,  $F(4, 104) = 3.50, p = .010$ . Post-hoc comparisons ( $MS = 0.79, df = 104.00$ ) showed that in the central LPP, the positive category ( $M = -1.12, SD = 0.34$ ) was significantly different from the negative ( $M = -2.04, SD = 0.34, p = .004$ ) and neutral categories ( $M = -1.97, SD = 0.34, p = .013$ ).

## DISCUSSION

This is the first study to inquire into the relationship between vagal tone level and brain affective information-processing in an ERP task in an adult population. Our results indicate that there are differences between the ways in which high and low vagal tone groups process emotional information at different ERP components, suggesting that vagal tone level is accompanied by particular strategies for information-processing at middle and late latencies. In the EPN, we observed a higher discrimination between emotional categories in the right hemisphere for the HVT group; however, both groups exhibited a lateralization effect. Also, higher LPP modulation was evident in the HVT group, regardless of the type of category. Although the P1 component showed a valence effect, there was no evidence for a group difference. In the behavioral task, no differences could be observed between the HVT and LVT groups, showing that affective variations in picture processing among groups can be more readily detected at an electrophysiological level.

The P1 is an early visual component that has been previously described at latencies similar to those observed in this study at occipito-temporal sites. It is modulated by face (Holmes, Vuilleumier, & Eimer, 2003) and body (Van Heijnsbergen, Meeren, Grèzes, & de Gelder, 2007) emotional content, and it possibly reflects an early visual mechanism for rapid emotion detection based on rough visual cues of the body and face (Van Heijnsbergen et al., 2007). These cues are consistent with the kind of stimuli (i.e., human situations) used in the present study, although these are to some extent more complex than the rough stimuli used in previous studies by other authors. Also, laterality effects observed in the right hemisphere have been previously described (Eger, Jedynak, Iwaki, & Skrandies, 2003; Van Heijnsbergen et al., 2007).

The EPN is a middle latency component that has been associated with early and late stages of information-processing, selectively for each affective category (Schupp et al., 2004a, 2004b). Di Russo, Taddei, Apnile, and Spinelli (2006) suggested that information-processing within a 200–300 ms window would reflect early discrimination and response selection processes. Also, Schupp et al. (2004a) have stated that processing indexed by the EPN is modulated by perceptual features that facilitate further evaluation of arousing stimuli. In the present study, the negative category showed higher amplitude in the EPN, followed by neutral and positive pictures.

Although a considerable number of studies have found a similar modulation, differing from neutral, for both emotional (pleasant, unpleasant) categories of pictures, an increasing number of studies have reported a differential modulation for the positive stimuli when compared to both neutral and negative in an early time window, such as the EPN. For example, Cuthbert, Schupp, Bradley, Birbaumer, and Lang (2000) observed that, within the time range of the EPN (200–300 ms), responses to positive pictures differed significantly from responses to both neutral and negative ones; Keil et al. (2002) reported a similar effect in the 120–150 ms time window and notably also a lateralization pattern in the late P3 window, with enhanced positivity for pleasant content. De Cesarei & Codispoti (2006) found a larger positivity in the early 150–300 ms window for both negative and neutral pictures compared to positive; and finally, Pastor et al. (2008) observed, in the same time window (150–300 ms), that viewing of pleasant pictures resulted in lower amplitude values over occipital sites compared to neutral and negative pictures. The results observed in our study are therefore consistent with this body of evidence, as the positive category differed significantly from both neutral and negative in our results.

Lateralization effects are in line with the literature (De Cesarei & Codispoti, 2006; Junghöfer et al., 2001). More interesting for the scope of this study are differences according to vagal tone in the EPN at the right hemisphere, pointing to a higher affective discrimination for the HVT in relation to LVT. Moreover, differences in waveforms (positive – negative) further confirm this finding, adding support to the hypothesis that a more accurate discrimination between affective categories exists for the HVT group when compared to the LVT group, at early categorization stages of processing.

Consistently with lateralization findings, some brain imaging studies have found a higher activation of right-sided structures within associative visual cortices in the processing of affective salient stimuli, when compared to left-sided activation (Bradley et al.,

2003; Lang et al., 1998; Sabatinelli, Lang, Keil, & Bradley, 2006). In light of our results, this evidence suggests that differences in interhemispheric activity between high and low vagal tone groups may in part be due to variations in the engagement degree of visual cortices in face of high relevant affective information, a process likely driven by interactions between more anterior regions of the brain (e.g., the amygdala; Davis & Whalen, 2001) and visual areas. It can be added to this hypothesis that the higher recruitment of right occipital areas in the HVT group might facilitate the tuning of perceptual areas, thus allowing for a more accurate discrimination between positive and negative emotional stimuli, when compared to lower levels of vagal tone. In sum, the lateralization effect suggests a more accurate early modulation of EPN for the HVT that is possible driven by a higher participation of right visual cortices, which is specific for valence content and may reflect early encoding facilitated by emotional content of visual stimuli (Schupp et al., 2003).

The LPP is a late component of the ERP that has been well replicated in several studies (Cacioppo, Crites, Gardner & Berntson, 1994; Crites, Cacioppo, Gardner & Berntson, 1995; Schupp et al., 2000, 2004a, 2004b). It peaks typically around 300–400 ms after the stimulus at medial sites, and is modulated by affective content. Differences between the HVT and LVT groups are generalized in this component, in spite of the kind of hedonic category. The LPP has been theoretically interpreted as a mandatory process of initial semantic categorization, and is indicative of the reflexive activation of the motivational neural networks that modulate emotional engagement (Pastor et al., 2008). Furthermore, some evidence has shown that this component (together with other late components of the ERP, such as P300 and the SW) may be involved in memory formation (Palomba, Angrilli, & Mini, 1997). The group effects observed in the present study show differential processing for all categories, suggesting that the HVT group had a greater activation of the neural networks that underlie the higher-order stages of information-processing.

The theoretical framework that accounts for the differential processing of affective information claims that the affect system has evolved from a bidimensional organization, to being responsible for motivated behavior (Cacioppo, Gardner, & Berntson, 1999; Lang, 1995). This can be further divided into two motivational systems: an aversive system that facilitates defensive and protective behaviors and an appetitive system responsible for the approach to pleasant stimuli when safety is perceived. The kind of task used in the present study follows the line of experimental paradigms that assume that unpleasant

and pleasant categories of pictures differentially activate the aversive or appetitive motivational systems, respectively. This study is the first to account for differences in the way that relevant affective stimuli are processed differently by the brain, at diverse stages of information-processing, according to vagal tone level. Specifically, the early discrimination stages indexed by the EPN component of the ERP show particular differences between the HVT and LVT groups for affective categories. Thus, it can be stated that there is an adaptive value of more accurate stimuli discrimination linked to differential engagement of the motivational systems by affective stimuli for the HVT group, in comparison to the LVT group. In fact, the organization of successful behavioral strategies depends on the efficient extraction of critical information from the environment (Öhman, Flykt & Lundqvist, 2000).

The notion that vagal tone may be related to differences in the way the brain extracts relevant information from the environment is concordant with research on vagal tone and diverse affective variables (see Beauchaine, 2001). At a theoretical level, the polyvagal theory of Porges (2003a, 2003b) emphasizes the role of evolution in the organization of the nervous system—particularly the vagus—and social behavior, accounting for three different evolutionary levels of the autonomic nervous system: (1) a myelinated vagus linked to social communication, self-soothing, and calming; (2) a sympathetic-adrenal system responsible for active avoidance by mobilization; and (3) an unmyelinated vagus responsible for immobilization, passive avoidance, and death feigning. The first of these autonomic evolved levels is well developed in mammals and particularly in primates, fostering what has been called the “social engagement system.” One prediction of the polyvagal theory is that individuals who exhibit higher cardiovagal tone levels would also express more social adaptive behaviors, and the opposite would be accompanied by more difficulties in affective and social regulation. If the differences seen in this study in the way HVT and LVT brains extract and process information are taken into account, the adaptive value of a high vagal function, as the polyvagal theory states, can be supported.

Possible neural sources that underlie the emotional modulation of the ERPs are suggested by previous imagery studies. On one hand, an increased activity in visual cortices occurs when viewing pleasant and unpleasant stimuli when compared to neutral ones (Bradley et al., 2003; Lane, Reiman, Ahern, & Schwartz, 1997; Lang et al., 1998a, 1998b; Sabatinelli et al., 2006), which has been confirmed with ERP modulations for the EPN and LPP components (Schupp et al., 2003). As well, several studies have

shown that emotional content triggers specific responses in the amygdala, which in turn activates sensory cortical areas and therefore allows for a more accurate perceptual processing when affective stimuli are presented (Armony & Dolan 2002; Lang et al., 1998a; Morris et al., 1998). On the other hand, positive correlations have been observed among parasympathetic cardiac HF domain measures and the activity of different limbic-related structures, such as the insular and ventromedial prefrontal cortex (Gianaros, Van Der Veen, & Jennings, 2004) or the anterior and ventral cingulate cortex (Matthews, Paulus, Simmons, Nelesen & Dimsdale, 2004; O'Connor, Gündel, McRae, & Lane, 2007) in cognitive tasks, and in the medial prefrontal cortex, the caudate nucleus, the periaqueductal gray and the mid-insular area in response to emotional stimuli (Lane et al., 2009). Taking this evidence together with lateralization effects, it can be hypothesized that limbic and cortical structures participating in functional networks that are activated by emotional stimuli may be differentially recruited in the high and low vagal tone conditions (see also Ibañez, Gleichgerrcht, & Manes, in press; Thayer & Lane, 2000).

Since the two groups were not significantly different in terms of age or gender, and all participants belonged to a similar educational level (undergraduate students), differences cannot be explained in terms of socio-demographic variability between groups. In fact, groups were equivalent in relevant variables that affect ERPs, except for vagal tone level, excluding the possibility of ERP differences between groups secondary to other variables.

The goal of our study was to assess the participation of the body and peripheral organs (measured by vagal tone) in relation to central processing (measured by ERPs). Our report is the first to show a peripheral–central relationship occurring in response to affective social information in adults. This is a new branch of research and our study does have some limitations, to be addressed in future studies. Although numerous studies on IAPS/ERPs have already been performed, showing an occipito-temporal EPN and centro-parietal LPP, those components are altered by several aspects of the design such as stimulus features (i.e., complexity, size, color, frequency), gender of participants, and type of task (Cano, Class, & Polich, 2009; Codispoti, Ferrari, De Cesarei, & Cardinale, 2006; Delplanque, N'diaye, Scherer, & Grandjean, 2007; Lang et al., 1998b; Rozenkrants, Olofsson, & Polich, 2008; Rozenkrants & Polich, 2008). Paradigm-dependent effects must be specifically addressed in future studies of vagal tone group differences.

In the same line, although pleasant and unpleasant pictures are usually associated with lower (more negative) occipito-temporal positivity compared to neutral pictures (Codispoti, Ferrari & Bradley, 2007; Keil

et al., 2002; Schupp et al., 2004a), the reported effects are not always in the same direction. Therefore, specific effects (task or stimuli-dependent) on early components, EPN and LPP relation to valence and the influence of arousal should be studied in further vagal tone research. Regarding early components (e.g., P1), the controversies found throughout the literature result from differences on task and recording methodology. When studies use dense arrays and short time windows for stimulus presentation (i.e., 200 ms), P1 effects are present (Carretié, Mercado, Hinojosa, Martin-Loeches, & Sotillo, 2004; Junghöfer et al., 2001; Schupp et al., 2003). Dense arrays allow for the consideration of several different possible ROIs in order to better detect valence category differences. In addition, fast presentation times enhance early components generation. Most classic studies of IAPS used stimulus durations longer than 500 ms, reducing the magnitude of early effects, but when time presentation is around 120–300 ms, early effects are reliable (Schupp et al., 2003, 2004a, 2006).

In our results, a weakness in the LPP category modulation can be observed, since stimuli selected were moderate in arousal. It is well known that the LPP is more sensitive to arousal than to emotional content. Arousal is the primary determinant of LPP, and valence minimally influences LPP amplitude (Cano et al., 2009; Rozenkrants et al., 2008; Rozenkrants & Polich, 2008), which is consistent with our LPP results showing a small emotional effect of valence. As presented in our data, valence effects are typically observed for early and EPN (100–300 ms), and arousal effects are observed for later (300–800 ms) components, with only a small effect of valence category in this time window (Codispoti et al., 2007; Olofsson et al., 2008; Rozenkrants & Polich, 2008). Because our explicit goal was to look at the valence of emotional effects and not arousal effects, we chose stimuli that did not possess high arousal values. Future studies may address other effects, such as arousal, presentation time or task-dependent effects and their possible interaction with emotional content in the differences between LVT and HVT groups in the P1, EPN, and LPP time windows. These studies will be important to further elucidate the nature of stimuli response, as recent studies have started to describe the distinct underlying brain systems that may mediate valence and arousal of affective stimuli differently (Nielen et al., 2009).

The LPP observed in the IAPS tasks has been recently identified as P300 (Cano, Class, & Polich, 2009; Rozenkrants, Olofsson, & Polich, 2008; Rozenkrants & Polich, 2008; see a review in Olofsson et al., 2008). The P300 is now thought to be composed of several processes that reflect attentional and memory-engaged

mechanisms. In particular, the integrated view of P300 as assessed by Polich (2007) can orient future studies of vagal tone differences and ERP/IAPS designs. This view assesses two components (P3a and P3b) with differences in scalp localization (more anterior and more posterior, similar to those obtained in our LPP results) and in function. In this view, P3a originates from stimulus-driven frontal attentional mechanisms during task processing (focal attention), whereas P3b originates from temporal-parietal activity associated with attention and subsequent memory processing (context maintenance). Since there are topographic and functional features related to P300, further studies can test the integrated theory of P300 as a potential background for highlighting the ERPs differences and relating subjacent mechanisms observed in each group-specific pattern with different vagal tone levels.

As an alternative hypothesis, it can be proposed that RSA might influence only the ERPs amplitude (modulator variable) rather than the emotional discrimination process. However, our data seem not to support this notion, since higher amplitude of the ERPs in the HVT group can only be observed in some temporal windows and this effect is not generalized to all components. On one hand, the early P1 component did not show group differences, so an absolute ERP amplitude difference cannot be assumed. On the other, the EPN window does not support the alternative hypothesis either. Although there is a general higher amplitude in this group restricted to right hemisphere, the most relevant finding is actually the higher differentiation of positive and negative stimuli by the HVT group, in the ERP as well as in the difference waveforms (positive – negative). This finding is indicative of a more accurate discrimination between positive and negative categories of stimuli in the HVT group. This effect cannot be accounted for by higher ERP amplitude alone. Finally, the general higher modulation of the LPP in the HVT group is the only result that does not contradict the alternative hypothesis of the RSA as a moderator effect over the ERPs. LPP does not show valence affects but a general group effect. Since the LPP component is mainly sensitive to arousal levels of the stimuli (instead of valence effects, Hurtado, Gonzalez, Haye, Manes, & Ibanez, 2009; Olofsson et al., 2008) it could be the case that higher levels of RSA influence higher levels of arousal in the HVT group, giving rise to the general higher amplitude effect. If that were the case, it would imply a different explanation from the alternative hypothesis. In sum, ERP modulation seems to be differentially modulated according to valence and arousal parameters of the stimuli within each group, rather than being a consequence of a general amplitude effect for

the HVT group. However, future studies should address this topic by implementing precise experimental designs to determine whether specific aspects of emotional information (such as valence or arousal) are influencing different components of the ERPs and how those relate to vagal tone, or whether vagal tone moderates the sensitivity of the ERP to affective stimuli.

Finally, it is important to highlight the fact that HVT and LVT differences in response to stimuli were found only at the electrophysiological level, with no significant group differences observed on the behavioral task, a finding that has been previously reported in IAPS studies (e.g., Hot, Yasuhiko, Mandai, Kobayashi, & Sequeira, 2006). Reporting ERP changes without overt behavioral differences is not a new topic in the ERP literature (Gray et al., 2004; Ibáñez, Haye, González, Hurtado, & Henríquez, 2009; Ibañez, Lopez, & Cornejo, 2006; Ibáñez, Manes, Escobar, Trujillo Andreucci, & Hurtado, 2010; Ibáñez, San Martín, Dufey, Bacquet, & Lopez, 2008a; Ibáñez, San Martín, Hurtado, & López, 2008b; Kotchoubey, 2006), and even more so in psychiatric populations (Guerra et al., 2009). This finding is crucial for several reasons that have direct theoretical and clinical implications. First, it reveals that physiological responses may dictate essential aspects of human social interactions (e.g., the way we react to someone else's behavior) that may not necessarily reach consciousness or explicit behavior. In this sense, the results of this study can be useful in debating specific aspects of behavioral models in social neuroscience (e.g., the somatic marker hypothesis; see Ibáñez et al., 2009). As well, electrophysiological measures of this caliber may contribute to the identification of relevant affective response patterns that may help distinguish the behavioral phenotype of several neuropsychiatric disorders and, ultimately, complement differential diagnosis, which is otherwise established through clinical, functional, and neuropsychological assessment. In addition to its potential contribution to diagnosis, electrophysiological measures like the ones employed in the present study may also help in the design of therapeutic approaches for a wide variety of conditions. For example, patients with chronic fatigue syndrome have been shown to exhibit reduced vagal tone (Sisto et al., 1995), suggesting that interdisciplinary treatment of psychiatric conditions could also focus on the modulation of autonomic functioning as part of comprehensive treatment programs, or even use electrophysiological measures as an indicator of treatment evolution and effectiveness.

One limitation of this study is that only baseline vagal tone was assessed. It would be of great interest to introduce dynamic measures of vagal reactivity,

since it points to behavioral and attentional regulation that facilitates orientation to stimuli (for a discussion see Santucci et al., 2008). ERP technique poses a challenge for simultaneous assessment of both cerebral and physiological activity, as most affective paradigms require briefer periods of stimuli presentation than physiological recordings. Van Hecke et al. (2009) have implemented a design that allows for the joint assessment of both RSA and continuous EEG (although they did not evidence any relationship between the two variables); however, it is important to consider that quantitative EEG and ERPs estimate different aspects of brain activity. Future works should consider the study of baseline vagal tone, vagal reactivity and emotional processing in a single experiment, either implementing a modified ERP design that considers both cerebral and peripheral recording time requirements or exploring other brain activity measures such as quantitative EEG.

In conclusion, this is the first report that inquires into the relationship between vagal tone level and the cerebral response to affective salient information assessed by ERPs. The results show that differences between high and low vagal tone levels are related to differences in the ERPs at middle and late latencies. The HVT group showed a clear differentiation between pleasant and unpleasant categories at the EPN component on the right hemisphere, when compared to the LVT. This would imply that a higher vagal tone is associated with a more accurate strategy to encode and discriminate affective relevant information in relation to a lower vagal tone, which may foster further processing at higher order levels (e.g., of semantic categorization or memory storage), as the LPP differences between groups suggest. Future replication is necessary to assess the stability of these findings and their generalization.

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## REFERENCES

- Appelhans, B., & Lueken, L. (2006). Heart rate variability as an index of regulated emotional responding. *Review of General Psychology, 10*, 229–240.
- Armony, J., & Dolan, R. (2002). Modulation of spatial attention by fear-conditioned stimuli: An event-related fMRI study. *Neuropsychologia, 40*, 817–826.
- Beauchaine, T. (2001). Vagal tone, development, and Gray's motivational theory: Toward an integrated model of autonomic nervous system functioning in psychopathology. *Development and Psychopathology, 13*, 183–214.
- Bradley, M., & Lang, P. (1994). Measuring emotion: The Self-Assessment Manikin and the semantic differential. *Journal of Behaviour Therapy & Experimental Psychiatry, 25*, 49–59.
- Bradley, M., Codispoti, M., Cuthbert, B., & Lang, P. (2001a). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion, 3*, 276–298.
- Bradley, M., Codispoti, M., Sabatinelli, D., & Lang, P. (2001b). Emotion and motivation: II. Sex differences in picture processing. *Emotion, 1*, 300–319.
- Bradley, M., Sabatinelli, D., Lang, P., Fitzsimmons, J., King, W., & Paramtap, D. (2003). Activation of the visual cortex in motivated attention. *Behavioral Neuroscience, 117*, 369–380.
- Butler, E., Wilhem, F., & Gross, J. (2006). Respiratory sinus arrhythmia, emotion, and emotion regulation during social interaction. *Psychophysiology, 43*, 612–622.
- Cacioppo, J. T., Gardner, W. L., & Berntson, G. G. (1999). The affect system has parallel and integrative processing components: Form follows function. *Journal of Personality and Social Psychology, 76*, 839–855.
- Cacioppo, J., Crites, S., Gardner, W., & Berntson, G. (1994). Bioelectrical echoes from evaluative categorizations: I. A late positive brain potential that varies as a function of trait negativity and extremity. *Journal of Personality and Social Psychology, 67*, 115–125.
- Calkins, S. (1997). Cardiac vagal tone indices of temperamental reactivity and behavioral regulation in young children. *Developmental Psychobiology, 31*, 125–135.
- Calkins, S., Smith, C., Gill, K., & Johnson, M. (1998). Maternal interactive style across contexts: Relations to emotional, behavioral, and physiological regulation during toddlerhood. *Social Development, 7*, 350–369.
- Cano, M., Class, Q., & Polich, J. (2009). Affective valence, stimulus attributes, and P300: Color vs. black/white and normal vs. scrambled images. *International Journal of Psychophysiology, 71*, 17–24.
- Carretié, L., Mercado, F., Hinojosa, J., Martin-Loeches, M., & Sotillo, M. (2004). Valence-related vigilance biases in anxiety studied through event-related potentials. *Journal of Affective Disorders, 78*, 119–130.
- Codispoti, M., Ferrari, V., & Bradley, M. (2007). Repetition and event-related potentials: Distinguishing early and late processes in affective picture perception. *Journal of Cognitive Neuroscience, 19*, 577–586.
- Codispoti, M., Ferrari, V., De Cesarei, A., & Cardinale, R. (2006). Implicit and explicit categorization of natural scenes. *Progress in Brain Research, 156*, 53–65.
- Crites, S., Cacioppo, J., Gardner, W., & Berntson, G. (1995). Bioelectrical echoes from evaluative categorization: II. A late positive brain potential that varies as a function of attitude registration rather than attitude report. *Journal of Personality and Social Psychology, 68*, 997–1013.
- Cuthbert, B., Schupp, H., Bradley, M., Birbaumer, N., & Lang, P. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology, 52*, 95–111.
- Davis, M., & Whalen, P. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry, 6*, 13–34.
- De Cesarei, A., & Codispoti, M. (2006). When does size not matter? Effects of stimulus size on affective modulation. *Psychophysiology, 43*, 207–215.
- Delplanque, S., N'diaye, K., Scherer, K., & Grandjean, D. (2007). Systematic measure of spatial frequencies for IAPS pictures by a discrete wavelet analysis. *Journal of Neuroscience Methods, 165*, 144–150.

- Demaree, H., Robinson, D., Everhart, D., & Schmeichel, B. (2004). Resting RSA is associated with natural and self-regulated responses to negative emotional stimuli. *Brain and Cognition*, *56*, 14–23.
- Di Russo, F., Taddei, F., Apnile, T., & Spinelli, D. (2006). Neural correlates of fast stimulus discrimination and response selection in top-level fencers. *Neuroscience Letters*, *408*, 113–118.
- Doussard-Roosevelt, J., McLenny, B., & Porges, S. (2001). Neonatal cardiac vagal tone and school-age developmental outcome in very low birth weight infants. *Developmental Psychobiology*, *38*, 56–66.
- Doussard-Roosevelt, J., Porges, S., Scalon, J., Alemi, B., & Scalon, K. (1997). Vagal regulation of heart rate in the prediction of developmental outcome for very low birth weight preterm infants. *Child Development*, *68*, 173–186.
- Eckberg, D. (1983). Human sinus arrhythmia as an index of vagal cardiac outflow. *Journal of Applied Physiology*, *54*, 961–966.
- Eger, E., Jedynak, A., Iwaki, T., & Skrandies, W. (2003). Rapid extraction of emotional expression: Evidence from evoked potential fields during brief presentation of face stimuli. *Neuropsychologia*, *41*, 808–817.
- Eslinger, P., Robinson-Long, M., Realmuto, J., Moll, J., Deoliveira-Souza, R., Tovar-Moll, F., et al. (2008). Developmental frontal lobe imaging in moral judgment: Arthur Benton's enduring influence 60 years later. *Journal of Clinical and Experimental Neuropsychology*, *2*, 1–12.
- Fabes, R., & Eisenberg, N. (1997). Regulatory control and adults' stress-related responses to daily life events. *Journal of Personality & Social Psychology*, *73*, 1107–1117.
- Forgas, J. (1995). Mood and judgement: The affect infusion model (AIM). *Psychological Bulletin*, *117*, 39–66.
- Frazier, T., Strauss, M., & Steinhauer, S. (2004). Respiratory sinus arrhythmia as an indicator of emotional response in young adults. *Psychophysiology*, *41*, 75–83.
- Frith, C. & Singer, T. (2008). The role of social cognition in decision making. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *363*, 3875–3886.
- Gianaros, P., Van Der Veen, F., & Jennings, J. (2004). Regional cerebral blood flow correlates with heart period and high-frequency heart period variability during working memory tasks: implications for the cortical and subcortical regulation of cardiac autonomic activity. *Psychophysiology*, *41*, 521–530.
- Gratton, G., Coles, M., & Donchin, E. (1983) A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484.
- Guerra, S., Ibáñez, A., Martín, M., Bobes, M. A., Reyes, A., Mendoza, R., et al. (2009). N400 deficits from semantic matching of pictures in probands and first-degree relatives from multiplex schizophrenia families. *Brain and Cognition*, *70*(2), 221–230.
- Haley, D., & Stansbury, K. (2003). Infant stress and parent responsiveness: Regulation of physiology and behavior during still-face and reunion. *Child Development*, *74*, 1534–1546.
- Harris, T., & Fiske, S. (2007). Social groups that elicit disgust are differentially processed in mPFC. *Social Cognitive and Affective Neuroscience*, *2*, 45–51.
- Hastings, P., Nuselovici, J., Utendale, W., Coutya, J., McShane, K., & Sullivan, C. (2008). Applying the polyvagal theory to children's emotion regulation: Social context, socialization, and adjustment. *Biological Psychology*, *79*, 299–306.
- Holmes, A., Vuilleumier, P., & Eimer, P. (2003). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research*, *16*, 174–184.
- Hot, P., Yasuhiko, S., Mandai, O., Kobayashi, T., & Sequeira, H. (2006). An ERP investigation of emotional processing in European and Japanese individuals. *Brain Research*, *1122*, 171–178.
- Huffman, L., Bryan, Y., del Carmen, R., Pedersen, F., Doussard-Roosevelt, J., & Porges, S. (1998). Infant temperament and cardiac vagal tone: Assessments at twelve weeks of age. *Child Development*, *69*, 624–635.
- Hurtado, E., Gonzalez, R., Haye, A., Manes, F., & Ibanez, A. (2009). Contextual blending of ingroup/outgroup face stimuli and word valence: LPP modulation and convergence of measures. *BMC Neuroscience*, *10*, 69.
- Ibáñez, A., Gleichgercht, E., & Manes, F. (in press). Clinical effects of insular damage in humans. *Brain Structure and Function*.
- Ibáñez, A., Haye, A., González, R., Hurtado, E., & Henríquez, R. (2009). Multi-level analysis of cultural phenomena: The role of ERP approach to prejudice. *The Journal for Theory in Social Behavior*, *39*, 81–110.
- Ibáñez, A., Lopez, V., & Cornejo, C. (2006). ERPs and contextual semantic discrimination: Evidence of degrees of congruency in wakefulness and sleep. *Brain and Language*, *98*(3), 264–275.
- Ibáñez, A., Manes, F., Escobar, J., Trujillo, N., Andreucci, P., & Hurtado, E. (2010). Gesture influences the processing of figurative language in non-native speakers. *Neuroscience Letters*, *471*, 48–52.
- Ibáñez, A., San Martin, R., Dufey, M., Bacquet, S., & Lopez, V. (2008a). ERPs studies of cognitive processing during sleep. *International Journal of Psychology*, *44*, 290–304.
- Ibáñez, A., San Martin, R., Hurtado, E., & López, V. (2008b). ERP studies of cognitive processing during sleep. *International Journal of Psychology*, *44*(4), 290–304. DOI: 10.1080/00207590802194234
- Jabbi, M., & Keysers, C. (2008). Inferior frontal gyrus activity triggers anterior insula response to emotional facial expressions. *Emotion*, *8*, 775–780.
- Junghöfer, M., Bradley, M., Elbert, T., & Lang, P. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, *38*, 175–178.
- Katz, L. (2007). Domestic violence and vagal reactivity to peer provocation. *Biological Psychology*, *74*, 154–164.
- Keil, A., Bradley, M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. (2002) Large-scale neural correlates of affective picture processing. *Psychophysiology*, *39*, 641–649.
- Lane, R., McRae, K., Reiman, E., Chen, K., Ahern, G., & Thayer, J. (2009). Neural correlates of heart rate variability during emotion. *NeuroImage*, *44*, 213–222.
- Lane, R., Reiman, E., Ahern, G., & Schwartz, G. (1997). Neuroanatomical correlates of happiness, sadness, and disgust. *American Journal of Psychiatry*, *154*, 926–933.
- Lang, P. (1980). Behavioral treatment and bio-behavioral assessment: Computer applications. In J. B. Sidowski,

- J. H. Johnson, & T. A. Williams (Eds.), *Technology in mental health care delivery systems* (pp. 119–137). Norwood, NJ: Ablex.
- Lang, P. (1995). The emotion probe. Studies of motivation and attention. *American Psychologist*, *50*, 372–385.
- Lang, P., Bradley, M., & Cuthbert, B. (1998a). Emotion, motivation and anxiety: Brain mechanisms and psychophysiology. *Biological Psychiatry*, *44*, 1248–1263.
- Lang, P., Bradley, M., & Cuthbert, B. (2005). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-6*. Gainesville, FL: University of Florida.
- Lang, P., Bradley, M., Fizzimmons, J. R., Cuthbert, B., Scott, J., Moulder, B., et al. (1998b). Emotional arousal and activation of the visual cortex: An fMRI analysis. *Psychophysiology*, *35*, 199–210.
- Leppänen, P., Guttorm, T., Pihko, E., Takkinen, S., Eklund, K., & Lyytinen, H. (2004). Maturational effects on newborn ERPs measured in the mismatch negativity paradigm. *Experimental Neurology*, *190*, 91–101.
- Levenson, R. (1999). The intrapersonal functions of emotions. *Cognition and Emotion*, *13*, 481–504.
- Light, K., Kothandapani, R., & Allen, M. (1998). Enhanced cardiovascular and chatecholamine responses in women with depressive symptoms. *International Journal of Psychophysiology*, *28*, 157–166.
- Linnemeyer, S., & Porges, S. (1986). Recognition memory and cardiac vagal tone in 6-month-old infants. *Infant Behavior and Development*, *9*, 43–56.
- Lyonfields, J., Borkovec, T., & Thayer, J. (1995). Vagal tone in generalized anxiety disorder and the effect of aversive imagery and worrisome thinking. *Behavior Therapy*, *26*, 257–266.
- Matthews, S., Paulus, M., Simmons, A., Nelesen, R., & Dimsdale, J. (2004). Functional subdivisions within anterior cingulate cortex and their relationship to autonomic nervous system function. *NeuroImage*, *22*, 1151–1156.
- Morris, J., Friston, K., Buchel, C., Frith, C., Young, A., Calder, A., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.
- Movius, H., & Allen, J. (2004). Cardiac vagal tone, defensiveness, and motivational style. *Biological Psychology*, *68*, 147–162.
- Nielen, M., Heslenfeld, D., Heinen, K., Van Strien, J., Witter, M., Jonker, C., et al. (2009). Distinct brain systems underlie the processing of valence and arousal of affective pictures. *Brain and Cognition*, *71*, 387–396.
- O'Connor, M., Guendel, H., McRae, K., & Lane, R. (2007). Baseline vagal tone predicts BOLD response during elicitation of grief. *Neuropsychopharmacology*, *32*, 2184–2189.
- Öhman, A., Flykt, A., & Lundqvist, D. (2000). Unconscious emotion: Evolutionary perspectives, psychophysiological data, and neuropsychological mechanisms. In R. D. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion* (pp. 296–327). New York: Oxford University Press.
- Oken, B., & Chiappa, K. (1986). Statistical issues concerning computerized 48 analysis of brain wave topography. *Annals of Neurology*, *19*, 493–494.
- Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Olofsson, J., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, *77*, 247–265.
- Palomba, D., Angrilli, A., & Mini, A. (1997). Visual evoked potentials, heart rate responses and memory to emotional pictorial stimuli. *International Journal of Psychophysiology*, *27*, 55–67.
- Pastor, M., Bradley, M., Löw, A., Versace, F., Moltó, J., & Lang, P. (2008). Affective picture perception: Emotion, context, and the late positive potential. *Brain Research*, *1198*, 145–151.
- Polich, J. (2007) Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*, 2128–2148.
- Porges, S. (1985). *Method and apparatus for evaluating rhythmic oscillations in aperiodic physiological response systems*. US patent 4.510.944.
- Porges, S. (2003a). The polyvagal theory: Phylogenetic contributions to social behavior. *Physiology & Behavior*, *79*, 503–513.
- Porges, S. (2003b). Social engagement and attachment: A phylogenetic perspective. *Annals of the New York Academy of Sciences*, *1008*, 31–47.
- Porges, S., Doussard-Roosevelt, J., & Maiti, A. K. (1994). Vagal tone and the physiological regulation of emotion. *Monographs of the Society for Research in Child Development*, *59*, 167–186.
- Porter, F., Porges, S., & Marshall, R. (1988). Newborn pain cries and vagal tone: Parallel changes in response to circumcision. *Child Development*, *59*, 495–505.
- Rechlin, T., Weis, M., Spitzer, A., & Kaschka, W. (1994). Are affective disorders associated with alterations of heart rate variability? *Journal of Affective Disorders*, *32*, 271–275.
- Riveros, R., Manes, F., Hurtado, E., Escobar, M., Reyes, M., Cetkovich, M., et al. (2010). Context-sensitive social cognition is impaired in schizophrenic patients and their healthy relatives. *Schizophrenia Research*, *116*, 297–298.
- Rozenkrants, B., Olofsson, J., & Polich, J. (2008) Affective visual event-related potentials: Arousal, valence and repetition effects for normal and distorted pictures. *International Journal of Psychophysiology*, *67*, 114–123.
- Rozenkrants, B., & Polich, J. (2008) Affective ERP processing in a visual oddball task: Arousal, valence, and gender. *Clinical Neurophysiology*, *119*, 2260–2265.
- Sabatinelli, D., Lang, P., Keil, A., & Bradley, M. (2006). Emotional perception: Correlation of functional MRI and event-related potentials. *Cerebral Cortex*, *17*, 1085–1091.
- San Martín, R., Manes, F., Hurtado, E., Isla, P., & Ibáñez, A. (in press). Size and probability of rewards modulate the feedback error-related negativity associated with wins but not losses in a monetarily rewarded gambling task. *NeuroImage*.
- Santucci, A., Silo, J., Shaw, D., Gentzler, A., Fox, N., & Kovacs, M. (2008). Vagal tone and temperament as predictors of emotion regulation strategies in young children. *Developmental Psychology*, *50*, 205–216.
- Schupp, H., Cuthbert, B., Bradley, M., Cacioppo, J., Ito, T., & Lang, P. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology*, *37*, 257–261.
- Schupp, H., Cuthbert, B., Bradley, M., Hillman, Ch., Hamm, A., & Lang, P. (2004b). Brain process in emotional perception: Motivated attention. *Cognition and Emotion*, *18*, 593–611.
- Schupp, H., Junghöfer, M., Weike, A., & Hamm, A. (2003). Emotional facilitation of sensory processing in the visual cortex. *Psychological Science*, *14*, 7–13.

- Schupp, H., Junghöfer, M., Weike, A., & Hamm, A. (2004a). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology*, *41*, 441–449.
- Schupp, H., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A., & Hamm, A. (2006). Stimulus novelty and emotion perception: The near absence of habituation in the visual cortex. *Cognitive Neuroscience and Neuropsychology*, *17*, 1107–1110.
- Sisto, S., Tapp, W., Drastal, S., Bergen, M., DeMasi, I., Cordero, D., et al. (1995). Vagal tone is reduced during paced breathing in patients with the chronic fatigue syndrome. *Clinical Autonomic Research*, *5*, 139–143.
- Spalding, T., Jeffers, L., Porges, S., & Hatfield, B. (2000). Vagal and cardiac reactivity to psychological stressors in trained and untrained men. *Medicine and Science in Sports and Exercise*, *32*, 581–591.
- Thayer, J., & Lane, R. (2000). A model of neurovisceral integration in emotion regulation and dysregulation. *Journal of Affective Disorders*, *61*, 201–216.
- Van Hecke, A., Lebow, J., Bal, E., Lamb, D., Harden, E., Kramer, A., et al. (2009). Electroencephalogram and heart rate regulation to familiar and unfamiliar people in children with autism spectrum disorders. *Child Development*, *80*, 1118–1133.
- Van Heijnsbergen, C., Meeren, H., Grèzes, J., & de Gelder B. (2007). Rapid detection of fear in body expressions, an ERP study. *Brain Research*, *1186*, 233–241.
- Wager, T., Davidson, M., Hughes, B., Lindquist, M., & Ochsner, K. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, *59*, 1037–1050.
- Yeragani, V., Pohl, R., Balon, R., Ramesh, C., Glitz, D., Jung, I., et al. (1991). Heart rate variability in patients with major depression. *Psychiatry Research*, *37*, 35–46.