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

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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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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 $M = 4.29$, $SD = 0.51$).[1]

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

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[1] 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 MΩ input impedance, 0.7 μV RMS/1.4 μV pp noise, and NetStationTM 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

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 × 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 × Group interaction, $F(2, 25) = 0.87$, ns, was observed.

ERPs

P1. 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 × ROI, $F(1, 26) = 5.53$, $p = .026$. The HVT group presented greater lateralization difference (right: $M = 7.01$, $SD = 0.70$; left: $M = 4.64$,
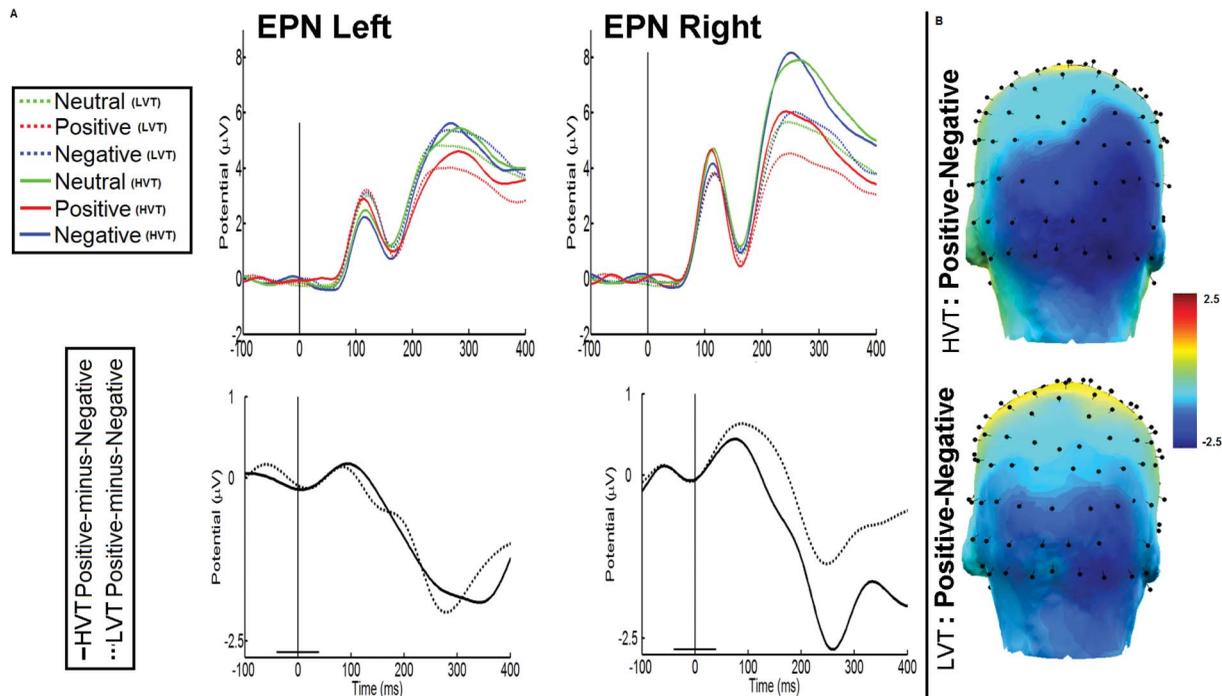
Figure 1. Early posterior negativity (EPN) effects. Left and right ROI waveforms (top) and difference waveforms (bottom, positive – negative subtraction); to the right are topographic maps showing the voltage difference (positive – negative) over the scalp for each group of participants (HVT and LVT Groups).
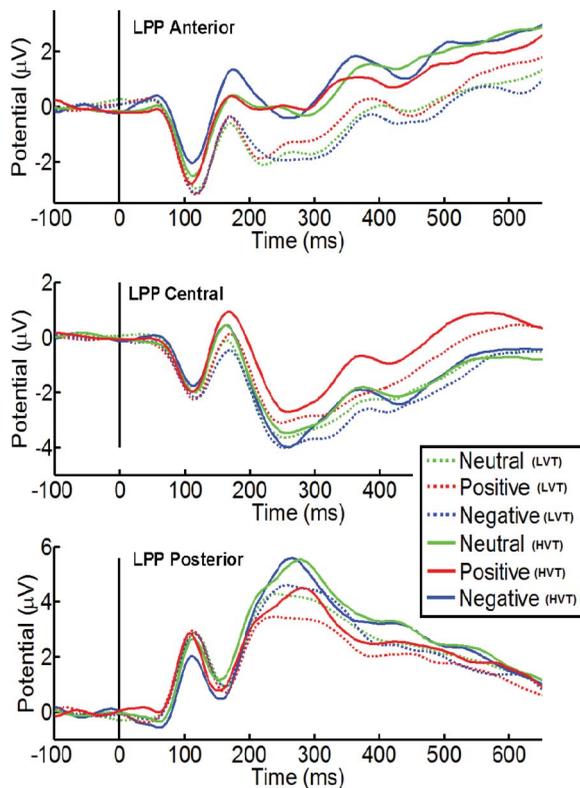
Figure 2. Triple interaction between the Regions of interest, Group of participants and Category. The amplitude graph shows that the greater differences between the groups of participants and category type occurred mostly in the right hemisphere.

$SD = 0.54$) 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 × Category × 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 × 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-subject 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 × 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 × 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).
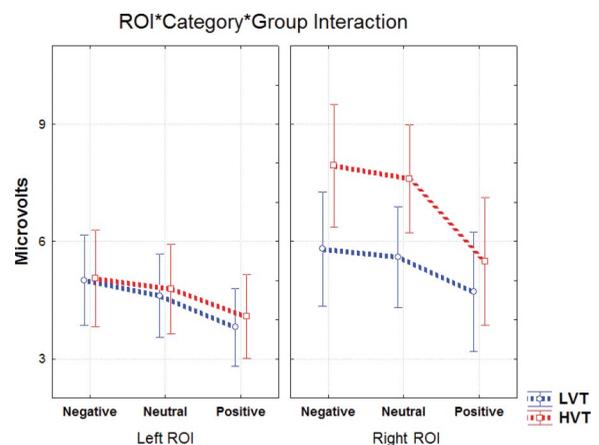
Figure 3. LPP component distribution on the midline and ERPs corresponding to the LPP for each category and each group of participants.

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 × 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 Martin, Dufey, Bacquet, & Lopez, 2008a; Ibáñez, San Martin, 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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