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Affective picture modulation: Valence, arousal, attention allocation and motivational significance

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ABSTRACT

The present study analyses the modulatory effects of affective pictures in the early posterior negativity (EPN), the late positive potential (LPP) and the human startle response on both the peripheral (eye blink EMG) and central neurophysiological levels (Probe P3), during passive affective pictures viewing. The affective pictures categories were balanced in terms of valence (pleasant; unpleasant) and arousal (high; low). The data shows that EPN may be sensitive to specific stimulus characteristics (affective relevant pictures versus neutral pictures) associated with early stages of attentional processing. In later stages, the heightened attentional resource allocation as well as the motivated significance of the affective stimuli was found to elicit enhanced amplitudes of slow wave processes thought to be related to enhanced encoding, namely LPP,. Although pleasant low arousing pictures were effective in engaging the resources involved in the slow wave processes, the highly arousing affective stimuli (pleasant and unpleasant) were found to produce the largest enhancement of the LPP, suggesting that high arousing stimuli may are associated with increased motivational significance. Additionally the response to high arousing stimuli may be suggestive of increased motivational attention, given the heightened attentional allocation, as expressed in the P3 probe, especially for the pleasant pictures. The hedonic valence may then serve as a mediator of the attentional inhibition to the affective priming, potentiating or inhibiting a shift towards defensive activation, as measured by the startle reflex.

1. Introduction

Emotions have been conceptualized as adaptive action dispositions (Izard, 1993; Lang, 1979) functionally preparing the organism for either avoidance (defensive system) or approach (appetitive system) related behaviours. These action dispositions may compete for ongoing mental resources, affecting stimulus appraisal and coping responses (Davidson, 2001; Frijda, 1986; Lang et al., 1997). Individual survival is dependent on the dynamic balance between these appetitive and defensive behaviours (Lang et al., 1997).

With the use of high temporal resolution methods, it has been shown to be possible to detect subtle changes in the cognitive and motor processing induced by affectively laden stimuli: the activity of the central nervous system (ERPs) and the peripheral nervous system response (e.g., electromyography — EMG).

The modulation of ERPs by affectively laden pictures has been widely addressed by research on affective and cognitive processing (Lang and Bradley, 2010). However, only recently have researchers started systematically exploring the interactions between the two types of valence (pleasant versus unpleasant) and arousal (high versus low) to assess their relative contributions in several ERP latencies (Briggs and Martin, 2009; Conroy and Polich, 2007; Rozenkrants et al., 2008).

Multiple ERP components are sensitive to affective pictures. For example, the early posterior negativity (EPN), the P300 and the late positive potential (LPP), have shown increased amplitude for both pleasant and unpleasant, when compared with neutral pictures (e.g. Cacioppo et al., 1994; Cuthbert et al., 2000; Keil et al., 2002; Schupp et al., 2004a); . These results have been interpreted as reflecting increased allocation of attentional resources (i.e. motivated attention) to motivationally relevant stimuli (e.g. Cuthbert et al., 2000; Foti et al., 2009; Hajcak et al., 2007; Hajcak and Olvet, 2008; Schupp et al., 2000, 2003a, 2004a). Other studies found an enhanced processing of the affective stimulus (i.e. motivated significance) with high arousal affective pictures, when compared with neutral or relaxing ones, reflected by the larger amplitudes on the late positive components (Hinojosa et al., 2009; Schupp et al., 2000).

In fact, the study of different ERP components allows the identification of different stages of the affective processing. Thus, while the EPN is associated with early selective attention to the stimulus, the LPP seems to reflect the initial attentional processing (along with

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the P300), as well as the sustained processing associated with encoding mechanisms (Foti et al., 2009).

In addition to ERP, the use of the startle response has been widely used to study the modulatory effects of valence and arousal in attention (Lang, 1995). The startle response is an evolutionary primitive fear reflexive reaction to the presentation of a sudden and intense sensorial probe, most typically an acoustic burst (Sokolov and Worters, 1963). It primarily consists of a stereotyped action pattern of somatic and facial muscles (Ekman et al., 1985), with the activation of both the autonomic and central nervous systems (Soto et al., 2005). Depending on the intensity, it can generate either a whole-body defensive response (Sokolov and Worters, 1963), an electromyographic (EMG) response associated with eye blinking and an evoked related potential (Probe P3).

Priming subjects with a stimulus of a contradictory affective valence significantly interferes with the magnitude of the startle response. Thus, the presentation of unpleasant stimuli (e.g., pictures, music, films) increases the magnitude of the startle reflex, while the presentation of pleasant stimuli significantly attenuates it (Lang et al., 1990).

Additionally, the startle probe also elicits a pronounced positive ERP wave referred as the startle P3 Probe peaking around 300 ms (Bradley et al., 2006; Cuthbert et al., 2000). While the eye-blink reflex is a good peripheral nervous system index of automatic subcortical affective processing, the P3 Probe represents a central nervous system marker of cortical cognitive-emotional regulation.

The P3 Probe is considered to be an index of the amount of resources allocated during the processing of affective pictures (i.e., workload measure)(Bradley et al., 2006). As greater attention is allocated to affectively laden pictures, fewer resources will be available to the sound probe. Therefore, lower probe amplitudes would indicate that more attentional resources are allocated to affectively laden pictures (Bradley et al., 2006; Schupp et al., 1997). This interpretation was also supported by studies where the reaction times to secondary probes were slower when viewing affective, compared to neutral pictures (Bradley et al., 1999; De Cesarei and Codispoti, 2008). One of the first studies exploring the mediators of the P3 Probe (Schupp et al., 1997) showed that, contrary to the eye blink response, the P3 is primarily modulated by the level of arousal, with attenuated auditory P3 waves for high arousal, affective stimuli, either pleasant or unpleasant.

Research on picture perception, following the multi-process startle modulation (Bradley et al., 2006) shows that instead of a single defensive response (i.e. the eye-blink reflex), the activation of the defense system is better explained by a cascade of several physiological responses (Bradley and Lang, 2007). The defense cascade (e.g. Bradley et al., 2001b; Bradley and Lang, 2000; Lang et al., 1997; Ohman and Wiens, 2003) states that stimuli activating the defensive system will orient our attention leading to increased sensory intake and resource allocation. As the stimulus becomes increasingly threatening, the active defense system starts to mobilize the available resources in order to prime defensive activation, thus potentiating the reflex. Appetitive inhibition of the reflex occurs with increasingly attention allocation to the appetitive stimulus (e.g. high arousing pleasant one), that could act as a single process of attentional inhibition or in conjunction with inhibition of the defensive system (Bradley et al., 2006). Both pleasant and unpleasant pictures with low to moderate arousal, as well as pleasant high arousing pictures may be responsible for startle inhibition, whereas unpleasant high arousal pictures may elicit startle potentiation (Cuthbert et al., 1996).

In sum, the multi-process model of startle modulation states that emotional autonomic responses to affective reactive stimuli are characterized by an initial orienting response followed by subsequent defense/appetitive activation.

Although startle probe and EMG have been already studied before (e.g. Amrhein et al., 2004; Ferrari et al., 2011), the present study focus on affective pictures categories balanced in terms of valence and arousal in response to a startle probe; as well as with EPN and LPP in response to the same pictures, in a passive viewing task. Therefore, the present study has two main objectives: (1) to test the effects of different categories of valence (pleasant; unpleasant) and arousal (high; low) on two event-related potentials (Early Posterior Negativity (EPN) and Late Positive Potential (LPP)) in response to passive picture viewing; and (2) to analyse the relative contributions of those valence (pleasant; unpleasant) and arousal (high; low) categories in modulating the human startle response on both the peripheral (eye blink EMG) and central neurophysiological levels (Probe P3).

2. Methods

2.1. Participants

Fifteen female university student volunteers (mean age: 20.27; SD: 1.87) participated in the study. All of the participants were healthy, with normal or corrected-to-normal visual and hearing acuity, self-reported right-handedness and without a present or past history of neurological or psychiatric disorder; they had not taken any medication or psychotropic drugs during the 4 weeks prior to the study. Participants were advised to avoid alcohol, cigarettes and caffeinated drinks on the day of the experiment, and none reported fatigue due to insufficient sleep. All of the participants gave their informed consent prior to their inclusion in the study and were awarded academic credits in an introductory psychology course. None of the participants were familiar with the protocols used in the study, including the IAPS (Lang et al., 2005) pictures.

The study was approved by the local ethics committee and was in accordance with the Declaration of Helsinki.

2.2. Stimulus material

A total of one hundred and twenty five pictures were used, which were taken from the IAPS database: 25 pleasant high arousing (PH), 25 pleasant low arousing (PL), 25 unpleasant high arousing (UH), 25 unpleasant low arousing (UL), and 25 neutral (NL).[1]

The startle stimulus was a 105 dB, 50 ms burst of white noise with instantaneous rise/fall times. Startle tones started 2500 ms after the onset of the picture, allowing the possibility to extract the first 1000 ms of each picture presentation and to examine the electric brain potentials in a passive picture viewing task, prior to the delivery of the startle tone.

2.3. Procedure and experimental design

The participants remained seated in a comfortable chair at an approximate distance of 1.5 meters to a 48.3 cm screen (19 inches) in an electrically isolated laboratory with attenuated light and sound. They were instructed not to move during the recording. Each picture was presented at approximately a 14.7° visual angle.

All of the participants were instructed that pictures of different affective content would be presented on a computer screen and to view the picture slide for the entire time it remained on the screen. They were also told that they might hear some noises, which they were instructed to ignore.

[1] The IAPS (Lang et al., 2005) pictures used in the experiment were the following: Pleasant Low (Valence: 7.37 (0.72); Arousal: 4.16 (0.55)): 2000, 2005, 2010, 2025, 2030, 2040, 2050, 2057, 2070, 2080, 2091, 2153, 2154, 2165, 2170, 2299, 2304, 2306, 2310, 2311, 2332, 2340, 2341, 2360, 2370; Unpleasant Low (Valence: 3.92 (1.17); Arousal: 4.00 (0.62)): 2095, 2100, 2110, 2190, 2221, 2230, 2271, 2272, 2276, 2278, 2280, 2312, 2383, 2399,2455, 2490, 2491, 2520, 2590, 2682, 2750, 2753, 9220, 9265, 9331; Pleasant High (Valence: 6.68 (0.36); Arousal: 6.44 (0.29)): 4607, 4643, 4647, 4651, 4652, 4656, 4658, 4659, 4660, 4664, 4666, 4670, 4672, 4676, 4677, 4680, 4681, 4683, 4687, 4689, 4690, 4694, 4695, 4800, 4810; Unpleasant High (Valence: 1.69 (0.25); Arousal: 6.64 (0.57)): 3000, 3010, 3015, 3016, 3030, 3053, 3060, 3061, 3062, 3063, 3064, 3068, 3069, 3071, 3080, 3100, 3102, 3110, 3120, 3130, 3140, 3150, 3168, 3170, 3266; Neutral(Valence: 4.95 (0.31); Arousal: 2.97 (0.52)): 7002, 7020, 7025, 7030, 7031, 7034, 7038, 7040, 7042, 7043, 7044, 7050, 7052, 7053, 7055, 7056, 7058, 7059, 7060, 7090, 7100, 7110,7130,7140,7150

Twenty-five pictures per category served as target stimuli in startle-probed trials, and 25 additional pictures for each category were paired in terms of content with the previous ones and served as non-startle trials. They were presented in 5 blocks of 50 pictures each. The pictures were pseudo-randomised in such a way that two pictures of the same category were always separated by at least one picture of a different category.

In the experiment, each picture was presented for 5000 ms, with the startle probe being delivered at 2500, 3250 or 4500 ms after picture onset. The three probe times occurred with equal frequencies for each picture category. Each picture was preceded by a fixation cross appearing in the middle of the screen, and the inter-stimulus interval varied between 1000 and 2500 ms to reduce expectancy effects. Pictures were pseudo-randomised, in such a way that two pictures of the same category were always separated by at least one picture of a different category. There was a 50% chance of a startle tone being delivered.

Startle probes were presented binaurally, at a constant intensity, over headphones carefully placed to not interfere with electrode recordings (namely T7 and T8).

The participants did not rate the affective content of the pictures, as such an evaluation task could potentially have an impact on the task design. Instead of asking for a general rating at the end of the experiment or double viewing each picture, the normative ratings were used.

2.4. Physiological recording and data reduction

Electroencephalographic activity was recorded with a QuickAmp™ system, with a 32-electrode Acticap™ System inserted in a cap with a frontopolar ground and average referenced, in accordance with the International 10–20 System (Jasper, 1958). The EEG signal was passed through a 0.1 to 70 Hz (12 dB/octave slope) analog band-pass filter, with a notch filter at 50 Hz, before being sampled at 500 Hz. An ocular movement (EOG) recording was obtained with two electrodes located supra- and infraorbitally to the right eye (VEOG). All impedances were maintained below 20 KΩ (on Acticap™ active electrodes).

After signal storage, ocular artefacts were corrected off-line using the algorithm Gratton et al. (1983). The EEG was then segmented, so 2000-ms segments (500 ms prestimulus baseline) associated with each presentation of the picture and 1100-ms segments (200 ms prestimulus baseline) associated with each probe sound presentation were extracted. Segments with signals exceeding ± 100 mV were automatically rejected, and all of the remaining segments were individually inspected to identify those still showing artefacts, excluding those from subsequent averaging. Segments were then corrected to the mean voltage of the pre-stimulus recording period (baseline). Finally, the signal was passed through a 0.1 to 20 Hz (12 dB/octave slope) digital band-pass filter.

The eye-blink component of the startle reflex was measured by recording electromyographic activity from the orbicularis oculi muscle beneath the left eye. Ag/AgCl miniature electrodes were attached with a constant inter-electrode distance of 2.5 cm across subjects. The raw signal was sampled at 500 Hz. Responses to the startle probes were scored manually and defined as an EMG peak in a time window from 20 to 120 ms after probe presentation. Trials with excessive baseline shifts or movement artefacts were excluded, and trials with no detectable reaction were scored as zero. Startle response magnitudes were then standardised within subjects to correct for the disproportionate influence of outliers (Globisch et al., 1999; Hamm et al., 2007). The raw data were first z- and then T-transformed for each subject.

2.5. Data analysis

For ERP recordings, five averaged ERP waveforms were obtained for each participant (PH, PL, NH, NL and Neutral) and stimulus type (Picture and Probe sound presentation). In order to analyse the different components, the average of electrodes was carried out according to the topographic distribution reported in previous studies. Therefore, for the picture-viewing task, the average of five parieto-occipital sites (PO9, PO10, O1, O2 and Oz) was carried out in order to analyse the EPN component (e.g. Foti et al., 2009; Schupp et al., 2003a, 2003b, 2004b, 2006a, 2006b), and the average of four electrode sites (Cz, Pz, CP1 and CP2) was carried out in order to analyse the LPP component (Foti and Hajcak, 2008; Hajcak et al., 2007; Keil et al., 2002; Schupp et al., 2000). For startle tone, the average of four electrode sites (Cz, Pz, CP1 and CP2) was carried out in order to analyse the Probe P3 component (Ferrari et al., 2011).

In order to measure the components, mean amplitudes were extracted in the time intervals where the amplitude was maximal: for the picture viewing waveforms, 200–250 ms (EPN) and 400–800 ms (LPP); for the startle tone waveforms, 250–350 ms (Probe P3).

2.6. Statistical analysis

To analyse the effects of the picture content on the ERP components and the EMG amplitude, four different one way repeated measures ANOVA with five levels (pleasant high arousing, unpleasant high arousing, pleasant low arousing, unpleasant low arousing and neutral).

When the assumption of sphericity was not met, the Greenhouse–Geisser correction was applied to the degrees of freedom in all cases, with the corrected probabilities and partial eta-squared (η_p^2) effect-size statistics reported. When the ANOVAs showed significant effects due to the main factors and their interactions, post-hoc analyses of the mean values were carried out using paired multiple comparisons (adjusted with a Bonferroni correction). The criterion for statistical significance was set at $p<0.05$. The partial eta squared is also presented (η_p^2). All of the statistical analyses were performed with PASW for Windows and Mac (version 19.0.1).

3. Results

3.1. ERPs related to passive picture viewing

3.1.1. Early posterior negative

There was a main effect of hedonic content ($F(4,56)=4.559$, $p=.02503$, $\eta_p^2=.177$). The bonferroni pairwise post-hoc tests revelead that pleasant high arousing (M = 2.937,SE = .795) (p = .019), pleasant low arousing (M = 2.824,SE = .968) (p = .009), unplesant high arousing (M = 2.384,SE = .827) (p = .006) and unpleasant low arousing (M = 2.283,SE = .798) (p = .003) showed statistically significant larger amplitudes than neutral pictures (M = 4.348,SE = 1.003) (Fig. 1).

3.1.2. Late positive potential

There was a main effect of hedonic content in the averaged late positive potential ($F(4,56)=49.479$, $p=<.001$, $\eta_p^2=.779$), with the post-hoc comparisons revealing that both pleasant high arousing pictures (M = 6.051, SE = .868) and unpleasant high arousing pictures (M = 5.483, SE = .700) showed larger amplitudes than both pleasant low arousing (M = 2.533, SE = .598), unpleasant low arousing (M = 1.472, SE = .548) and neutral (M = 1.118, SE = .641) ($p<.001$). Pleasant low arousing showed significantly larger amplitude than neutral (p = .005). No differences were found between the two affective high arousing categories (p = 1.000), between the two affective low arousing ones (p = .078), and between unpleasant low arousing and neutral (p = 1.000) (Fig. 1).

3.2. Electrophysiological correlates of the startle response

3.2.1. Probe P3

As shown in Fig. 1, a large positive wave, the P3 Probe, can be observed in the 250 to 350 ms interval.

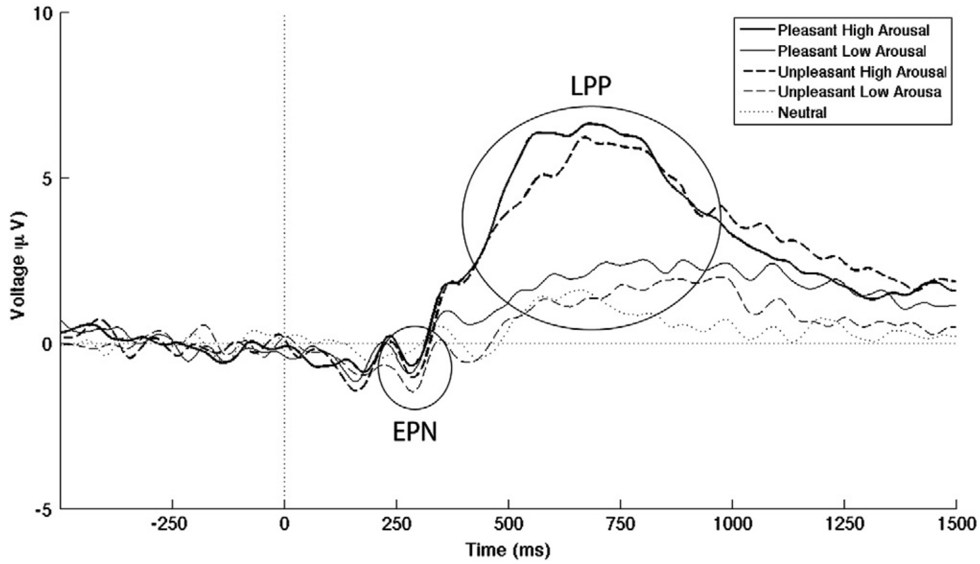

Fig. 1. Grand average ERP waveforms for passive picture viewing.

There was a main effect of picture category on the Probe P3 ($F(4,56)=19.555, p=<.001, \eta_p^2=.583$). The post-hoc comparisons revealed that Probe P3 amplitude was significantly smaller in the pleasant high arousing condition ($M=5.122$, $SE=.821$) than either unpleasant high arousing condition ($M=6.902$, $SE=1.009$) ($p=.005$), pleasant low arousing ($M=8.039$, $SE=.889$) ($p<.001$), unpleasant low arousing ($M=8.537$, $SE=1.093$) ($p<.001$) and neutral ($M=7.340$, $SE=1.023$) ($p=.010$). Also there was a significant amplitude reduction in the unpleasant high arousing condition when compared to the pleasant low arousing ($p=.005$) and unpleasant low arousing condition ($p=.002$). No other differences were found between the other categories (Fig. 2).

3.2.2. Startle eye blink EMG

There was a main effect of picture category on the EMG amplitude ($F(4,56)=13.565, p=<.001, \varepsilon=.534, \eta_p^2=.492$). Pleasant high arousing pictures ($M=49.653, SE=.031$) significantly attenuated the EMG amplitude when comparing to both unpleasant high arousing ($M=50.310, SE=.084$) and neutral ($M=49.948, SE=.040$) ($p<.001$) as well as both pleasant ($M=49.991, SE=.047$) and unpleasant low arousing ones ($M=50.119, SE=.073$) ($p=.001$). Although not statistically significant, the unpleasant high arousing pictures potentiated the EMG amplitude when comparing to neutral ($p=.070$) and pleasant low arousing ones ($p=.085$) (Fig. 3).

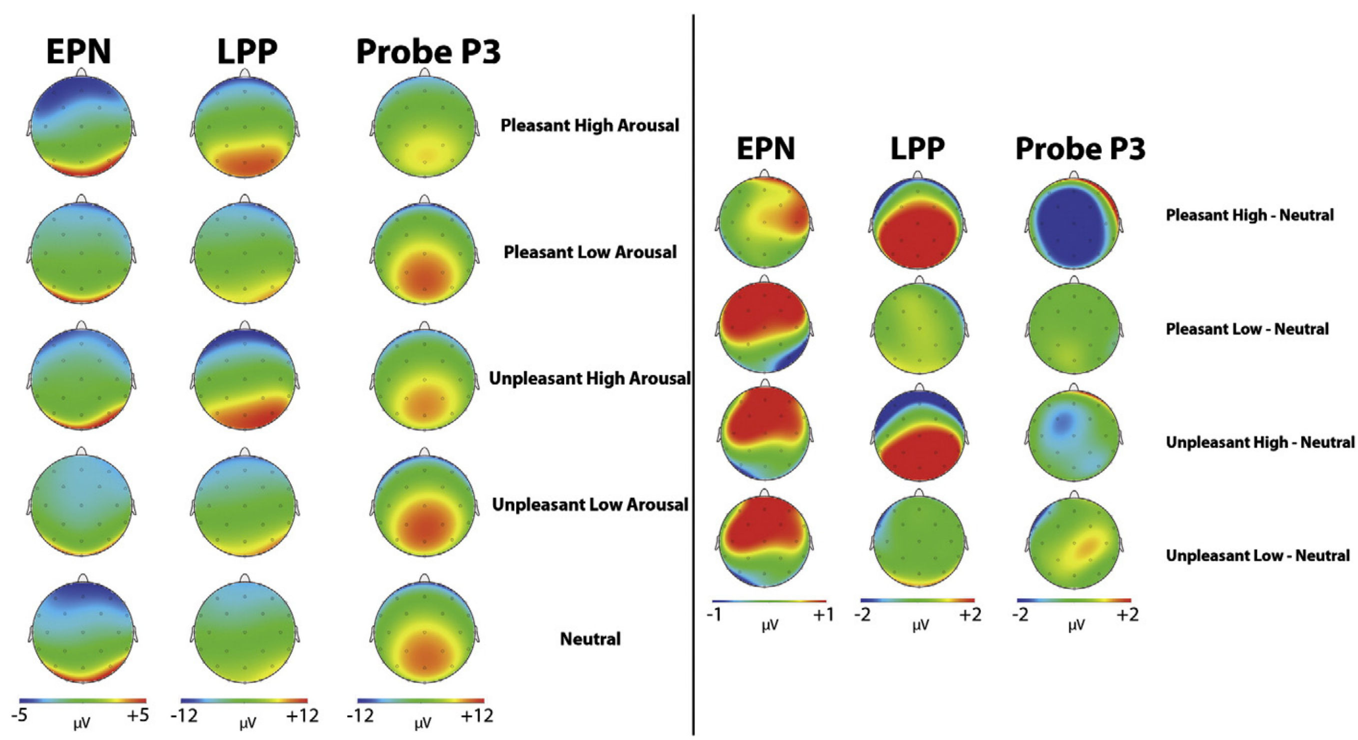

Fig. 2. Scalp topography maps. Left Panel: scalp topographies for early posterior negativity, late positive potential and P3 Probe. Right Panel: Scalp topographies differences from neutral pictures for early posterior negativity, late positive potential and P3 Probe.

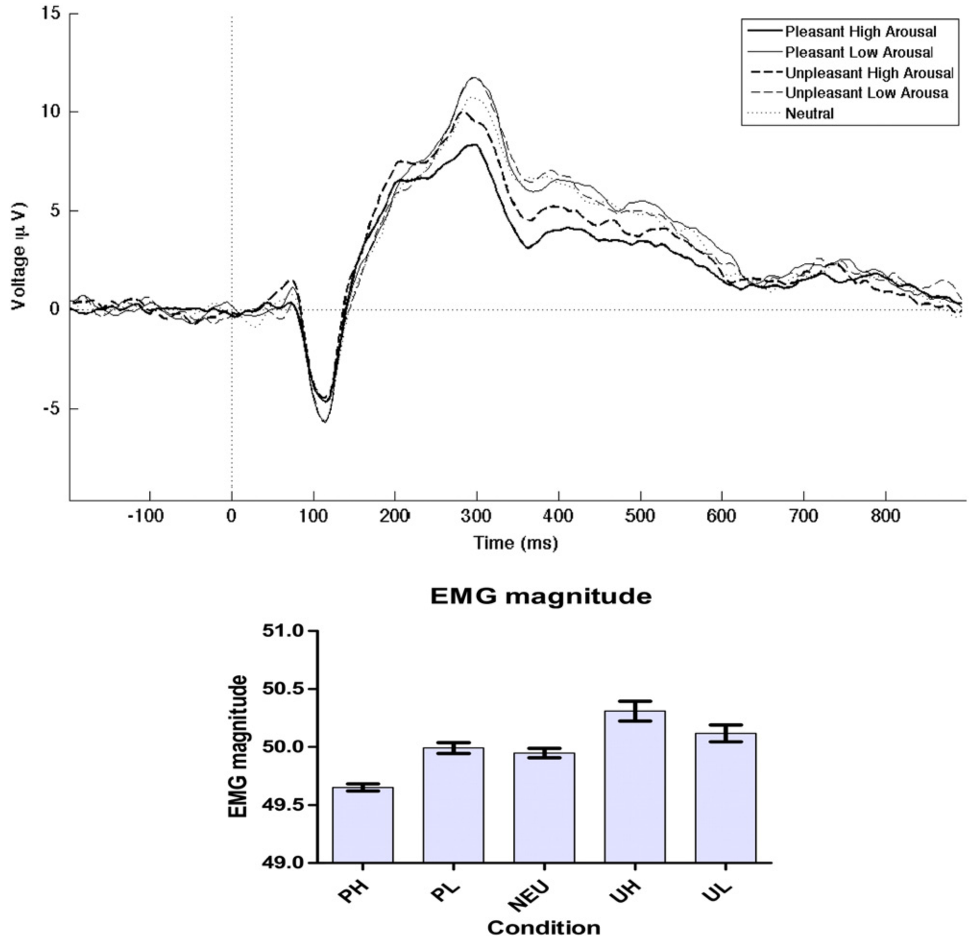

Fig. 3. Grand average ERP and EMG histogram. For the EMG histogram, the columns represent the means plotted with the SEM error bars. PH — pleasant high arousal; PL — pleasant low arousal; UL — unpleasant low arousal; UH — unpleasant high arousal; NEU — neutral.

4. Discussion

The present study found an increased negativity of the early posterior negativity (EPN) amplitude for both high arousing (pleasant and unpleasant) and low arousing (pleasant and unpleasant) when compared to neutral pictures, within the 200–250 ms latency range. This data is consistent with previous studies (Junghofer et al., 2001; Peyk et al., 2009; Schupp et al., 2007a, 2007b), showing that the EPN is modulated by affective arousing pictures when compared to neutral. Similar results on EPN have been interpreted as an index of "natural selective attention," reflecting early facilitated perception of motivationally relevant stimuli (Schupp et al., 2003a, 2003b, 2004b). In other words, EPN modulation may reflect an early stage of stimulus selection, based on specific stimuli characteristics, in order to allow room for further processing (Dolcos and Cabeza, 2002; Schupp et al., 2004a, 2004b).

Following the early stage selection processes, the results also indicate a significant effect of picture category in the late positive potential (LPP), especially for highly arousing pictures. High arousing pictures (pleasant and unplesant) elicited most pronouced LPP amplitudes than both pleasant and unpleasant low arousing and neutral pictures. Also, pleasant low arousing picures elicited larger amplitudes than neutral, but no valence differences were found between low and high arousing categories. This data is also consistent with previous studies (e.g. Amrhein et al., 2004; Cuthbert et al., 2000; Keil et al., 2002; Olofsson and Polich, 2007; Palomba et al., 1997; Schupp et al., 2000), which have found a more pronounced LPP amplitude to the pleasant and unpleasant compared to neutral pictures. This effect is more pronounced in high arousing pictures than in the less arousing pictures of the same valence. These results for the LPP have been interpreted as both, an index of "motivated attention" and "motivated significance." That is, LPP seems to be modulated by the continuing perceptual analysis of intrinsic relevant stimuli involved in memory mechanisms (Azizian and Polich, 2007; Cuthbert et al., 2000; Schupp et al., 2000, 2004a), as well as by the activation of the defensive and appetitive subsystems (Ferrari et al., 2011; Lang et al., 1997).

In sum, both the EPN and the LPP components have shown to be responsive to stimulus of different valence and arousal categories in passive picture viewing, suggesting that greater sensory intake and processing occurs from very early stages, enhancing later cognitive processing and memory encoding.

As expected the processing of affective pictures affected the response to a new, startling, stimulus. Indeed, the processing of pictures of different arousal and valence modulated the startle response to a probe at both the peripheral (startle blink EMG) and central nervous system levels (Probe P3).

Pleasant high arousing pictures produced significantly smaller EMG amplitudes when compared to all the other stimuli (with the exception of pleasant low arousing). The present data is consistent with previous reports showing that pleasant highly arousing pictures contribute to the inhibition of the EMG startle response (Lang et al., 1990). The inverted pattern found with the eye blink attenuation for the high arousing pleasant condition with the eye-blink enhancement for the unpleasant high arousing has been found in several other studies (e.g. Bradley et al., 2001b, 2006).

The present study, consistent with previous ones (Cuthbert et al., 2001; Schupp et al., 2004a), found an effect of both pleasant and unpleasant highly arousing pictures on the P3 Probe. This component seems to reflect the amount of attentional resources allocated to the startle stimulus (Cuthbert et al., 2001), being used as a measure of motivated attention (Lang et al., 1997). The data also suggests that significant affective content (high arousal pictures) may attract large amount of attentional resources probably to potentiate an approach or withdrawal action disposition. However, pleasant high arousing pictures were found to produce smaller P3 Probe amplitudes than unpleasant high arousing ones. This is also consistent with the literature, where a pleasant picture was found to be more effective in engaging visual attention, therefore reducing the attentional resources allocated to the startle probe (Bradley et al., 1990, 2006; Carretie et al., 2001; Simons and Zelson, 2007).

Therefore, the presentation of affective pictures seemed to attract participants' attention, and the startle reflex was found to be sensitive to the dynamic interplay of attentional and affective processing. In the case of high arousing pictures, there was a reduced orientation to other stimuli in the environment (in the case of the present study, a startle probe), modulating the response to these stimuli, according to what is suggested by the multi-process model of affective eye-blink modulation (Bradley et al., 2006). Physiological responses sequentially change at different levels of defensive activation. When the activation is still relatively low, at early stages of defense, the perceptual processing is facilitated. With increased levels of activation, oriented attention starts to switch to metabolic mobilization for active defense. The arousal intensity of these affective pictures seems to be modulating the level of attention allocation to the sound probes. For example, less processing of sound probes occurs in the context of a less intense aversive foreground (Anthony and Graham, 1985) and more processing of the sound probe occurs in a highly aversive foreground, resulting in a less inhibitory influence of attention (Lang et al., 1997).

Probably in the pleasant high arousing condition, there is greater inhibitory influence of attention in the defensive reflex (Bradley et al., 2006) whereas for unpleasant high arousal condition, the inhibitory influence of attention was smaller, thus potentiating (although not statistically significant) the defensive activation (Lang et al., 1997). What is not clear is whether this appetitive inhibition is a part of a single attentional process or due to interplay between attention and defensive reflex inhibition (Bradley et al., 2006).

At the same time, for the low arousing affective categories (both pleasant and unpleasant) when compared with neutral stimuli, the initial increase of sensory intake, orienting and resource allocation did not affect the blink magnitude. For the unpleasant low arousing condition this has been interpreted as an inhibitory effect due to increased attentional demands that will reduce the defensive response (Bradley et al., 2006). This is also consistent with the notion that in order to potentiate the reflex, there needs to exist a high defensive activation (Bradley et al., 2006).

In sum, the present study shows that EPN may be sensitive to specific stimulus characteristics (affective relevant pictures versus neutral pictures) associated with early stages of attentional processing. In later stages, the heightened attentional resource allocation as well as the motivated significance of the affective stimuli was found to elicit enhanced amplitudes of slow wave processes thought to be related to enhanced encoding, namely LPP. Although pleasant low arousing pictures were effective in engaging the resources involved in the slow wave processes, the highly arousing affective stimuli (pleasant and unpleasant) were found to produce the largest enhancement of the LPP, suggesting that high arousing stimuli may are associated with increased motivational significance. Additionally the response to high arousing stimuli may be suggestive of increased motivated attention, given the heightened attentional allocation, as expressed in the P3 probe, especially for the pleasant pictures. The hedonic valence may then serve as a mediator of the attentional inhibition to the affective priming, potentiating or inhibiting a shift towards defensive activation, as measured by the startle reflex. The small sample size and the restriction to female participants may present limitations to the generalisation of the present findings. While several authors reported differences between genders (e.g., Bradley et al., 2001a), other studies have suggested otherwise (e.g., Rozenkrants and Polich, 2008). Future studies should address this question with larger samples and paired gender analyses. Another possible limitation of this study is related to the stimuli selection. Differences in valence between low and high arousal pictures and differences in arousal between pleasant and unpleasant pictures should carefully be addressed in order to avoid no desirable effects on psychophysiological measures. Also, for the present study different groups of pictures were created according to valence and arousal ratings with some degree of content consistency (e.g., most of the pleasant high arousing pictures used in this study are erotica, whereas the unpleasant high arousing pictures are basically mutilations). However, as the study from Bradley et al. (2001b) showed, the startle modulation is greater for erotic, mutilation and threat (varying with arousal level). The same study also showed specific pattern modulation for faces. The present study cannot provide light to these questions; nonetheless future studies should address these aspects, with a careful selection of the stimuli content and planning for specific content analysis.

Author's notes

Special authorship status: Jorge Leite and Sandra Carvalho share equal responsibility for the content of this article.

Conflicts of interest

The authors do not have any conflicts of interest, financial or otherwise, to disclose.

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