

Are Females More Responsive to Emotional Stimuli? A Neurophysiological Study Across Arousal and Valence Dimensions

C. Lithari · C. A. Frantzidis · C. Papadelis ·
Ana B. Vivas · M. A. Klados · C. Kourtidou-Papadeli ·
C. Pappas · A. A. Ioannides · P. D. Bamidis

Received: 9 February 2009 / Accepted: 14 December 2009 / Published online: 31 December 2009
© The Author(s) 2009. This article is published with open access at Springerlink.com

Abstract Men and women seem to process emotions and react to them differently. Yet, few neurophysiological studies have systematically investigated gender differences in emotional processing. Here, we studied gender differences using Event Related Potentials (ERPs) and Skin Conductance Responses (SCR) recorded from participants who passively viewed emotional pictures selected from the International Affective Picture System (IAPS). The arousal and valence dimension of the stimuli were manipulated orthogonally. The peak amplitude and peak latency of ERP components and SCR were analyzed separately, and the scalp topographies of significant ERP differences were

documented. Females responded with enhanced negative components (N100 and N200), in comparison to males, especially to the unpleasant visual stimuli, whereas both genders responded faster to high arousing or unpleasant stimuli. Scalp topographies revealed more pronounced gender differences on central and left hemisphere areas. Our results suggest a difference in the way emotional stimuli are processed by genders: unpleasant and high arousing stimuli evoke greater ERP amplitudes in women relatively to men. It also seems that unpleasant or high arousing stimuli are temporally prioritized during visual processing by both genders.

Keywords Emotions · Gender differences · Event related potentials · Skin conductance

C. Lithari · C. A. Frantzidis · M. A. Klados · C. Pappas ·
P. D. Bamidis (✉)
Laboratory of Medical Informatics, Medical School, Aristotle
University of Thessaloniki, P.O. Box 323, 54124 Thessaloniki,
Greece
e-mail: bamidis@med.auth.gr

C. Papadelis
Laboratory of Functional Neuroimaging, Center for Mind/Brain
Sciences, Matarello, Italy

A. B. Vivas
Psychology Department, City Liberal Studies (Affiliated
Institution of the University of Sheffield), Thessaloniki, Greece

C. Kourtidou-Papadeli
Greek Aerospace Medical Association and Space Research,
Thessaloniki, Greece

A. A. Ioannides
Laboratory for Human Brain Dynamics, Brain Science Institute
(BSI), RIKEN, Wako, Saitama, Japan

A. A. Ioannides
Laboratory for Human Brain Dynamics, AAI Scientific and
Cultural Services Ltd., Galaxias Center, Nicosia, Cyprus

Introduction

Over the last few years there has been a renewed interest about sex differences in brain and cognition. This interest is partly due to the increasing amount of literature showing structural and chemical differences between the brain of males and females in both animals (Zhang et al. 2008; Xiong et al. 2007) and humans (Canli et al. 2002; Cahill and McGaugh 1998; Lang 1968, 1984). Sex differences have also been documented in cognitive processes such as memory, emotion, and vision (see Cahill 2006 for a review). Within this field, the topic of sex differences in emotional processing has attracted particular interest due to its potential application in understanding psychopathology. For instance, gender differences in the prevalence of mood disorders such as depression and anxiety may be related to the differential response of females and males to stress (Cahill 2006).

Only few studies have so far investigated gender differences in emotions, and most of them report significant differences. Thus, for instance, unpleasant pictures from International Affective Picture System (IAPS, Lang et al. 1997) elicited more robust P300 effects in terms of both amplitude and latency in the left hemispheres of females, while they elicited a stronger P300 component in the right hemisphere of males (Gasbarri et al. 2007). Females responded with a much larger N200 component to IAPS (Lang et al. 1997) emotional pictures depicting humans than to those containing scenes (Proverbio et al. 2008). Similarly, Han et al. (2008) found that the amplitude of the P300 was generally larger for painful relative to neutral stimuli in both sexes, but this effect was stronger for females. These findings agree with the hypothesis that women are generally more responsive to emotional stimuli and more particularly to danger-related stimuli (Williams and Gordon 2007).

The findings from event related potentials (ERPs) studies appear to be also supported from neuroimaging studies employing fMRI (Canli et al. 2002; Cahill 2003; George et al. 1996; Pardo et al. 1993; Schneider et al. 2000; Wrase et al. 2003). Stimuli of different valence (film clips) produced a differential time course and intensity of prefrontal cortex activation, with overshoot and undershoot being more pronounced in males in an fMRI study (Leon-Carrion et al. 2006). Kemp et al. (2004) used steady-state probe topography and reported that the processing of unpleasant images is associated with widespread frontal latency reductions in females, but not in males. These findings support the notion that males and females seem to perceive, process, and respond differently to emotional stimuli.

Studies with auditory stimuli also report gender differences with emotional tones of voice indicating the significance of a spoken utterance. Schirmer et al. (2005) showed that even though both sexes appear to detect pre-attentively changes in voice, only women recruit additional processing resources when the change in voice is of emotional valence. Also, females are found to use earlier the emotional prosody during word processing as compared to men (Schirmer et al. 2002). Thus in general, these findings appear to support the claim of women's superior emotion recognition proposed by Hall (1978).

Although these studies converge to some general conclusion, the findings are not conclusive yet, partially due to large discrepancies among the studies in terms of aspects of emotion measured and the type of stimuli employed. For instance, some studies have investigated the expression of emotions in terms of facial movements and self-reports of experienced emotion (Kring and Gordon 1998; Wild 2003), whereas others have looked at neurophysiological correlates of emotions with autonomic

responses (e.g., skin conductance) (Bradley et al. 2001; Kring and Gordon 1998). Similarly, researchers have used a variety of stimuli to induce emotional experiences; emotional films (Aftanas et al. 1997; Kring and Gordon 1998; Cahill 2003), pictures (Codispoti et al. 2006; Cahill 2003; Cuthbert et al. 2000; Schupp et al. 2006; for a review see Oloffson et al. 2008), pictures of specific content (e.g., emotional faces or social stimuli) (Gerber et al. 2008; Proverbio et al. 2008), emotional words (Alfano and Cimino 2008), music and sounds (Schirmer et al. 2002, 2005; Krumhansl 2002; Bachorowski and Owren 2003; Panksepp and Bernatzky 2002). While emotional films seem to be quite effective, they are difficult to standardize in terms of the basic visual processes, because responses elicited by different frames overlap. In addition, during exposure to both emotional films and music, the effect of each frame or note is embedded within the context established by its predecessors in a highly idiosyncratic way for each participant. On the other hand, emotional words include the verbal information and its perception, which may affect the study of emotional perception itself. In this sense, the IAPS collection (Lang et al. 1997), which contains standardized images rated for emotional valence and arousal may provide a convenient alternative for the investigation of emotional processing.

There is no agreement in literature about how valence and arousal may interact to induce emotional experiences. The bi-dimensionality theory of emotions proposes that the nature of emotional experience, or at least its 'affective core', is primarily determined by two main dimensions: pleasure and arousal (Russell 1980, 1989; Reisenzein 1994; Barrett 1998). Valence ranges from attraction and pleasure to aversion and displeasure, whereas arousal is a more general property of the stimulus and refers to the level of activation, regardless of the direction (whether pleasant or unpleasant) and it should not be confused with affective intensity (Barrett and Russell 1999). This proposal would be consistent with an underlying bi-motivational system: the appetitive (approach) and the aversive (avoidance) motivational system that vary along the arousal dimension (Cacioppo and Bernston 1994; Lang et al. 1998). It also derives from theory, that valence and arousal are two orthogonal, independent dimensions of the emotional stimulus. Other theories propose that these two dimensions are relatively dependent. Williams and Gordon (2007) have proposed that potentially dangerous stimuli are typically high arousing, what they called a "mismatch". On the other hand, reward-related stimuli are typically predictable, what they termed as a "match". Although, it is true that valence and arousal co-vary in the real world (Lang et al. 1997), recent studies suggest that these two dimensions interact and need to be taken into account when

studying emotional processing (Cuthbert et al. 2000; Robinson et al. 2004).

In line with this, there are at least four previous reports considering the possible interaction of arousal and valence during selecting IAPS stimuli in the experimental design, as in the present one. Most of these studies (Keil et al. 2002; Dolcos and Cabeza 2002; Delplanque et al. 2006) used emotional versus non emotional (neutral) stimuli to study arousal effects, whereas Gianotti et al. (2008) manipulated valence and arousal orthogonally getting to a different experimental design. The latter study assumed different neural assemblies for high and low arousal, as well as, for pleasant and unpleasant stimuli. Their results also revealed that valence information was extracted before that of arousal. These studies were mainly focused on the temporal analysis of emotional perception, whereas none of them reported gender differences.

Another aspect that has been addressed in the literature of emotional processing is the autonomic responses. Emotions elicited by stimuli often lead to autonomic responses that survive even when the stimulus is masked (Ekman et al. 2007). In this sense, simultaneous recordings of central and autonomic nervous responses are more likely to advance our understanding of emotional processing. Recent studies have attempted to integrate brain activity measures with more than one simultaneous peripheral physiological measurements, such as Skin Conductance Response (SCR), heart rate, and facial electromyography (EMG) (Bernat et al. 2006; Cuthbert et al. 2000; Kring and Gordon 1998). The electrodermal activity has been found to be more responsive to pleasant and unpleasant pictures than neutral ones, while the high arousing pictures evoked greater SCR amplitudes as compared to low arousing ones (Bernat et al. 2006). In terms of sex differences, women were found to elicit greater physiological reactivity (i.e., SCR, facial EMG) than men to emotional material, especially if the material was of negative valence (Bradley et al. 2001; Chentsova-Dutton and Tsai 2007).

In the present study, we investigated potential differences in emotional processing between genders by measuring ERPs and SCRs when participants were passively exposed to emotional pictures selected from the IAPS collection. The valence and arousal dimensions of the pictures were orthogonally manipulated, since recent research suggests that these two dimensions may interact (Cuthbert et al. 2000). Based on findings from previous studies, we hypothesized that emotional stimuli will reveal gender differences in ERPs and SCRs. In this sense, females may appear more responsive to emotional stimuli at ERP components relative to males. This difference is presumed to be greater for unpleasant stimuli.

Materials and Methods

Participants

Twenty-eight healthy, right-handed volunteers (14 females and 14 males) participated in the study with a mean age of 28.2 ± 7.5 for males, and 27.1 ± 5.2 for females (mean \pm SD). Participants with a history of psychiatric or neurological illness or under medication were excluded from the study. All participants had normal (10/10) or corrected to normal vision. Participants were kindly asked to refrain from any alcohol and caffeine consumption the day before and the day of the experiment; they were also asked to sleep as adequately and comfortably as possibly achievable the night before the recordings. Each participant signed an informed consent form prior to his/her participation and completed a short questionnaire. All participants were paid for their participation. An approval from the local Ethical Committee was granted for this study.

Experimental Procedure

Participants were seated on an armchair and a PC screen was placed in front of their eyes in a distance of 80 cm. The room temperature was constantly controlled during the experiment. The experiment started with a 30-s recording, during which participants were asked to keep their eyes open and fixate to a cross appearing in the center of the screen; this was followed by similar measurement with eyes closed. The aim of both recordings was to identify and correct any possible technical problems before the actual recordings (see below), as well as, to provide test data for performing the artifact rejection algorithms used later in the analysis. One hundred and sixty pictures were selected for the experiment. Pictures were categorized in four groups (4×40 pictures) according to arousal and pleasure ratings, as explained below.

The emotion evocative pictures were presented to participants in a random order. Stimulus delivery was controlled by the presentation software (Neurobehavioral systems, Albany, CA). Each single epoch consisted of a 500 ms pre-stimulus and a 2 s post-stimulus period. In the pre-stimulus period, a white fixation cross was presented on the screen in a black background. The stimulus appeared on the screen for 1 s after which the cross came up again. The total duration of the experiment was less than 5 min. The procedure was concluded with a repetition of the initial 30 s recordings, with eyes open and then closed. Most of the participants (13/14 males, 13/14 females) rated the presented pictures in terms of valence and arousal following the IAPS rating scales through a web-based online questionnaire.

Stimuli

Visual stimuli were pictures from the IAPS collection; these were selected along with their emotional content defined in terms of their pleasure and arousal ratings. The selected stimuli divided the pleasure-arousal 2D space by naturally forming four groups of pictures: pleasant and high arousing (PHA),¹ pleasant and low arousing (PLA),² unpleasant and high arousing (UHA),³ and unpleasant and low arousing (ULA).⁴ Figure 1 shows how the performed selection populated the four corners of the pleasure-arousal plane so that arousal and pleasure effects were well-separated (Bradley and Lang 1994; Lang et al. 1997). Since males and females have rated IAPS pictures differently across pleasure and arousal (Lang et al. 1997), we tried to maintain similar affective content level for both genders. To this direction, we considered as many common pictures as possible. However, few of the pictures for males and females were different, but of similar affective content level. In order to test that the two sets of pictures were equal, we conducted *t*-tests for both arousal and valence. The gender-specific ratings of the presented pictures, as provided by the IAPS collection, are presented in Table 1, accompanied by our participants' group ratings. None of the comparisons between stimuli used for males and those

¹ **PHA for males:** 1720, 1811, 4001, 4006, 4141, 4142, 4150, 4180, 4210, 4220, 4225, 4232, 4240, 4250, 4255, 4290, 4300, 4310, 4311, 4320, 4607, 4608, 4651, 4652, 4658, 4659, 4660, 4664.1, 4670, 4681, 4683, 8080, 8185, 8186, 8190, 8340, 8400, 8499, 8501. **PHA for females:** 2150, 2216, 2303, 2345, 2389, 2550, 4460, 4470, 4490, 4503, 4510, 4520, 4532, 4533, 4537, 4538, 4542, 4561, 4572, 4598, 4599, 4607, 4608, 4609, 4611, 4626, 4656, 4659, 4660, 4670, 4680, 4681, 4687, 4689, 4695, 5621, 5629, 7502, 8030, 8034.

² **PLA for males:** 1450, 1601, 1610, 1620, 1750, 1812, 1900, 1920, 2050, 2070, 2235, 2260, 2299, 2303, 2360, 2370, 2388, 2501, 2530, 2550, 2650, 2660, 4614, 5000, 5001, 5010, 5020, 5030, 5200, 5831, 5891, 7080, 7325, 7340, 7545, 7900, 8330, 8497. **PLA for females:** 2000, 2010, 2037, 2152, 2260, 2299, 2304, 2311, 2360, 2370, 2388, 2395, 2398, 2501, 2510, 2530, 2540, 2598, 2620, 5000, 5010, 5020, 5030, 5200, 5520, 5551, 5611, 5631, 5711, 5720, 5750, 5760, 5764, 5779, 5800, 5811, 5891, 7039, 7340, 7545.

³ **UHA for males:** 1525, 2681, 2683, 2688, 2703, 2811, 3000, 3010, 3015, 3030, 3053, 3060, 3068, 3069, 3071, 3080, 3100, 3102, 3110, 3120, 3130, 3150, 6230, 6250.1, 6300, 6313, 6350, 6510, 6540, 6550, 6560, 6570, 8485, 9040, 9252, 9410, 9630, 9635.1, 9810, 9902. **UHA for females:** 2683, 2691, 2730, 2981, 3000, 3010, 3015, 3030, 3051, 3053, 3063, 3064, 3068, 3069, 3071, 3080, 3100, 3102, 3110, 3120, 3140, 3150, 3168, 3170, 3191, 3225, 3266, 3400, 3500, 3530, 5971, 6021, 6022, 6190, 6200, 6210, 6212, 6230, 6243, 6250.

⁴ **ULA for males:** 2095, 2100, 2141, 2200, 2205, 2206, 2210, 2214, 2375.1, 2393, 2399, 2440, 2490, 2570, 2700, 2715, 2722, 2750, 2753, 3017, 3301, 4490, 4510, 4550, 4561, 7006, 7025, 7031, 7150, 7170, 7187, 9220, 9265, 9280, 9290, 9331, 9360, 9421, 9571. **ULA for females:** 2399, 2490, 2491, 2590, 2722, 2750, 4001, 4210, 4230, 4233, 4240, 4290, 4635, 5120, 5130, 5534, 6010, 6241, 6800, 6930, 7031, 7036, 7044, 7046, 7054, 7060, 7130, 7150, 7180, 7184, 7211, 7224, 7234, 7484, 7491, 7700, 7705, 7920, 8496, 9000.

used for females reached statistical significance ($P > 0.05$). That is, although some of the pictures were different for males and females, they were equal in terms of valence and arousal dimensions. The pictures were further tested for complexity (picture's histogram entropy), overall Apparent Contrast ($AC = \text{standard deviation of luminance matrix} / \text{mean of luminance matrix}$, Delplanque et al. 2007), as well as for AC for each color level, and there were no significant differences between stimuli for males and females for each of the picture categories ($P > 0.05$).

Electrophysiological Recordings

EEG/ERP

EEG/ERP measurements were recorded from 19 active sites distributed across the scalp according to the International system 10–20 (Jasper 1958) and with reference electrodes positioned at the mastoids. The recordings, were performed with a Nihon Kohden 911 (Nihon Kohden, Japan) EEG recording device. All electrode impedances were maintained at less than 5 k Ω . Electrooculographic (EOG) activity was also recorded via four Ag–AgCl electrodes placed one above, and one below the left eye and two at the outer canthus of both eyes. The sampling rate for all measurements was 500 Hz.

SCR

The skin conductance was recorded during the entire experiment by an in-house device using a pair of Ag–AgCl electrodes. The electrode pairs were supplied with constant current and the voltage changes, representing the inverse conductance value, were recorded using a DC amplifier (SCRmin $\sim 0.01 \mu\text{Siemens}$ and SCRmax $\sim 1 \mu\text{Siemens}$). The sampling rate for the recording of digitized data was set at 500 Hz.

Data Analysis

All EEG/ERP recordings were initially band-pass filtered (low-pass IIR filter with cut-off frequency 40 Hz, high-pass IIR filter with cut-off frequency: 0.5 Hz). The INFOMAX Independent Component Analysis (ICA) algorithm was applied to the filtered EEG data for removing the biological artifacts (i.e., eye movements, eye blinks, cardiac signal, and muscle artifacts) (Jung et al. 2000). The analysis and extraction of the artifacts was performed off-line on a PC by means of the EEGLAB software (version 5.03) coded in MATLAB (Delorme and Makeig 2004). Two independent and experienced electrophysiologists reviewed the components and decided for their rejection. The ERPs were

Fig. 1 Valence and arousal ratings of images used for males and females

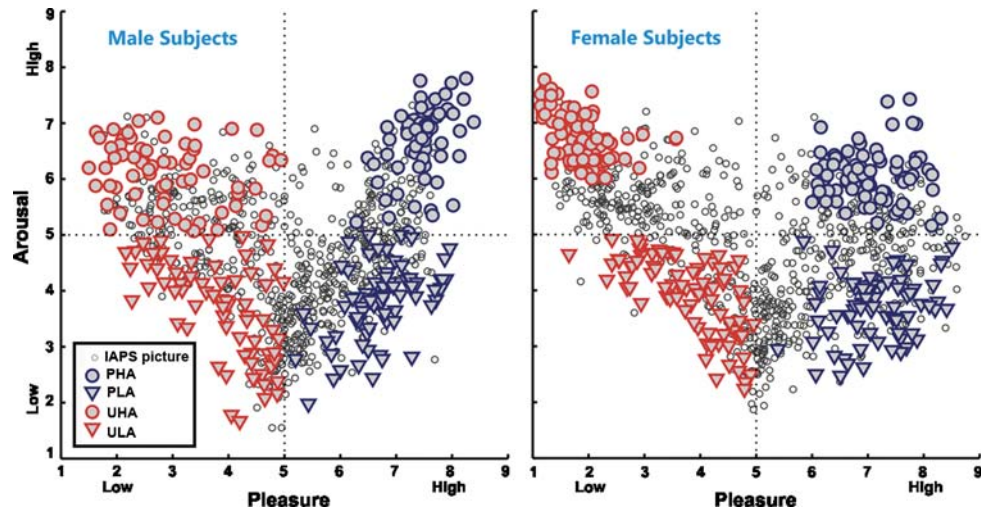


Table 1 The gender-specific ratings of the presented stimuli as provided by the IAPS collection and as rated by participants of this study

		Males		Females	
		IAPS	Participants	IAPS	Participants
Pleasure	Pleasant	7.18 ± 0.66	6.92 ± 0.63	7.15 ± 0.67	7.03 ± 0.58
	Unpleasant	3.05 ± 0.96	3.52 ± 1.36	2.89 ± 1.41	3.17 ± 1.64
Arousal	High arousing	6.64 ± 0.56	6.50 ± 1.13	6.46 ± 0.62	6.78 ± 1.25
	Low arousing	3.51 ± 0.80	4.34 ± 0.93	3.59 ± 0.71	4.28 ± 0.73

t-Tests were performed to ensure that there were no significant differences between pictures used for males and those for females

averaged in respect to the stimulus onset from –200 to 1000 ms reducing the background noise to a point where the event-related signals can be seen in the data. This resulted in a complex waveform that is made up of a number of distinct components (Fig. 2). For all electrodes and each participant, the averaged ERP waveforms were estimated for each of the four picture categories. The grand averaged ERP waveforms were also calculated for each picture, category, and electrode site, referenced to a 500 ms baseline preceding picture onset.

The SCR measurements were also digitally filtered off-line by using the EEGLAB software. A low-pass short IIR filter was used with cut-off frequency at 2.5 Hz. The average signal was computed for each picture category from –500 to 2000 ms. The grand average was also calculated among all participants. The SCR amplitude was scored manually and defined as the largest increase in electrodermal activity in a time window ranging from 500 to 2000 ms post-stimulus (Amrhein et al. 2004).

The baseline-to-peak amplitudes of each component and each participant were submitted to separate repeated ANOVA measures with gender as the between participants factor and stimulus valence (positive and negative) and

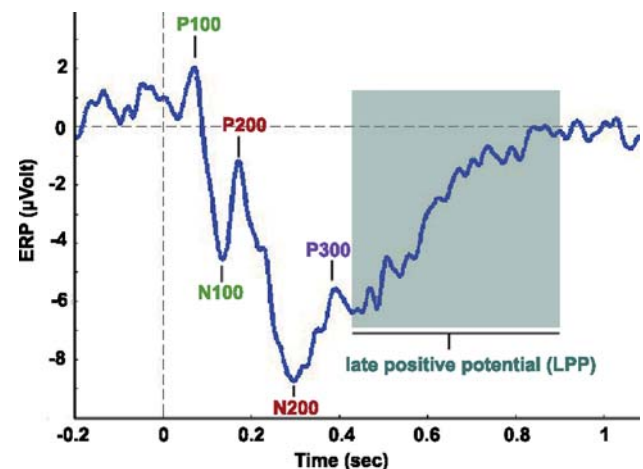


Fig. 2 ERP components of a typical grand average waveform. Early components are marked with green and middle ones with red color. P100 usually is seen around 100 ms (maximum between 70 and 130 ms in our study), followed by N100 (minimum between 90 and 170 ms in our study), a peak with opposite polarity. P200 is obvious after 200 ms (maximum between 180 and 230 ms) followed by N200 (minimum between 200 and 300 ms) of opposite polarity. P300 is the next positive peak (between 300 and 400 ms) followed by the late positive potential (LPP), whose duration is from 400 to 900 ms

arousal (high and low) as the within participants factors. The statistical analysis was performed for all EEG electrodes. For simplicity reasons as well because of the absence of laterality, only the statistic results from the central electrodes (Fz, Cz, and Pz) are presented here in detail. The F -values from the repeated measures of ANOVA statistical analysis for the main effects were used to form the topographies of ERP differences illustrating the gross underlying brain regions modulated by gender, arousal, and valence effects for each component. Fifteen topographies (five components \times three effects) were finally calculated. In summary, the ERP data are represented in terms of components' amplitude, latency, and F -topography.

Results

Two early (P100 and N100), two middle (P200 and N200) and one late components (P300), were recognized on the average ERPs for each participant and electrode. The grand average among subjects is presented in Fig. 2. The mean latencies for each component and each of the central electrodes are presented in Table 2. As for SCRs, one peak

Table 2 Mean latencies and standard deviation of each component on electrodes Fz, Cz, Pz averaged across participants and picture categories

Mean latencies of components			
Latency (ms)	Fz	Cz	Pz
P100 (max in 70–130 ms)	90.9 \pm 1.5	91.7 \pm 1.9	95.6 \pm 1.8
N100 (min in 90–170 ms)	140.9 \pm 1.6	137.7 \pm 1.7	131 \pm 3.8
P200 (max in 180–230 ms)	195.6 \pm 4.6	200.4 \pm 5.1	208.6 \pm 2.8
N200 (min in 200–300 ms)	275.2 \pm 8.5	272.9 \pm 8.1	264.5 \pm 8.5
P300 (max in 300–400 ms)	372.6 \pm 4.7	368.59 \pm 5.2	364.2 \pm 6.3

was recognized on the average waveform that was at 1.03 ± 0.18 s.

The early and middle ERP peaks elicited significant differences between males and females with respect to peak amplitude, with females showing greater absolute responses, as shown below. The ERP waveforms for the electrodes studied are shown in Fig. 3 and the P -values are shown in Table 3. The SCR recordings revealed a main effect of arousal replicating previous studies. Topographies of ERP differences reveal the gross underlying brain regions where gender, arousal, and valence effects are prominent.

Fig. 3 Grand average ERPs of Fz, Cz, and Pz for males (left) and females (right). Arousal effects on the amplitude of P300 are evident; *dashed lines* are more positive than the *solid ones*. The regions in zoom show the valence effects on N200 amplitudes of Fz and Cz where unpleasant pictures (*red lines*) evoked more negative responses. The zoomed regions of electrode Pz also depict the valence effect on latency for males, since *red lines* (unpleasant) evoke faster N200 responses, as well as, the arousal effect on latency for females, since *dashed lines* (high arousal) evoke faster N200 responses

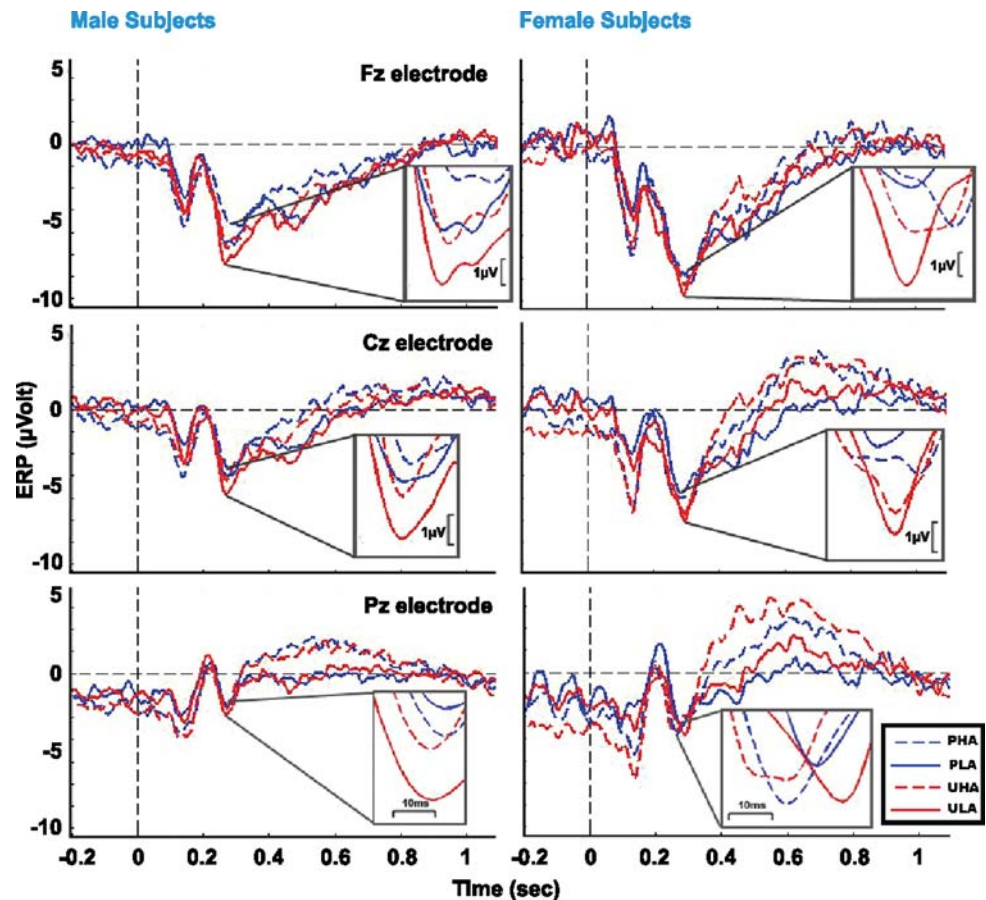


Table 3 *P*-values of the ANOVA show significant main effects on peak amplitudes

Electrode	Peak	Effect		
		Gender	Arousal	Valence
Fz	P100		$F(1,26) = 26.13, P < 0.001$	
	N100		$F(1,26) = 25.3, P = 0.0001$	
	P200			
	N200			$F(1,26) = 15.2, P = 0.0001$
	P300			$F(1,26) = 4.11, P = 0.05$
Cz	P100		$F(1,26) = 32.66, P < 0.0001$	
	N100	$F(1,26) = 4.35, P = 0.047$		$F(1,26) = 4.35, P = 0.047$
	P200			$F(1,25) = 5.61, P = 0.025$
	N200			$F(1,26) = 9.83, P = 0.0042$
	P300		$F(1,26) = 7.38, P = 0.012$	
Pz	P100		$F(1,26) = 25.91, P < 0.0001$	
	N100	$F(1,26) = 5.66, P = 0.025$	$F(1,26) = 26.1, P < 0.0001$	$F(1,26) = 8.24, P = 0.008$
	P200			
	N200	$F(1,26) = 4.54, P = 0.043$		
	P300		$F(1,26) = 37.34, P < 0.0001$	

The gender effect is dominant on N100 and N200, with females eliciting more negative responses than males, whereas arousal affects early and late components. Valence affects early, middle, and late components, with unpleasant pictures eliciting greater negativity than positive ones

Amplitudes of ERP Components

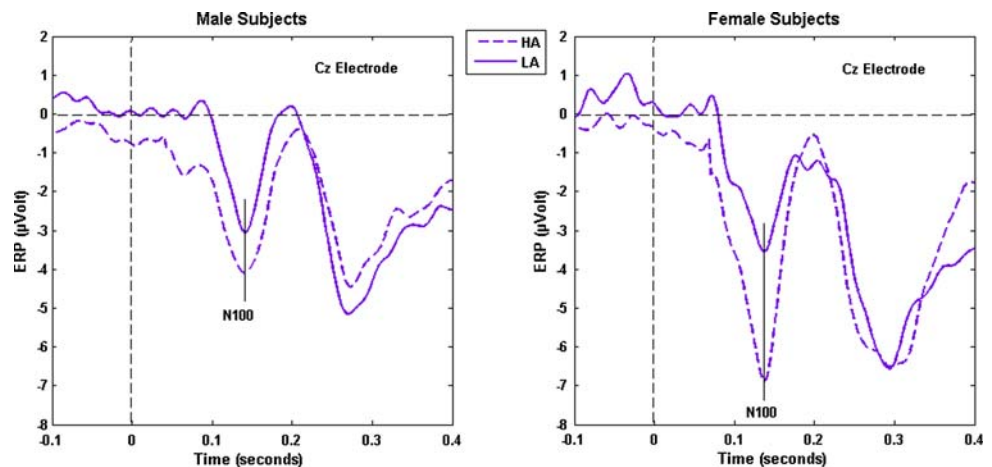
The analysis of peak amplitudes yielded significant main effects of gender, arousal and valence on early, middle, and late components (Fig. 3). Table 3 shows the significant *P*-values for the main effects of each component.

The gender effect was prominent on the negative components for the Cz and Pz electrodes, revealing a greater reaction to emotional stimuli for females. Women showed greater negativity ($-7.48 \mu\text{V}$) as compared to males ($-5.07 \mu\text{V}$) on the early N100 component on Pz. The same effect was also revealed for Cz. As for middle components, female responses on N200 of the Pz electrode were again more negative ($-5.78 \mu\text{V}$) than those of males ($-3.29 \mu\text{V}$).

There was a strong main effect of arousal on the early component P100 on all three central electrodes. Low arousing pictures elicited higher positivity than high arousing stimuli did. The N100 component was also affected by arousal on electrodes Fz and Pz, with high arousing stimuli eliciting greater negativity than low arousing pictures. For example, on Fz, the N100 amplitude was more negative ($-7.54 \mu\text{V}$) for high arousing stimuli, than for low arousing ($-5.91 \mu\text{V}$). Finally, P300 revealed arousal effects on Cz and Pz; i.e., on Pz, P300 amplitudes were higher for high arousing pictures ($2.86 \mu\text{V}$), than for low arousing ones ($1.18 \mu\text{V}$).

Valence effects are also prominent on central channels, not only for middle peaks, but also for early and late ones. On negative components (N100 and N200) the unpleasant

Fig. 4 Gender by arousal interaction is evident as the difference between high arousing (HA) and low arousing (LA) is greater in females than in males on N100 on Fz and Cz electrode



emotional stimuli elicit responses with greater negativity on all central electrodes as compared to pleasant pictures; that is, unpleasant pictures evoked greater negativity on N200 of Fz ($-9.6 \mu\text{V}$) than pleasant ones ($-8.46 \mu\text{V}$). The same effect was observed on N100 of Cz and Pz and N200 of Cz. On the other hand, on positive components (P200 of Cz and P300 of Fz), pleasant pictures provoke responses with greater positivity than unpleasant ones.

Interactions were also evident on the early component N100. On frontal and central electrodes (Fz, Cz) there were significant gender by arousal interactions. In order to analyze the gender by arousal interactions further, we collapsed the data for valence and the results showed significant differences between high and low arousal conditions on both channels; i.e., on Fz, high arousing pictures evoked more negative N100 responses, than low arousing, for both males ($t(13) = -2.48, P = 0.028$) and females ($t(13) = -4.38, P = 0.0007$), with the difference being clearly greater for females (Fig. 4).

Finally, there was a significant gender by valence interaction on the N100 of Pz. In order to analyze this further again, we collapsed the data for arousal. Results showed significant higher negativity for females ($-8.31 \mu\text{V}$) as compared to males ($-5.21 \mu\text{V}$), but only for the unpleasant pictures ($t(26) = 2.61, P = 0.015$). Furthermore, amplitudes were significantly higher for the unpleasant pictures relatively to pleasant ones only for the female group ($t(13) = 2.73, P = 0.017$) (Fig. 5).

Latencies of ERP Components

Analysis of the peak latencies revealed significant effects for the N200 component on Pz electrode. Arousal ($F(1,26) = 5.1, P = 0.032$) and valence ($F(1,26) = 5.82, P = 0.023$) modulated this peak, with high arousing pictures eliciting faster responses than low arousing ones (Fig. 6), and unpleasant pictures also evoking earlier

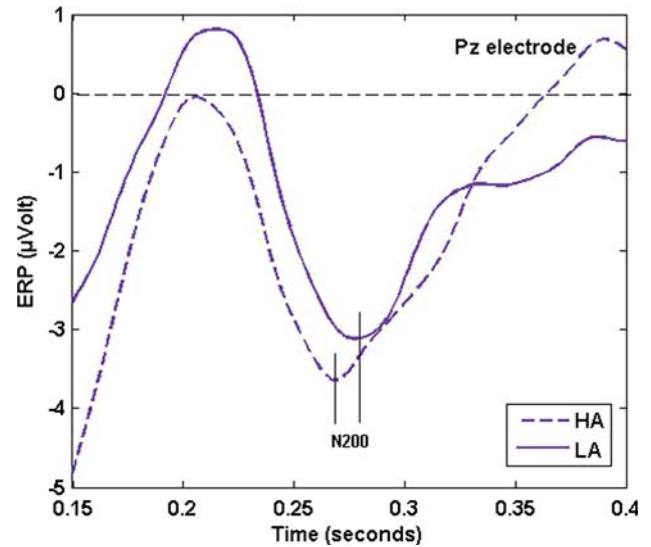


Fig. 6 High arousing pictures elicited faster N200 responses than low arousing ones on Pz electrode on both males and females ($F(1,26) = 5.1, P = 0.032$)

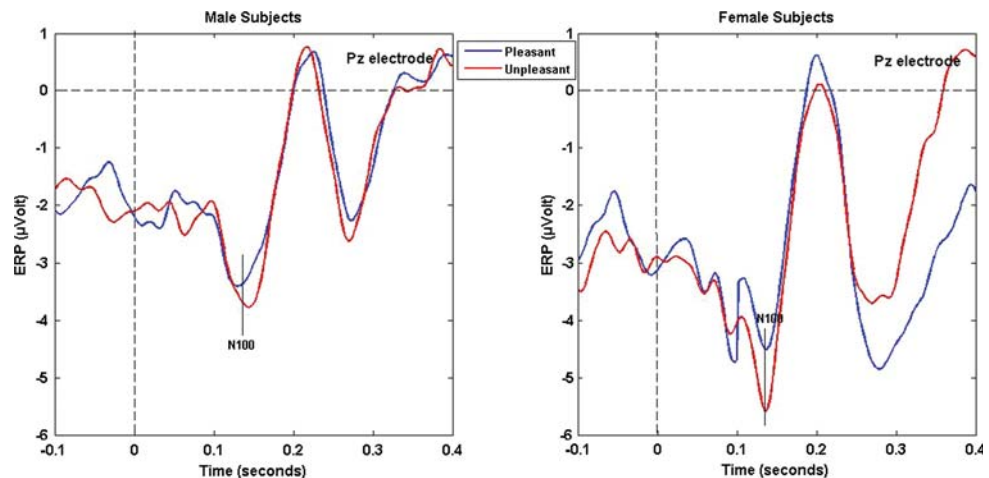
N200 components that pleasant ones for both genders (Fig. 7).

Topographies of ERP Differences

The gender effect is most prominent on negative components (N100 and N200) on the left hemisphere (Fig. 8a). This means that electrodes on the left hemisphere are those which differ between males and females during passive viewing of emotional stimuli. On P200 and P300 there is also a gender effect on the occipital right side.

Arousal (Fig. 8b) modulates all electrodes during early brain responses (P100 and N100). On P200 the brain region that differs between brain responses for high arousal and low arousal stimuli is the centroparietal region

Fig. 5 Gender by valence interaction is evident as only females exhibited difference between pleasant and unpleasant stimuli on N100 on Pz electrode



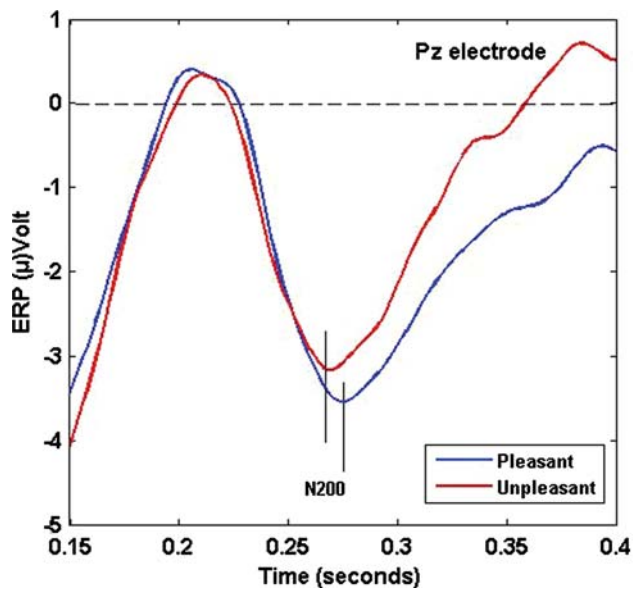


Fig. 7 Unpleasant pictures elicited faster N200 responses than pleasant ones on Pz electrode on both males and females ($F(1,26) = 5.82$, $P = 0.023$)

of the right hemisphere and the temporal region of the left hemisphere. On N200 the frontal lobe is involved. During the late component (P300), the central, parietal, and occipital electrodes are mostly affected, whereas the arousal effect is significant also on the frontal left part of the brain.

As for valence (Fig. 8c), it affects the early component N100 on the centroparietal sites mostly on the left hemisphere. On P200, the central region is affected by valence, whereas on N200 all prefrontal, frontal, and central electrodes differ in terms of processing stimuli of different valences. Finally, P300 is modulated by valence on occipital and right frontal electrodes.

SCR Amplitudes

The amplitude analysis of SCRs revealed a significant main effect of arousal ($F(1,24) = 9.67$, $P < 0.0048$). That is, highly arousing stimuli evoked greater responses (98.701 μ S) than low arousing ones (71.819 μ S). Also, there was a significant valence by arousal interaction ($F(1, 24) = 5.611$, $P < 0.026$). Planned t -tests showed significant differences between the high (113.05 μ S) and the low arousal (65.453 μ S) conditions, but only for the pleasant stimuli ($t(24) = 3.322$, $P < 0.003$).

Discussion

The aim of the present study was to investigate possible gender differences in the processing of emotional stimuli,

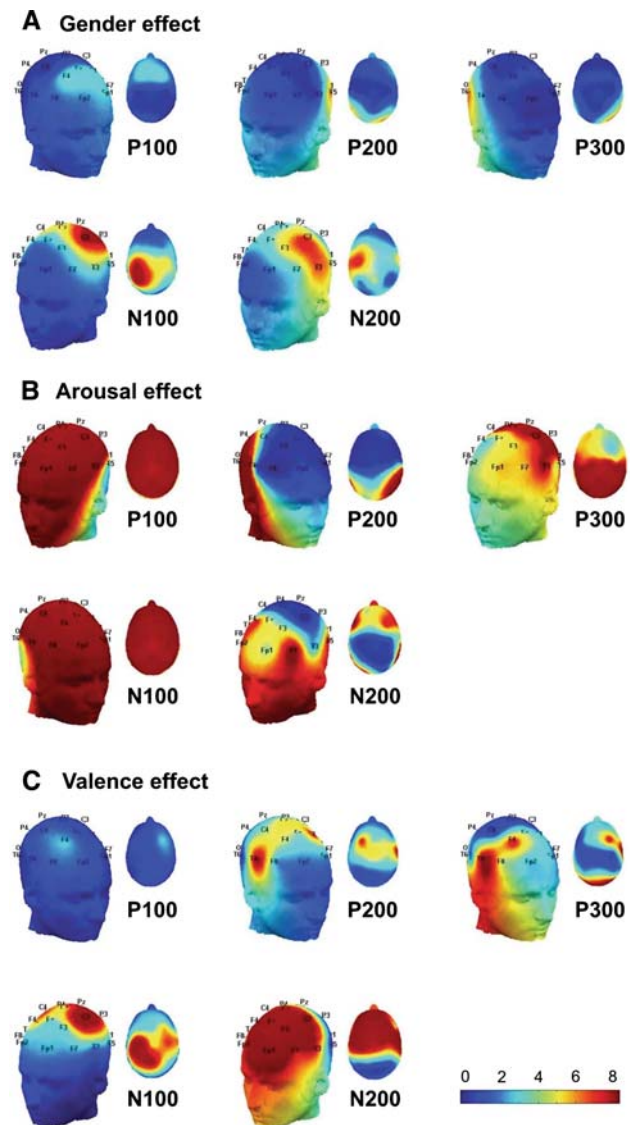


Fig. 8 Topographies of ERP amplitude differences extracted from statistical analysis of all electrodes; F -values were calculated and plotted. F -values greater than 4 represent significant main effects of gender (a), arousal (b), and valence (c) across components. Gender effects on N100 and N200 amplitude are significant on central and left hemisphere electrodes

using both ERPs and SCR measures. Unlike most of the previous studies, arousal and valence of the emotional stimuli were considered orthogonally as they seem to interact with each other (Cuthbert et al. 2000). We found that females responded with enhanced N100 and N200 in comparison to males to the visual stimuli, especially to the unpleasant ones. On the other hand, both genders responded faster to high arousing or unpleasant stimuli. As for scalp topographies, gender differences appeared to be more pronounced on central and left hemisphere areas.

Main Effects and Interactions Regarding Gender

Females showed greater negativity than males on negative components (N100 and N200) upon viewing emotional stimuli. This effect was further modulated by a gender by valence interaction on the N100 of Pz electrode; females exhibited greater negativity than males but only for the unpleasant stimuli. Similar findings were found for the arousal dimension and this is a relatively new finding in the field of gender differences. We observed arousal effects early on in the processing (N100) on frontal and central electrodes, and these effects were also modulated by gender; high arousing pictures evoked more negative response in females as compared to males. Thus, the present study adds to the existing literature in gender differences (Han et al. 2008; Chentsova-Dutton and Tsai 2007; Guillem and Mograss 2005; Kemp et al. 2004; Bradley et al. 2001; George et al. 1996; Pardo et al. 1993), showing that females respond more strongly not only to emotional or negative faces, pictures with human and sounds, but also to unpleasant emotional complex scenes of no specific content. More importantly, it shows that females respond with more negative early components to high arousing stimuli as well. This finding adds the electroencephalographic aspect to other previous electrophysiological findings regarding stronger autonomic responses, such as EMG, SCR, and heart rate, reported for women when viewing unpleasant pictures (Chentsova-Dutton and Tsai 2007; Kemp et al. 2004; Bradley et al. 2001; George et al. 1996; Pardo et al. 1993). It replicates and, in a way, generalizes the fact that women exhibited enhanced reactions to painful images (Han et al. 2008). More specifically, gender differences were identified on central and left hemisphere electrodes, as it is shown on the *F*-topographies, replicating previous EEG (Gasbarri et al. 2007) and fMRI studies (Canli et al. 2002; Cahill 2003) which indicated the over-activation of left hemisphere by females when viewing emotional stimuli.

It has been proposed that the amplitude of the middle component N200 reflects biased selective attention to task-relevant stimulus properties (e.g., color, shape, etc.) or biologically relevant stimuli such as those that are potentially dangerous (Schupp et al. 2006). We therefore suggest that selective attention in women appears to be more strongly tuned to biologically relevant stimuli. Since such differences can be mainly traced to a complex interaction or a feedback loop between underlying biological processes and social and cultural responses to values regarding gender (Brody 1997; Brody et al. 1993), one can speculate that gender differences may have been also influenced by evolutionary pressures. As a result, females, having a slighter physique, appear to exhibit a more rapid and stronger response to potentially dangerous stimuli (e.g.,

unpleasant and high arousing stimuli) which may have been useful to effectively nurture their offspring.

Despite the rather convincing evidence for gender differences in emotional processing, proposed not only by this study, but also by previous ones, there exist studies encompassing different interpretations. It has been proposed that gender differences on brain oscillations occur even during simple visual stimulation (Gutenkin and Basar 2007), and the gender differences in the emotional processing could be just an epiphenomenon of these intrinsic gender differences. These differences, found in the delta frequency band measured on parietal and occipital regions, are attributed to the basic sensory circuits which are differentiated by the “phyletic memory” (Fuster 1995; Basar 2004). However, the delta oscillations are found to affect mainly the P300 potential and the forthcoming slow wave activity (Oloffson et al. 2008). Consequently, if we had to do with an epiphenomenon, we should have observed gender differences on P300 on parietal and occipital regions as well, whereas we reported gender differences during early ERPs measured mainly in anterior areas. In addition, the fact that in our study valence and arousal interacted with gender, suggests that the parameters of the emotional stimuli affect the intrinsic gender differences to visual stimuli. Therefore, our findings can be interpreted as an enhancement of intrinsic gender differences by the arousal and valence of the stimuli, resulting to gender differences in terms of emotional processing.

Unlike other studies (Bradley et al. 2001; Chentsova-Dutton and Tsai 2007), autonomic responses (SCRs) were not modulated by gender. However, the validity of this conclusion may be compromised by a procedural limitation. It turned out that although, the ISI was long enough for a recognizable rise in the SCR to be seen in response to a stimulus; it was not long enough to separate different SCR components, i.e., for the SCR signal to return to its baseline level. To deal with this limitation, we employed the amplitude of SCR, a rather weak measure that may have obscured gender differences.

There was no significant three-way interaction of gender by valence by arousal. It seems that gender differences are not greater for stimuli that are both unpleasant and high arousing. This fact adds evidence to the independency of valence and arousal in the way both genders perceive and process emotional stimuli in terms of ERP responses.

To sum up, our data support the notion that females respond more in terms of ERP amplitudes to unpleasant or high arousing stimuli relative to males. The brain mechanisms responsible for these mechanisms are most likely localized in the central and left brain regions, as suggested by the brain topography analysis. The robust gender effect on negative components suggests that brain regions that recognize the valence of stimuli early on in the stream of

processing are more finely tuned. This conclusion is consistent with the evolutionary hypothesis of sex differences in emotional processing; the brain of men and women differ not only anatomically, but also functionally (Cahill 2005). Furthermore, these findings are relevant within the context of gender differences in the prevalence of mood disorders such as depression, and the post-traumatic stress disorder (PTSD). Both disorders are twice as likely to occur in women as in men (Kessler 2003; Kendler et al. 2001; Breslau et al. 1997), presumably because of the differential response of women to stressful stimuli of everyday life.

Main Effects and Interactions Regarding Valence (Pleasure) and Arousal

The analyses of the peak latency data yielded significant results, not reported in previous literature to our knowledge. The unpleasant and the high arousing stimuli appear to elicit faster responses in both genders. These findings suggest that the prioritization of emotional, unpleasant, and high arousing, stimuli is not only reflected in stronger brain activity (increased amplitude), but also in the temporal course of this activity, since it occurs faster than the processing of pleasant or low arousing stimuli. The faster response to unpleasant or high arousing stimuli can be seen in an evolutionary context, underlying the necessity for immediate reaction to potentially life-threatening stimuli and situations.

The effects of arousal and valence on ERP amplitudes are also in agreement with previous findings. Studies have shown that the early N100 component is associated with attentional process modulated by the valence dimension (for a review see Oloffson et al. 2008). The valence effect observed in our study was most prominent on N200 of Cz and Pz electrodes, with unpleasant pictures eliciting greater responses than pleasant ones. The amplitude modulations of early ERP components were greater for unpleasant stimuli, consistent with the suggestion that unpleasant stimuli preferentially attract attention early in the information processing system (Oloffson et al. 2008). Recent studies proposed that pleasant stimuli yielded more positive components, such as P300 (Cuthbert et al. 2000; Flaisch et al. 2008). Our study shows an enhancement of both positive (P300) and negative (N100 and N200) components for unpleasant stimuli.

Amplitudes of early components were strongly modulated by arousal on almost all electrodes as shown in Fig. 8b. Particularly, on the N100 component of Pz, high arousing stimuli evoked enhanced responses than low arousing ones. This finding adds to the study of Keil et al. (2003), where affectively arousing pictures were found to be associated with enhanced reactions at parieto-occipital

sites. An unexpected result was the greater positivity elicited by low arousing stimuli on the P100 component. Although it is not clear which factor contributed most for this effect, the early modulation of the ERP by the emotional and arousing properties of the stimulus support the hypothesis of preferential processing of affective stimuli.

As for the late, P300, component, which indexes attentional processes and initial memory storage of events (Polich 2007), arousal effects were significant on centro-parietal sites on both hemispheres, as it is shown in the topographies, in terms of amplitude. High arousing pictures evoked greater positivity than low arousing ones to both males and females. This is in line with previous results (Bradley et al. 2007; Cuthbert et al. 2000; Schupp et al. 2006; Schupp et al. 2007; Delplanque et al. 2006). Valence also seems to modulate P300 when arousal level is controlled (Cano et al. 2008; Conroy and Polich 2007; Cuthbert et al. 2000). Thus, studies have shown that pleasant pictures elicit greater positivity on P300 (Cano et al. 2008; Conroy and Polich 2007; Cuthbert et al. 2000). This finding was also supported by our study where the valence effect on P300 is prominent on occipital, temporal, and frontal regions as shown in the topographies (Figs. 8c).

Last but not least, although the skin conductance responses have lower temporal sensitivity than ERPs, they nevertheless produced clear results. High arousing pictures elicited higher SCR than low arousing did. This was expected and it is in agreement with past literature (Anonkin et al. 2006; Bradley et al. 2001).

Finally, we did not find a significant two-way valence by arousal interaction concerning ERPs, whereas such an interaction was present in the SCR data. That is, although both factors affected brain components, ERP amplitudes were not greater for unpleasant-high-arousing stimuli and pleasant-low-arousing stimuli as suggested by previous behavioral studies (Robinson et al. 2004) and the Continuum Model of Significance Processing (Williams and Gordon 2007). However, as regards autonomic responses, valence interacted with arousal in electrodermal activity measurements. As a result, we cannot clearly confirm or reject the hypothesis that valence and arousal are independently processed by human brain.

Limitations

We list here some limitations of our study that could in principle allow for modifications in the interpretation of our results.

The performed analysis may be limited as the side of differences on brain activation was considered in a rather gross way (left/right, frontal/central/posterior); in addition a relatively low number of electrodes (19) was used and

our choice of filtering (0.5–40 Hz) resulted to the elimination of high frequency EEG activity. Future EEG studies with high density electrodes may confirm and expand these results. Also, Magnetoencephalographic (MEG) studies could further examine emotional processing, as MEG provides better localization accuracy (Leahy et al. 1998) of a few mm (Papadelis et al. 2009).

Unlike most of the previous studies we manipulated orthogonally the valence and arousal dimensions of the stimuli, as they appear to interact (Cuthbert et al. 2000). We decided to select stimuli of similar affective content level for males and females, as the two genders perceive emotional context in a different way. However, IAPS collection in its current form does not provide enough pictures rated with similar ratings by both genders to perform such a study. In order to achieve similar affective content level of the stimuli for males and females, we used the gender-specific ratings provided by the IAPS collection. This limitation of IAPS collection has been discussed by previous studies. Cuthbert et al. (2000) report that ‘unpleasant pictures show a high positive correlation between valence and arousal that is particularly pronounced for female subjects.’ Rozenkrants and Polich (2008) selected images of similar affective content level; those whose mean ratings of males and females did not differ significantly (only 16 pictures of each category). We should take also into account that in previous studies involving male or female participants only, the gender-specific ratings and not the overall ones were selected for the experiment (Bernat et al. 2006; Anonkin et al. 2006).

In conclusion, our study provides evidence for gender differences in the way stimuli with different valence and arousal are processed. The subjective nature, however, of valence and arousal allows the possibility that the observed gender differences may be due, at least partly, to the presentation of different stimuli to the participants.

Acknowledgments This work has been benefited from a grant by the Greek General Secretariat for Research and Technology. Assistance with the experiment preparation and recordings from Mr. S. Tsemberlidis and Ms. G. Germanidou is also gratefully acknowledged.

Open Access This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

- Aftanas LI, Lotova NV, Koshkarov VI, Popov SA, Makhnev VP (1997) Non-linear forecasting measurements of the human EEG during evoked emotions. *Brain Topogr* 10:155–162
- Alfano KM, Cimino C (2008) Alteration of expected hemispheric asymmetries: valence and arousal effects in neurophysiological models of emotion. *Brain Cogn* 66:213–220
- Amrhein C, Muhlberger A, Pauli P (2004) Modulation of event-related brain potentials during affective picture processing: a complement to startle reflex and skin conductance response? *Int J Psychophysiol* 54:231–240
- Anonkin AP, Golosheykin S, Sirevaag E, Kristjansson S, Rohrbaugh JW, Heath AC (2006) Rapid discrimination of visual scene content in the human brain. *Brain Res* 1093:167–177
- Bachorowski J, Owren MJ (2003) Sounds of emotion production and perception of affect-related vocal acoustics. *Ann N Y Acad Sci* 1000:244–265
- Barrett LF (1998) Discrete emotions or dimensions? The role of valence focus and arousal focus. *Cogn Emot* 12:579–599
- Barrett LF, Russell JA (1999) The structure of current affect: controversies and emerging consensus. *Am Psychol Soc Bull* 8:10–14
- Basar E (2004) Memory and brain dynamics: oscillations integrating attention, perception, learning and memory. CRC Press, Boca Raton
- Bernat E, Patrick CJ, Benning SD, Tellengen A (2006) Effects of picture content and intensity on affective physiological response. *Psychophysiology* 43:93–103
- Bradley MM, Lang PJ (1994) Measuring emotion: the self-assessment manikin and the semantic differential. *J Behav Ther Exp Psychiatry* 25:49–59
- Bradley MM, Codispoti M, Sabatinelli D, Lang PJ (2001) Emotion and motivation II: sex differences in picture processing. *Emotion* 1:300–319
- Bradley MM, Hamby S, Low A, Lang PJ (2007) Brain potentials in perception: picture complexity and emotional arousal. *Psychophysiology* 44:364–373
- Breslau N, Davis GC, Andreski P, Peterson EL, Schultz LR (1997) Sex differences in posttraumatic stress disorder. *Arch Gen Psychiatry* 54:1044–1048
- Brody LR (1997) Gender and emotion: beyond stereotypes. *J Soc Issues* 53:369–394
- Brody LR, Hall JA, Lewis M, Haviland JM (1993) Gender and emotion. Guilford Press, New York
- Cacioppo JT, Bernston GG (1994) Relationships between attitudes and evaluative space: a critical review with emphasis on the separability of positive and negative substrates. *Psychol Bull* 115:401–423
- Cahill L (2003) Sex and hemisphere-related influences on the neurobiology of emotionally influenced memory. *Ann N Y Acad Sci* 985:163–173
- Cahill L (2005) His brain, her brain. *Sci Am* 292:40–47
- Cahill L (2006) Why sex matters for neuroscience. *Nat Rev Neurosci* 7:477–484
- Cahill L, McGaugh JL (1998) Mechanisms of emotional arousal and lasting declarative memory. *Trends Neurosci* 21:294–299
- Canli T, Desmond JE, Zhao Z, Gabrieli JDE (2002) Sex difference in the neural basis of emotional memories. *Proc Natl Acad Sci* 99:10789–10794
- Cano ME, Class QA, Polich J (2009) Affective valence, stimulus attributes and P300: colors vs. black/white and normal vs. scrambled images. *Int J Psychophysiol* 71:17–24
- Chentsova-Dutton YE, Tsai JL (2007) Gender differences in emotional response among European Americans and among Americans. *Cogn Emot* 21:162–181
- Codispoti M, Ferrari V, Bradley MM (2006) Repetitive picture processing: autonomic and cortical correlates. *Cogn Brain Res* 1068:213–220
- Conroy MA, Polich J (2007) Affective valence and P300 when stimulus arousal level is controlled. *Cogn Emot* 21:891–901

- Cuthbert BN, Schupp HT, Bradley MM, Birbaumer N, Lang PJ (2000) Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biol Psychol* 52:95–111
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134:9–21
- Delplanque S, Silvert L, Hot P, Rigoulot S, Sequeira H (2006) Arousal and valence effects on event-related P3a and P3b during emotional categorization. *Int J Psychophysiol* 60:315–322
- Delplanque S, N'diaye K, Scherer K, Grandjean D (2007) Spatial frequencies or emotional effects? A systematic measure of spatial frequencies for IAPS pictures by a discrete wavelet analysis. *J Neurosci Methods* 165:144–150
- Dolcos F, Cabeza R (2002) Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. *Cogn Affect Behav Neurosci* 2:252–263
- Ekman A, Flink R, Sundman E, Eriksson LI, Brudin L, Sandin R (2007) Neuromuscular block and the electroencephalogram during sevoflurane anaesthesia. *Neuroreport* 18(17):1817–1820
- Flaisch T, Stockburger J, Schupp HT (2008) Affective prime and target picture processing: an ERP analysis of early and late interference effects. *Brain Topogr* 20:183–191
- Fuster JM (1995) Memory in the cerebral cortex—an empirical approach to neural networks in the human and non-human primate. MIT Press, Cambridge, MA
- Gasbarri A, Arnone B, Pompili A, Pacitti F, Pacitti C, Cahill L (2007) Sex related hemispheric lateralization of electrical potentials evoked by arousing negative stimuli. *Brain Res* 1138:178–186
- George MS, Ketter TA, Parekh PI, Herscovitch P, Post RM (1996) Gender differences in regional cerebral blood flow during transient self-induced sadness or happiness. *Biol Psychiatry* 40:859–871
- Gerber AJ, Posner J, Gorman D, Colibazzi T, Yu S, Wang Z, Kangarlu A, Zhu H, Russell J, Peterson BS (2008) An affective circumplex model of neural systems subserving valence, arousal and cognitive overlay during the appraisal of emotional faces. *Neurophysiologia* 46:2129–2139
- Gianotti LRR, Faber PL, Schuler M, Pasqual-Marqui RD, Kochi K, Lehmann D (2008) First valence, then arousal: the temporal dynamics of brain electric activity evoked by emotional stimuli. *Brain Topogr* 20:143–156
- Guillem F, Mograss M (2005) Gender differences in memory processing: evidence from event-related potentials to faces. *Brain Cogn* 57:84–92
- Gutenkin B, Basar E (2007) Brain oscillations are highly influenced by gender differences. *Int J Psychophysiol* 65:294–299
- Hall JA (1978) Gender effects in decoding nonverbal cues. *Psychol Bull* 85:845–857
- Han S, Fan Y, Mao L (2008) Gender difference in empathy for pain: an electrophysiological investigation. *Brain Res* 1196:85–93
- Jasper H (1958) Report of committee on methods of clinical exam in EEG. *Electroencephalogr Clin Neurophysiol* 10:370–375
- Jung TP, Makeig S, Humphries C, Lee TW, Mckeown MJ, Iragui V, Sejnowski TJ (2000) Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37:163–178
- Keil A, Bradley MM, Hauk O, Rockstroh B, Elbert T, Lang P (2002) Large-scale neural correlates of affective picture processing. *Psychophysiology* 39:641–649
- Keil A, Gruber T, Muller MM, Moratti S, Stolarova M, Bradley MM, Lang PJ (2003) Early modulation of visual perception by emotional arousal: evidence from steady-state visual evoked brain potentials. *Cogn Affect Behav Neurosci* 3:195–206
- Kemp AH, Silberstein RB, Armstrong SM, Nathan PJ (2004) Gender differences in the cortical electrophysiological processing of visual emotional stimuli. *NeuroImage* 16:632–646
- Kendler KS, Thornton LM, Prescott CA (2001) Gender differences in the rates of exposure to stressful life events and sensitivity to their depressogenic effects. *Am J Psychiatry* 158:587–593
- Kessler RC (2003) Epidemiology of women and depression. *J Affect Disord* 74:5–13
- Kring AM, Gordon AH (1998) Sex differences in emotion: expression, experience and physiology. *J Pers Soc Psychol* 74:686–703
- Krumhansl CL (2002) Music: a link between cognition and emotion. *Curr Dir Psychol Sci* 11:45–50
- Lang PJ (1968) Fear reduction and fear behaviour: problems in treating a construct. In: Schlien J (ed) *Research in psychotherapy*, vol 3. American Psychological Association, Washington, DC, pp 90–103
- Lang PJ (1984) Cognition in emotion: concept and action. In: Izard CE, Kagan J, Zajonc RB (eds) *Emotions, cognition, and behaviour*. Cambridge University Press, New York, pp 192–226
- Lang PJ, Bradley MM, Cuthbert BN (1997) Motivated attention: affect, activation, and action. In: Lang PJ, Simons RF, Balaban M (eds) *Attention and orienting: sensory and motivational processes*. Erlbaum Associates, Hillsdale, NJ
- Lang PJ, Bradley MM, Cuthbert BN (1998) Emotion motivation and anxiety: brain mechanisms and psychophysiology. *Biol Psychiatry* 44:1248–1263
- Leahy RM, Mosher JC, Spencer ME, Huang MX, Lewine JD (1998) A study of dipole localisation accuracy for MEG and EEG using a human skull phantom. *Electroencephalogr Clin Neurophysiol* 107:159–173
- Leon-Carrion J, Damasb J, Izzetoglu K, Pourrezai K, Martin-Rodriguez JF, Barroso y Martin JM, Dominguez-Morales MR (2006) Differential time course and intensity of PFC activation for men and women in response to emotional stimuli: a functional near-infrared spectroscopy (fNIRS) study. *Neurosci Lett* 403:90–95
- Olofsson JK, Nordin S, Sequeira H, Polich J (2008) Affective picture processing: an integrative review of ERP findings. *Biol Psychol* 77:247–265
- Panksepp J, Bernatzky G (2002) Emotional sounds and the brain: the neuro-affective foundations of musical appreciation. *Behav Processes* 60:133–155
- Papadelis C, Poghosyan V, Fenwick PBC, Ioannides AA (2009) MEG's ability to localise accurately weak transient neural sources. *Clin Neurophysiol* 120:1958–1970
- Pardo JV, Pardo PJ, Raichle ME (1993) Neural correlates of self-induced dysphoria. *Am J Psychiatry* 150:713–719
- Polich J (2007) Updating P300: an integrative theory of P3a and P3b. *Clin Neurophysiol* 118:2128–2148
- Proverbio AM, Zani A, Adorni R (2008) Neural markers of greater female responsiveness to social stimuli. *BMC Neurosci* 9:56
- Reinsezein R (1994) Pleasure-arousal theory and the intensity of emotions. *J Pers Soc Psychol* 67:525–539
- Robinson MR, Storbeck J, Meier BP, Kirkeby BS (2004) Watch out! That could be dangerous: valence-arousal interactions in evaluative processing. *Pers Soc Psychol Bull* 30:1472–1484
- Rozenkrants B, Polich J (2008) Affective ERP processing in a visual oddball task: arousal, valence, and gender. *Clin Neurophysiol* 119:2260–2265
- Russell JA (1980) A circumplex model of affect. *J Pers Soc Psychol* 39:1161–1178
- Russell JA (1989) Measures of emotion. In: Plutchik R, Kellerman H (eds) *Emotion: theory, research and experience*, vol 4. Academic Press, San Diego, CA, pp 83–111
- Schirmer A, Kotz SA, Friederici AD (2002) Sex differentiates the role of emotional prosody during word processing. *Cogn Brain Res* 14:228–233

- Schirmer A, Striano T, Friederici AD (2005) Sex differences in the preattentive processing of vocal emotional expressions. *Neuroreport* 16:635–639
- Schneider F, Habel U, Kessler C, Salloum JB, Posse S (2000) Gender differences in regional cerebral activity during sadness. *Hum Brain Mapp* 9:226–238
- Schupp HT, Stockburger J, Codispoti M, Junghofer M, Weike AI, Hamm AO (2006) Stimulus novelty and emotion perception: the mean absence of habituation in the visual cortex. *Neuroreport* 17:365–369
- Schupp HT, Stockburger J, Junghofer M, Weike AI, Hamm AO (2007) Selective visual attention to emotion. *J Neurosci* 27:1082–1089
- Wild B (2003) Are emotions contagious? Evoked emotions while viewing emotionally expressive faces: quality, quantity, time course and gender differences. *Psychiatry Res* 102:109–124
- Williams LM, Gordon E (2007) Dynamic organization of the emotional brain: responsivity, stability and instability. *Neuroscientist* 13:349–370
- Wrase J, Klein S, Gruesser SM, Hermann D, Flor H, Mann K, Braus DF, Heinz A (2003) Gender differences in the processing of standardized emotional visual stimuli in humans: a functional magnetic resonance imaging study. *Neurosci Lett* 348:41–45
- Xiong Y, Mahmood A, Lu D, Gu C, Goussev A, Schallert T, Chopp M (2007) The role of gender in outcome after traumatic brain injury and therapeutic effect of erythropoietin in mice. *Brain Res* 1185:301–312
- Zhang XM, Zhu SW, Duan RS, Mohammed AH, Windblad B, Zhu J (2008) Gender differences in susceptibility to kainic acid-induced neurodegeneration in aged C57BL/6 mice. *Neurotoxicology* 29:406–412