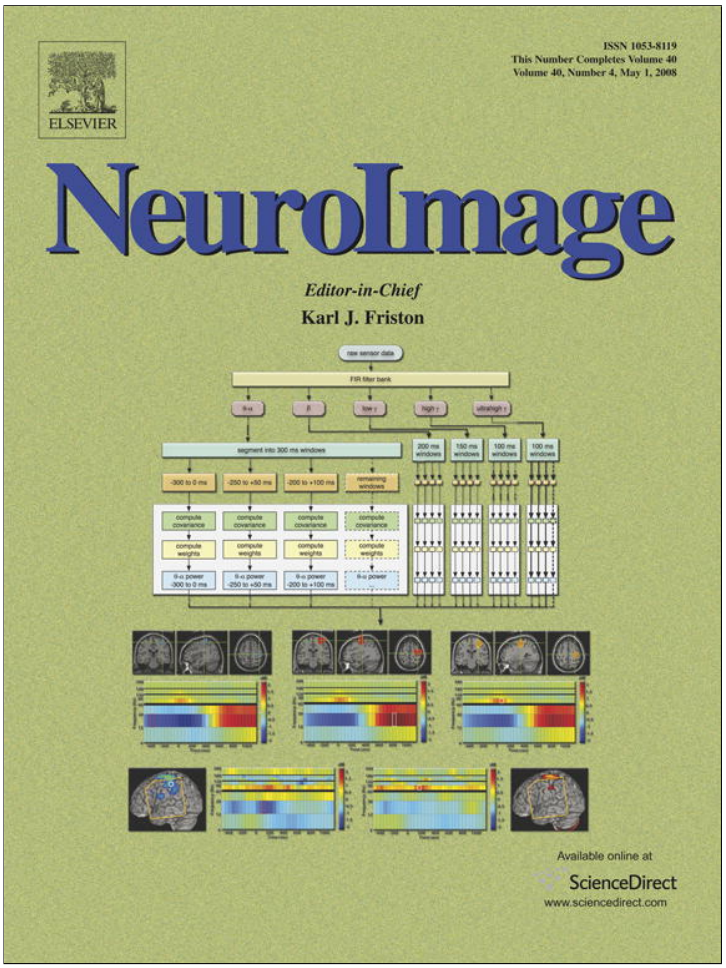

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The neural mechanism underlying the female advantage in identifying negative emotions: An event-related potential study

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Previous studies have extensively reported an advantage of females in identifying negative facial emotions as compared with males. Nevertheless, why females are better in performance relative to males during emotion recognition tasks is still unknown, and the neural mechanism(s) underlying this phenomenon has yet to be directly investigated. As facial affects convey emotional information which is adaptively important and the recognition of a given facial affect generally evokes individuals' emotion of the same type [Dimberg, U., 1997. Facial reactions: rapidly evoked emotional responses. J. Psychophysiol. 11, 115–123], the present study assumes that the female advantage in emotion recognition may result from the attenuated sensitivity of males to emotionally negative stimuli of lesser valence intensity compared to that of females. In contrast, each gender may be comparably sensitive to emotionally negative stimuli of enhanced salience as suggested by the emotional negativity bias. To test this hypothesis, event-related potentials were recorded for highly negative (HN), moderately negative (MN), and Neutral deviant images while subjects (15 males, 15 females) perform a standard/deviant categorization task, irrespective of the emotional valence of deviants. The results demonstrated more negative ERP deflections during HN condition than during MN and Neutral conditions at early N2 and later P3 components, irrespective of gender. Moreover, MN condition elicited significantly more negative deflections than the Neutral condition across N2 and P3 components only in females, and the MN−Neutral difference waveform in females during 250–450 ms interval was localized to the right prefrontal cortex. Thus, apart from the increased sensitivity of both genders to the highly negative stimuli, the present study demonstrated that women, instead of men, are sensitive to emotionally negative stimuli of lesser saliency, which may be an important mechanism underlying the female advantage in identifying negative emotions, and the right prefrontal cortex may be the neural basis underlying the female-specific sensitivity to emotionally negative stimuli of lesser salience.

Keywords: Gender differences; ERP; Emotional negativity bias; Right prefrontal cortex

Introduction

Considerable studies have revealed a gender-related dimorphism during the processing of emotional stimuli (Montagne et al., 2005; Brebner, 2003; Campanella et al., 2004; Hall, 1978; Schirmer et al., 2002; Miura, 1993; Scholten et al., 2005). Among these studies, one of the most noticeable observations is that males, as compared with females, are less capable of labeling negative affects. Apart from the early reports that females are of advantage to understanding emotional expressions from faces, gestures and voices, males were shown less accurate in recognizing emotions from faces, in particular, in recognizing negative emotions such as fear, disgust, and sadness (Hall, 1978; Miura, 1993). More recently, the studies related to psychosocial aspects of depression suggested that interpersonal communications through non-verbal emotional cues are more pronounced in females than in males (Campanella et al., 2004; Harris, 2001). Moreover, the study by Scholten et al. (2005) found that when asked to identify facial affects, healthy males had lower accuracy scores than healthy females in recognizing negative emotions, and the performances in male patients with schizophrenia were impaired to a greater extent compared with those in female patients. The similar results were also reported by Montagne et al. (2005), who observed that females were more accurate in labeling negative emotions like sadness and could identify negative facial affects (e.g. anger, disgust) at a lower emotional saturation level relative to males.

As stated above, it is apparent that males are less competent in identifying negative emotions as compared to females. This is likely

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to be attributed to the reduced sensitivity of males to emotionally negative stimuli relative to females since previous studies showed that the same emotionally negative pictures activated more neural substrates as well as greater cerebral activation values (e.g. in amygdala) in females relative to males (Wrase et al., 2003; Hofer et al., 2006; Orozco and Ehlers, 1998). In addition, the semantic processing is less susceptible to emotionally negative prosody in males relative to females, suggesting that the ongoing cognitive activities in males are less likely to be influenced by emotionally negative stimuli than those in females (Schirmer et al., 2004). Nevertheless, since emotional negativity bias that emotionally negative stimuli, due to their important adaptive values, are processed preferentially throughout the information processing stream has been well established (Ito et al., 1998; Delplanque et al., 2004; Huang and Luo, 2006; Yuan et al., 2007a,b), it seems unlikely that males have reduced sensitivity as compared with females to emotionally negative stimuli at all levels of valence intensity. In fact, the valence of the negative event is important as the human brain has differential sensitivity to emotionally negative events of varying valences, with greater emotional reactivity to extremely negative events than to moderately negative events even when individuals are engaged in a non-emotional task (Yuan et al., 2007a,b). On the other hand, it is often seen in life settings that males show fewer emotional responses to the negative events of lesser saliency, which, however, could elicit prominent emotional reactivity in females (most noticeably, prominent emotional responses are easily seen in females when they come across unpredictable beetles, which typically elicit less emotional reactivity in males). Thus, it is possible that males, similar to females, are sensitive to emotionally negative events with high salience as predicted by emotional negativity bias, whereas males may be less sensitive to negative stimuli of lesser valence intensity relative to females, which may be an important mechanism underlying the female advantage in identifying negative emotions.

Thus, the present study hypothesizes that humans, irrespective of gender, are sensitive to emotionally negative stimuli of high saliency such that both genders would show pronounced processing biases for highly negative stimuli at some information processing stages; however, as the valence intensity decreases to a moderate level, it is possible to observe a gender-related dimorphism that the brain sensitivity to the negative stimuli is preserved in females whereas this sensitivity is prominently reduced in males. As a result, females would still manifest prominent emotional responses to the lesser valenced negative stimuli whereas the emotional responses to the same stimuli in males would be unapparent, or even absent if subjects are engaged in a non-emotional task. For a test of this hypothesis, via high temporal resolution ERP technique, the present study mainly investigated the effect of gender on human emotional responses to negative stimuli of varying valences. As emotional responses are often triggered by unpredictable stimuli during non-emotional activities in the natural settings (most commonly in social interaction situations, some accidental words from other people offend us in a conversation) (Delplanque et al., 2005; Yuan et al., 2007a). Thus, the present study used an implicit emotional task that does not require subjects to evaluate valence, consequently to allow emotional responses in the laboratory setting to more closely resemble nature (Yuan et al., 2007a). More specifically, previous studies indicated that the early perceptual and attentional processes, as indexed by early P2 and N2 components, were modulated by emotional valence (Carreti′e et al., 2001, Huang and Luo, 2006, Carretie′ et al., 2004), and the later higher cognitive processes such as the stimulus evaluation and response decision making, as is typically reflected by late positive complex (LPC), are also influenced by emotional saliency (Ito et al., 1998; Yuan et al., 2007a,b). We predicted that some ERP components, such as attention-related N2 and evaluation-related P3, would see Gender by Valence interaction effects and manifest some temporal features of gender differences during the processing of emotional stimuli of varying valences.

The present study used a modified oddball paradigm that required subjects to make a standard/deviant distinction by pressing different keys, irrespective of the emotional valence of the deviants. Rather than requiring a single response for the deviants, we designed two responses to mask the true purpose of the experiment, so as to avoid a "relevance-for-task" effect that was repeatedly reported to obscure the effect of valence on ERPs (Carreti′e et al., 1996, 2001). Moreover, according to P.J Lang's theory of emotional dimensions (Lang, 1995), valence (ranging from unpleasant to pleasant) and arousal (ranging from calm to excited) are the two primary dimensions that should be considered in emotional studies. Thus, the emotional studies that address valence effect on ERPs need to control for arousal influences across valence conditions (Lang, 1995; Johnson, 1993). Because the present study focuses on the gender-related valence effect on ERPs, and arousal influence was indicated to mask the valence effect on ERPs non-specifically (Carretie' et al., 1997; Johnson, 1993), the stimulus materials used in the present study were the standardized emotional pictures whose valence and arousal values were normatively rated, consequently to facilitate the control for arousal influences on ERPs (Carretie′ et al., 1997; Johnson, 1993). Since a cultural bias for the International Affective Picture System (IAPS) has been reported in Chinese subjects (Huang and Luo, 2004), the pictures used to elicit emotional responses in the current study were from the native Chinese Affective Picture System (CAPS)[1] (Yuan et al., 2007a; Bai et al., 2005). In addition, as the arousal variation from emotional stimuli to Neutral stimuli would confound the emotional effect on ERPs, in the present study, emotional pictures were selected in such a way that the arousal level was matched across the three valence conditions, in particular, between the neutral images and the two valence-differed image groups.

Materials and methods

Subjects

As paid volunteers, 15 female (18–22 years; M=20.6 years) and 15 male (18–23 years; M=21.1 years) undergraduate students participated in the experiment. All subjects were healthy, right-handed, had normal or corrected to normal vision, and had no history of

[1] The standardized CAPS was developed in key laboratory of mental health, Chinese academy of sciences in order to avoid the cultural bias of emotional inducement found in Chinese participants when IAPS was used. The CAPS introduced a number of pictures characterized by oriental natural scenes and oriental faces. The development method of this native emotional picture system is similar to that of IAPS. For the CAPS development, originators first collected over 2000 pictures of various contents for the system development, and finally kept 852 pictures most of which are typical of Chinese cultures for the normative ratings. Chinese college students (gender-matched) were recruited to rate the valence, arousal, and dominance by a self-report 9-point rating scale for the 852 pictures of the system. The pretest for this system showed that CAPS is reliable across individuals in emotional inducement (the between-subjects reliability scores were 0.982 for valence and 0.979 for arousal). More details about CAPS are accessible in Bai et al. (2005).

affective disorder. All participants signed an informed consent form for the experiment. The experimental procedure was in accordance with the ethical principles of the 1964 Declaration of Helsinki (World Medical Organization, 1996).

Stimuli

The present study adopted the modified oddball paradigm which consisted of 6 blocks of 100 trials, and each block included 70 standard and three conditions of 10 deviants. All deviants were pictures taken from the Chinese Affective Picture System (CAPS). A natural scene of cup served as the frequent standard picture and 30 pictures grouped as either highly negative (HN), moderately negative (MN), or Neutral served as the deviants. The sequence of standard and deviant pictures was randomized for each subject. Three groups of deviant pictures were selected in such a way that they differed significantly in valence from one another [mean: HN = 1.85, MN = 3.52, Neutral = 5.46; $F(2,87) = 266.19$, $P < 0.001$. Max(HN) = 2.20, Min(MN) = 2.98] but were similar in arousal (mean: HN = 6.08, MN = 5.80, Neutral = 5.86; $F(2,87) = 1.49$, $P = 0.23$). All the pictures were identical in size and resolution (15 cm × 10 cm, 100 pixels per inch). In addition, the luminance level of the pictures used was tested prior to experiment, and the luminance level was matched across the three valence conditions. The contrast of the monitor was set to a constant value across subjects.

Behavioral procedures

Subjects were seated in a quiet room at approximately 150 cm from a computer screen with the horizontal and vertical visual angles below 6°. Prior to the experiment, all subjects were told that the purpose of the study was to investigate their ability to make a fast response selection and their ability to inhibit the prepotent response to the frequent picture when the deviant appears. At the end of each of the six blocks, accuracy rates for both standard and deviant stimuli were given to the subjects as a feedback of their performance. Each trial was initiated by a 300 ms presentation of a small black cross on the white computer screen; then, a blank screen whose duration varied randomly between 500 and 1500 ms was followed by the onset of picture stimulus. Each subject was instructed to press the "F" key on the keyboard with their left index finger as accurately and quickly as possible if the standard picture appeared and to press the "J" key with their right index finger if the deviant picture appeared. The stimulus picture was terminated by key pressing or was terminated when it elapsed for 1000 ms. Therefore, each subject was informed that their responses must be made under 1000 ms. Each response was followed by 1000 ms of a blank screen. Pre-training with 10 practice trials was used before formal experiment in order to familiarize subjects with the procedure, and the standard picture in pre-training was the same as that in the subsequent experiment whereas the deviants for pre-training were neutral pictures that were not selected for the formal experiment. All subjects achieved 100% accuracy on 10 practice trials prior to the formal experiment.

ERP recording and analysis

The EEG was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products), with the average reference on the left and right mastoids and a ground electrode on the medial frontal aspect. The vertical electrooculograms (EOGs) were recorded supra- and infra-orbitally at the left eye. The horizontal EOG was recorded from the left versus right orbital rim. The EEG and EOG were amplified using a DC ~100 Hz bandpass and continuously sampled at 500 Hz/channel. All inter-electrode impedance was maintained below 5 kΩ. Averaging of ERPs was computed off-line; trials with EOG artifacts (mean EOG voltage exceeding ±80 μV) and those contaminated with artifacts due to amplifier clipping, peak-to-peak deflection exceeding ±80 μV were excluded from averaging.

EEG activity for correct response in each valence condition was overlapped and averaged separately. ERP waveforms were time-locked to the onset of stimuli and the average epoch was 1200 ms, including a 200 ms pre-stimulus baseline. As shown by ERPs' grand average waveforms and topographical map (see Figs. 1 and 2), prominent central and frontal N2 components, and broadly distributed P3 components were elicited during all three valence conditions for both males and females. In addition, the ERP differences during HN, MN and Neutral conditions mainly distribute over central and frontal sites for both genders. Thus, the present study mainly measured and analyzed the peak latencies (from stimulus onset to the peak of each component) and amplitudes (baseline to peak) of N2 and P3 components. The following 15 electrode sites [Fz, FC3, FC4, FCz, FC1, FC2, C1, C2, Cz, C3, C4 (11 frontal and central sites), CP3, CP4, CPz and Pz (4 central-parietal and parietal sites)] were selected for statistical analysis of the P3 component (350~450 ms), and N2 (230~290 ms) was analyzed at the 11 frontal and central sites. A repeated measures analysis of variance (ANOVA) on the amplitude and latency of each component was conducted with Valence (three levels: HN, MN, Neutral) and Electrode sites as within-subjects factors and gender as between-subjects factor. As the present study focused on the effect of gender on human emotional responses to negative stimuli of varying valences, our analyses mainly focused on Gender by Valence interaction effect. The degrees of freedom of the F-ratio were corrected according to the Greenhouse–Geisser method.

Dipole analysis

The Brain Electrical Source Analysis program (BESA, Version, 5.0, Software) was used to perform dipole source analysis. For dipole source analysis, the four-shell ellipsoidal head model was used. In order to focus on the scalp electrical activity related to the females' emotional responses during MN condition, the averaged ERPs evoked during Neutral condition were subtracted from the ERPs evoked during MN condition. When the dipole points were determined, the software automatically determined the dipoles' location. The relevant residual variance criterion was used.

Results

Behavioral performance

The false responses or responses exceeding time limits were rare as nearly all 30 subjects achieved 100% accuracy rates for both standard and deviant stimuli. A two-way ANOVA on RT data for deviant stimuli (Valence as within-subjects factor whereas Gender as between-subjects factor) demonstrated no significant Valence effect, or Valence by Gender interaction effect [$F(2,56) = 0.96$, $P = 0.37$; $F(2,56) = 0.48$, $P = 0.58$]. The averaged RTs in females were 518.30 ± 53.01 ms for HN, 519.50 ± 59.86 ms for MN and 504.62 ± 63.77 ms for Neutral conditions, whereas the averaged RTs

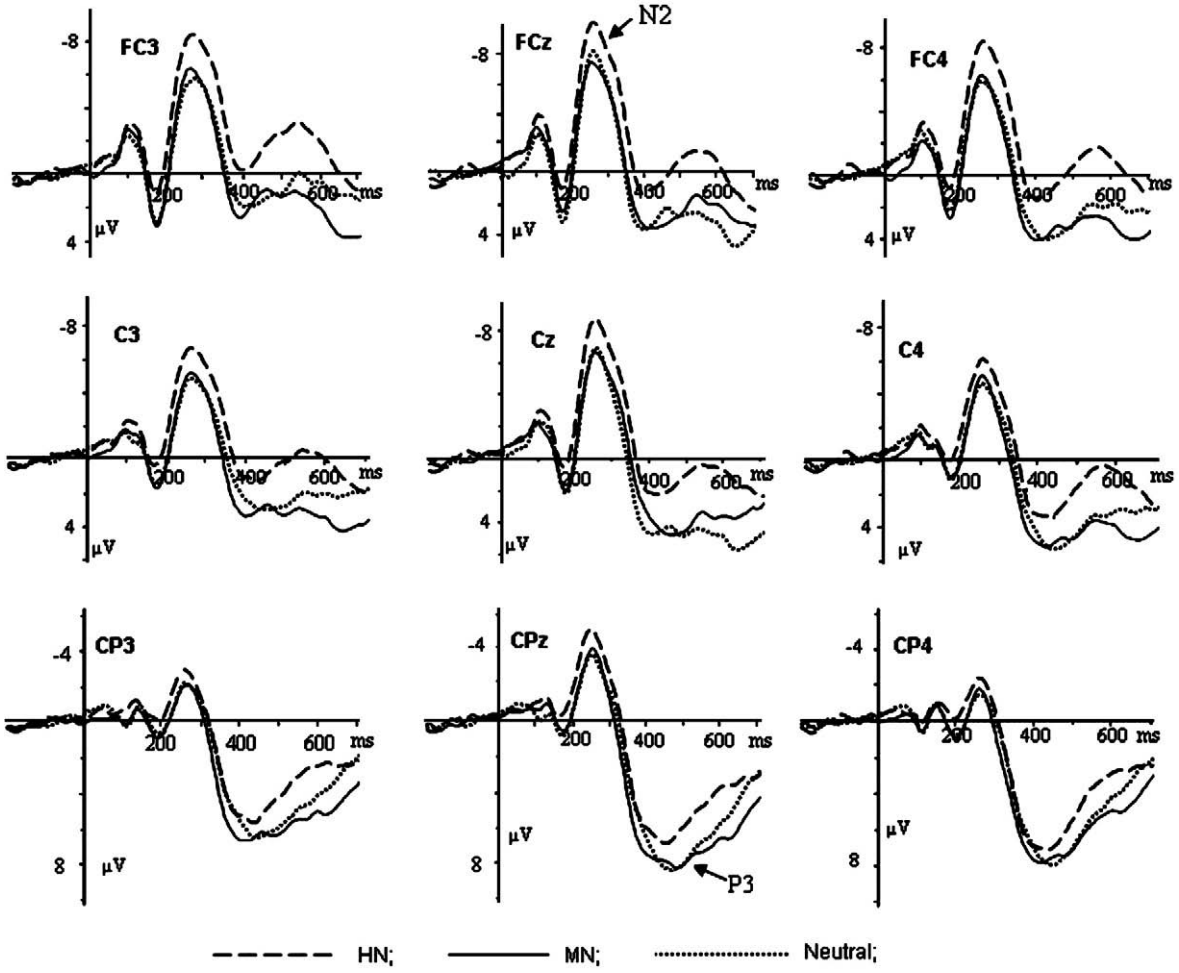

Fig. 1. The grand average ERPs for HN (dashed lines), MN (solid lines) and Neutral (dotted lines) conditions at the frontal–central (FC3, FCz, FC4), central (C3, Cz, C4), and central–parietal (CP3, CPz, CP4) electrode sites in male subjects.

in males were 553.20±76.72 ms for HN, 554.08±78.56 ms for MN and 551.19±58.80 ms for Neutral conditions. Further, Gender main effect was not significant, either [$F(1,28)=2.93$, $P=0.098$]. Thus, behavioral responses to the deviant pictures were not affected by differences in valence during the experiment, which indicates that the experimental design did preoccupy subjects in standard/deviant categorization task, thus effectively masking the true objective of the study.

ERP analysis

Despite early N1 and P2 components elicited by HN, MN and Neutral conditions, no Gender by Valence interaction effects were observed at these components (Figs. 1 and 2); thus, N1 and P2 components were not further addressed. In N2 component, the repeated measures ANOVA conducted on the amplitudes demonstrated very significant main effects for Valence and Electrode [$F(2,56)=12.56$, $P<0.001$; $F(10,280)=11.68$, $P<0.001$] and also a marginal effect of Valence by Gender interaction [$F(2,56)=2.98$, $P<0.07$]. The pairwise comparison for the valence main effect showed that HN condition elicited larger amplitudes than MN [$F(1,29)=10.86$, $P<0.01$] and Neutral [$F(1,29)=24.28$, $P<0.001$] conditions while the latter two conditions did not show significant amplitude differences [$F(1,29)=1.94$, $P=0.19$]. Larger amplitude was elicited in medial frontal–central sites (FC1, FCz and FC2) than other sites. The simple effects analyses on the Valence by Gender interaction effect revealed that a significant valence effect was observed in females [$F(2,28)=8.48$, $P<0.01$]. Larger amplitudes were elicited during HN condition than during MN condition [$F(1,14)=5.12$, $P<0.05$], which, in turn, elicited larger amplitudes than Neutral condition [$F(1,14)=9.06$, $P<0.01$]. Males also showed a significant valence effect [$F(2,28)=4.82$, $P<0.05$], and HN condition elicited larger amplitudes than MN and Neutral conditions [$F(1,14)=5.36$, $P<0.05$; $F(1,14)=11.86$, $P<0.01$]. However, in contrast with females, males showed no significant amplitude differences between MN and Neutral conditions ($F(1,14)=0.18$, $P=0.68$). No other significant main effects or interactions were found for N2 amplitudes and nor were the main effects or interactions for N2 latency.

The repeated measures ANOVA on P3 amplitudes showed significant main effects at valence and electrode sites [$F(2,56)=16.67$, $P<0.001$; $F(14,392)=25.22$, $P<0.001$], and also significant Gender by Valence interaction effect [$F(2,56)=3.97$, $P<0.05$] and Electrode by Valence interaction effect [$F(28,784)=7.35$; $P<0.001$]. Central–parietal and parietal sites recorded much larger P3b amplitudes than central and frontal sites, and the amplitude differences during HN, MN and Neutral conditions were largest at central and frontal sites (Figs. 1 and 2). HN condition elicited smaller amplitudes than MN

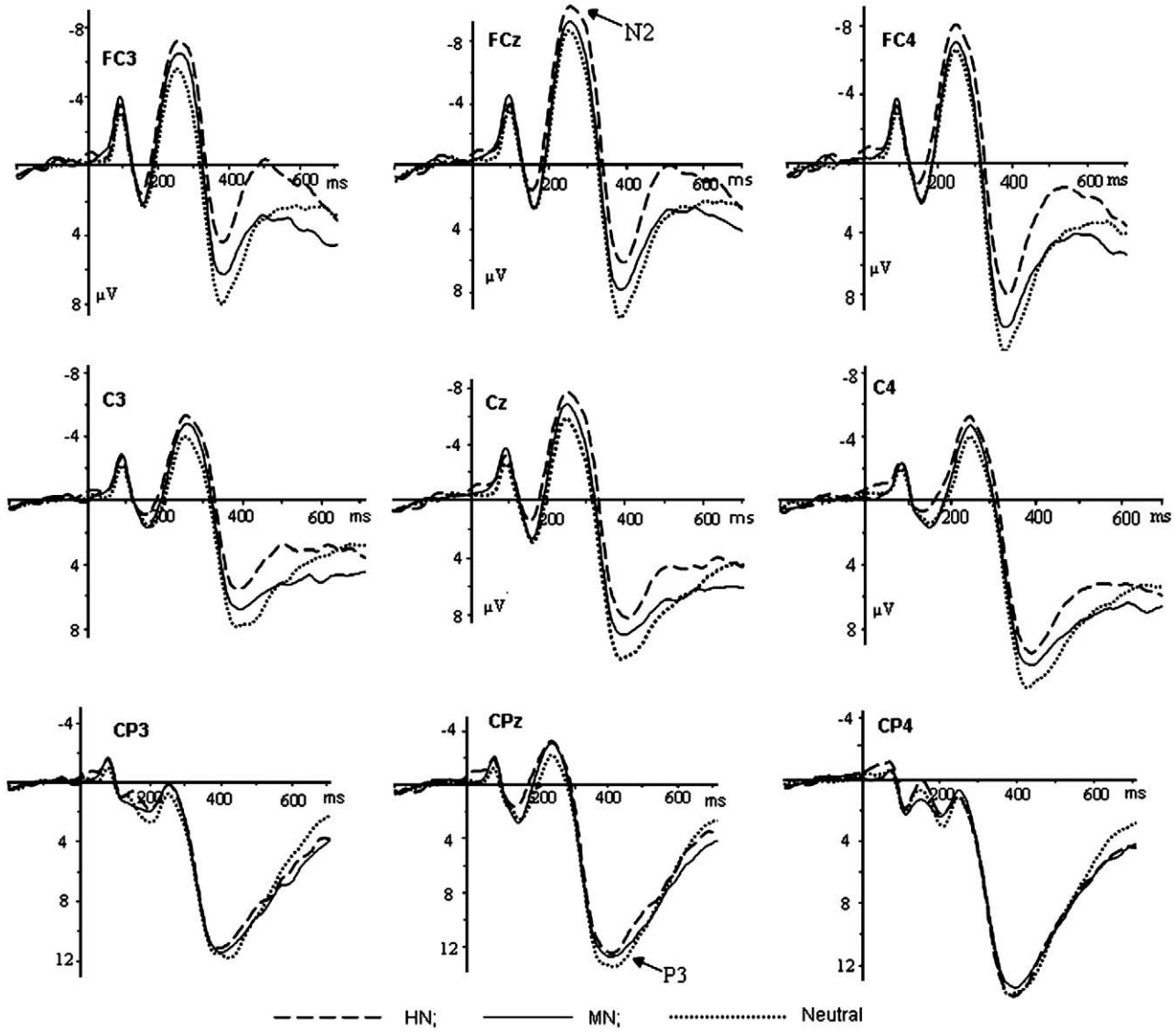

Fig. 2. The grand average ERPs for HN (dashed lines), MN (solid lines) and Neutral (dotted lines) conditions at the frontal–central (FC3, FCz, FC4), central (C3, Cz, C4), and central–parietal (CP3, CPz, CP4) electrode sites in female subjects.

and Neutral conditions. [$F(1,29)=12.14$, $P<0.01$; $F(1, 29)=37.79$, $P<0.001$]. In addition, the amplitude differences during MN and Neutral conditions were also significant [$F(1,29)=4.32$, $P<0.05$]. Simple effects analyses of the interaction effect between gender and valence demonstrated a significant valence effect in females [$F(2,28)=16.81$, $P<0.001$], and HN condition elicited smaller amplitudes than MN [$F(1,14)=9.03$, $P<0.01$], which, in turn, elicited significantly smaller amplitude than the Neutral condition [$F(1,14)=8.32$, $P<0.02$]. Males also showed a significant valence effect [$F(2,28)=4.44$, $P<0.05$], with amplitudes smaller in HN condition than in MN [$F(1,14)=4.69$, $P<0.05$] and Neutral conditions [$F(1,14)=10.68$, $P<0.01$]. However, in contrast with females, male subjects showed no significant amplitude differences during MN and Neutral conditions [$F(1,14)=0.154$, $P=0.701$]. Significant gender effect was also observed [$F(1,28)=5.46$, $P=0.027$], and the amplitudes elicited in females were larger than those in males across three valence conditions. As a main effect of gender signals gender differences in ERP response to rare deviants in general, it has been found that novelty processing is modulated by gender non-specifically (Nagy et al., 2003). Thus, this effect probably stems from gender differences in novelty processing and would not be discussed later. Lastly, a main effect of latency at electrode sites was also significant [$F(14,392)=7.20$, $P<0.001$], and posterior sites elicited longer latency than anterior sites. No other main effects or interactions were seen at this component.

Therefore, MN condition elicited significantly more negative ERP deflections than the Neutral condition across N2 and P3 components only in females (Figs. 1 and 2). Moreover, the amplitude differences during MN and Neutral conditions were largest at central and frontal electrode sites as shown by Figs. 2 and 3. In order to investigate the neural substrates underlying the female-specific emotional reactivity to the MN stimuli, the dipole source analysis (BESA, Version, 5.0, Software) was conducted on the MN−Neutral difference ERPs.

Based on the statistical results and the topography of the difference waveforms (Fig. 3), Principal Component Analysis (PCA)

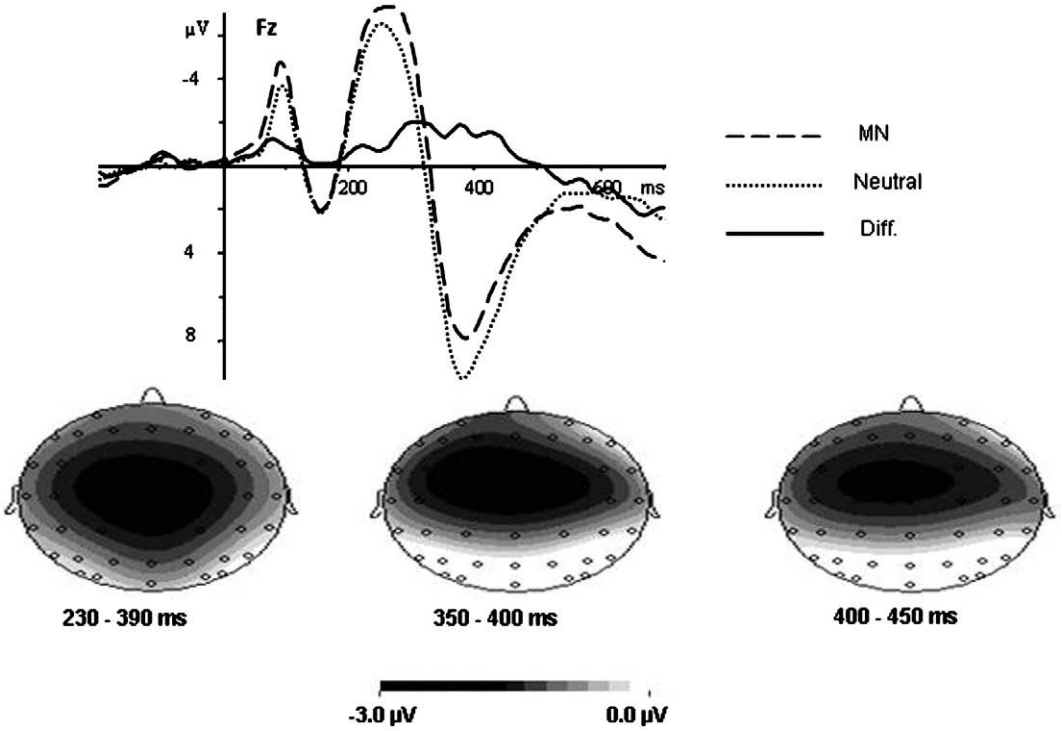

Fig. 3. Top: the average ERPs for MN (dashed line) and Neutral (dotted line) conditions and the MN minus Neutral difference waveform (solid line) at Fz. Bottom: topographical maps of voltage amplitudes for the MN−Neutral difference waveform during 230–290 ms (N2 component), 350–400 ms and 450–450 ms (P3 component) intervals.

of the MN−Neutral difference waveform was conducted at 250–450 ms interval, where the amplitude differences during MN and Neutral conditions were statistically significant and visibly prominent. PCA indicated that only one principal component was needed to explain 97.1% of the variance in the data during this interval. Therefore, only one dipole was fitted with no restriction as to the direction or location of the dipole. The results indicated that the dipole was located approximately in the right prefrontal cortex (Talairach coordinate values: $x=50.4$, $y=35.8$, $z=31.8$) and that the maximal strength of the dipole occurred at about 380 ms. This model best explained the data and accounted for most of the variance with a residual variance (RV) of 13.85% at the peak activity of the dipole (Fig. 4).

Discussion

In agreement with our hypothesis, the present study observed a gender-related dimorphism in processing emotionally negative stimuli of varying valences. Apart from prominent emotional responses of both genders to the highly negative stimuli, females further showed

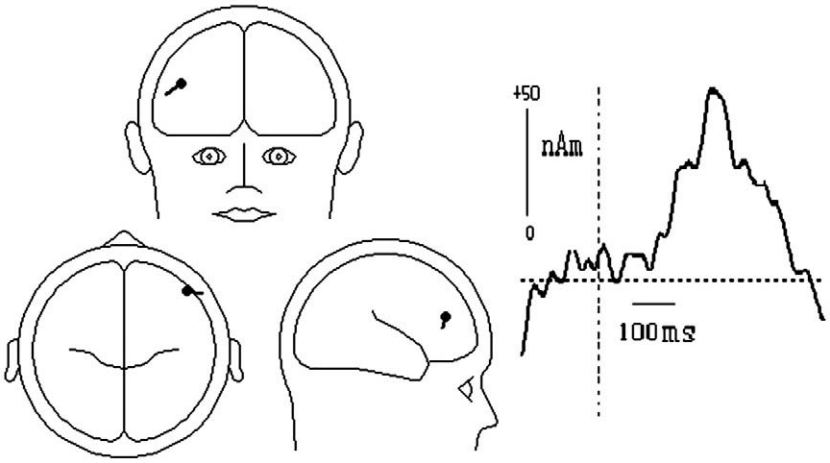

Fig. 4. Results of dipole source analysis of the MN minus Neutral difference wave at the 250–450 ms time window. The left side shows the mean dipole location and the right shows the source activity waveforms. The dipole is located approximately in the right prefrontal cortex (Talairach coordinate values $x=50.4$, $y=35.8$, $z=31.8$).

conspicuous sensitivity to the emotionality of the MN stimuli, whose emotional salience was largely reduced compared with that of the HN stimuli. In contrast, the emotional responses to the MN stimuli were absent in males in the present study. At 230–290 ms interval, we observed a significant valence main effect and a marginal Gender by Valence interaction effect on N2 amplitudes, and the N2 amplitudes displayed a central and frontal distribution. Previous studies using oddball paradigm have shown that prominent N2 component, whose amplitudes were largest at central sites, is typically elicited by infrequent deviant stimuli (Muller-Gass et al., 2006; Nagy et al., 2003; Yuan et al., 2007a; Carretie′ et al., 2004), and the appearance of this component represents a frontier between automatic and controlled phases of the orienting response that, as is widely accepted, directs individuals' attention to novel, potentially salient stimuli (Nagy et al., 2003; Yuan et al., 2007a; Carretie′ et al., 2004). Consistent with this evidence, HN stimuli elicited the largest N2 amplitudes of the three valence conditions across genders, which signals that humans, irrespective of gender, devote most attentional resources to HN stimuli due to their significant adaptive values (i.e. the highest emotional saliency).

Nevertheless, the more intriguing finding at N2 stage is that females showed an enhanced negativity during MN versus Neutral conditions, whereas N2 amplitudes were not significantly different between MN and Neutral conditions in males. This indicates that the emotional negativity of MN images was detected by females during this early attentional processing stage, and that MN stimuli recruited more attentional resources relative to Neutral stimuli in females, though the subjects were highly engaged in an overt standard/deviant categorization task. In contrast, males showed no obvious valence effect during the MN condition. Therefore, at N2 stage, only females showed a significant valence effect during MN condition, suggesting that the early attentional bias for negative stimuli of lesser affective intensity might be specific to females during a covert emotional task.

P3b (or LPC) signals the cognitive evaluation of stimuli's meaning (Yuan et al., 2007a; Ito et al., 1998). The present study observed a broadly distributed later P3 component whose amplitudes were largest at parietal sites. Evidently, the P3 we observed is a P3b component (Campanella et al., 2002, 2004, Delplanque et al., 2004). The statistical analysis showed a significant valence main effect and also a significant Gender by Valence interaction effect on P3 amplitudes. HN stimuli evoked the smallest P3b amplitudes of the three valence conditions, and Neutral stimuli evoked the largest. This is consistent with several lines of evidence that negative stimuli elicited smaller P3b amplitudes than Neutral stimuli over a wide range of recording sites during implicit emotional tasks (Delplanque et al., 2004; Carreti′e et al., 1996; Yuan et al., 2007a). It has been accepted that P3 and its underlying subprocesses reflect the neural inhibition of task-irrelevant information (Polich, 2007; Yuan et al., 2007a), and an inhibitory process most likely accounts for the smaller P3b amplitudes elicited by negatively valenced stimuli than by Neutral stimuli during covert emotional experiments (Yuan et al., 2007a). As such, the smaller P3 amplitudes elicited by negative stimuli versus Neutral stimuli in the current study may reflect an inhibitive process on task-irrelevant but information-laden emotionally negative information. For a subject to make a correct behavioral response to the stimulus (standard vs. deviants), all task-irrelevant information has to be inhibited. Therefore, the emotional negativity of HN stimuli, which is highest in information burden, should have required the strongest inhibitive process in both genders, which accounts for the smallest P3 amplitudes elicited by the HN stimuli across genders.

More importantly, the present study showed that females, instead of males, exhibited significantly smaller P3 amplitudes between MN and Neutral conditions (see Figs. 1 and 2). P3b signals a deliberative and controlled process that involves higher cognitive evaluation of stimulus meaning, and information is represented and analyzed more fully, with more factors considered and more experiences referenced at this stage (Yuan et al., 2007b; Huang and Luo, 2006). Thus, the significance of emotional information is evaluated, and stimuli of varying emotional values could be differentiated clearly during this stage (Huang and Luo, 2006; Ito et al., 1998; Yuan et al., 2007a). Whereas males showed no valence effect during MN condition even at this later stage, females exhibited prominent emotional responses not only to HN stimuli but also to the MN stimuli at P3 stage. Therefore, females seem indeed more able to detect and process emotionally negative information compared to males. Presumably, females are more able to detect the emotionally negative stimuli of lesser saliency in life settings which, in most cases, resemble the present experiment whose cognitive activity is irrelevant to affective evaluation (Yuan et al., 2007a; Delplanque et al., 2005). In contrast, it seems that males are only sensitive to emotionally negative events of enhanced saliency in life settings (Fig. 1). Taken together, it is apparent that females are of an advantage to detect the emotional negativity of lesser saliency and could manifest both early attentional and later evaluative biases for these moderately negative stimuli during an implicit emotional task.

As stated before, the female advantage in identifying negative emotions has been validated by considerable studies employing behavioral measures. Nevertheless, the possible reason(s) for this phenomenon has yet to be directly investigated, and neurophysiological correlates underlying this phenomenon were not addressed in previous studies. By use of ERP measures and manipulating the valence intensity of emotionally negative stimuli, the present study demonstrated prominent emotional responses to the highly negative stimuli across genders whereas only females manifested pronounced emotional responses to the moderately negative stimuli during a non-emotional task, which agrees with the observation by Montagne et al. (2005), who reported that when subjects were required to identify facial emotions, females could label negative emotions like disgust and anger at a lower level of affective saturation relative to males. The present study provided direct electrophysiological evidence to understand why behavioral studies consistently demonstrated a better performance during emotion recognition tasks in females versus males (Hall, 1978; Miura, 1993; Campanella et al., 2004; Scholten et al., 2005), and why females were able to label negative emotions (typically anger and disgust) at a lower saturation level than males (Montagne et al., 2005). Probably, as suggested by the present study, human beings, irrespective of gender, are sensitive to emotionally negative events of enhanced salience in natural settings, however, when the valence intensity of negative stimuli gets lesser, males would turn to be insensitive to the emotional negativity of these stimuli whereas females' sensitivity remains, although their cerebral activation may decrease compared to that evoked by the highly negative stimuli. Thus, it seems less easy for males to detect the emotionality of the negative stimuli of lesser salience as compared with females, which, to some degree, could account for the well-known female advantage in identifying negative emotions (Hall, 1978; Miura, 1993; Scholten et al., 2005). Based on these analyses, it should come as no surprise that females are often found more sensitive to delicate variability of people's affective states and also respond more intensely to issues signifying social rejection factor in interpersonal interaction situations (Hall, 1978; Stroud et al., 2002, Beehr et al., 2003).

Although quite a few brain mapping studies demonstrated that similar neural networks are involved in processing emotionally negative scenes and negatively facial emotions (Hariri et al., 2003; Liberzon et al., 2003; Morris et al., 1998; Britton et al., 2006), carefulness should still be exercised, however, when we apply the current findings to the explanation of female advantage in identifying negative facial emotions as there remains a possible discrepancy between emotionally evocative scenes and facial expression of emotion in terms of emotional inducement (Hariri et al., 2002; Britton et al., 2006): Facial emotions may elicit more emotion recognition/perception, and evocative pictures may elicit more direct experience of emotion (Britton et al., 2006). As well, though facial expressions of emotion have proven to be "emotionally contagious" such that the perception of emotionally expressive faces can evoke the corresponding emotional experiences in a subject (Wild et al., 2001; Dimberg, 1997), and even though neural structures mediating the recognition of negative facial emotions (e.g. amygdala, ventromedial prefrontal cortex etc.) were repeatedly shown to be also involved in processing negative emotions elicited by emotionally negative scenes (Yang et al., 2002; Adolphs et al., 2001; Britton et al., 2006; Yuan et al., 2007b), identifying negative affects does not exactly entail the same processes as experiencing emotional negativity. As a higher cognitive activity, facial emotions recognition may involve some other mental elements in addition to the typical emotional responses, such as category judgment, mental state decoding etc. (Sabbagh et al., 2004). Thus, given the fact that the enhanced sensitivity of females over males to emotionally negative stimuli of lesser saliency most likely accounts for the better performance of females in identifying negative emotions (Hariri et al., 2003; Britton et al., 2006; Wild et al., 2001; Adolphs et al., 2001), it is still likely that possible gender differences in other mental processes (if they do exist) also contribute to this phenomenon. Therefore, it is more appropriate for the present study to conclude that the female-specific sensitivity to the lesser valenced negative stimuli is an important, instead of the sole, mechanism underlying the female advantage in identifying negative emotions.

As shown by Fig. 3, the MN−Neutral difference ERPs mainly activated frontal–central scalp regions during 250–450 ms interval, implying that neural substrates mediating the female-specific emotional sensitivity to the MN stimuli may locate within the cortical frontal network. The present dipole analysis demonstrated an important role of the right prefrontal cortex in mediating women's greater emotional reactivity to the moderately negative stimuli, which agrees with the frontal–central distribution of the MN−Neutral difference wave. This dipole model is supported by several lines of evidence from neural imaging studies. Aside from the established role of the right hemisphere in emotional processing, in particular, in processing negative emotions (Mitchell et al., 2003; Esslen et al., 2004; Holt et al., 2005;Yuan et al., 2007b), the right prefrontal cortex was demonstrated to play a key role in processing different types of negative emotions (Esslen et al., 2004), and the right prefrontal cortex was activated across genders when subjects viewed emotionally negative images and were required to induce the corresponding emotions (Hofer et al., 2006). More importantly, employing an automated tissue segmentation procedure, the study by Gur et al. (2002) demonstrated that whereas both genders had identical volume of amygdala and hippocampus, women had larger orbital frontal cortices than men after correcting for cranial volume, resulting in larger ratio of orbital–frontal gray matter to amygdala volume in women. Further, Gur et al. (2002) suggested that the larger volume of cortex devoted to emotional modulation in females may relate to behavioral evidence for gender differences in emotional processing (Gur et al., 2002). On grounds of the present dipole analysis and the above evidence, the current study suggests that the right prefrontal cortex, possibly, larger volume of the right orbitofrontal cortex in females may be the neural basis of the female-specific sensitivity to the emotionally negative stimuli of lesser valence intensity. However, due to the limitations of ERP measures in spatial resolution, the present study could not determine precisely which region(s) of the right prefrontal cortex mediates females' affective responses to the MN stimuli, although the right orbitofrontal cortex is implicated. Thus, conducting a further experiment employing measures of high spatial resolution is necessary to clarify the neural bases underlying women's increased sensitivity to the negative stimuli of lesser saliency.

Conclusion

The present study demonstrated a gender-related dimorphism in neural responses to emotionally negative stimuli of varying valences during a covert emotional task. Aside from the prominent emotional responses of both genders to the highly negative stimuli, females showed remarkable attentional and evaluative biases for the moderately negative stimuli whereas males showed neither biases for these stimuli. This suggests that the well-known female advantage in identifying negative emotions may be attributable to the unique sensitivity of females to negative stimuli of lesser emotional saliency. The dipole analysis suggests that females' unique sensitivity to emotionally negative stimuli of lesser saliency may have a neurobiological basis in the right prefrontal cortex.

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