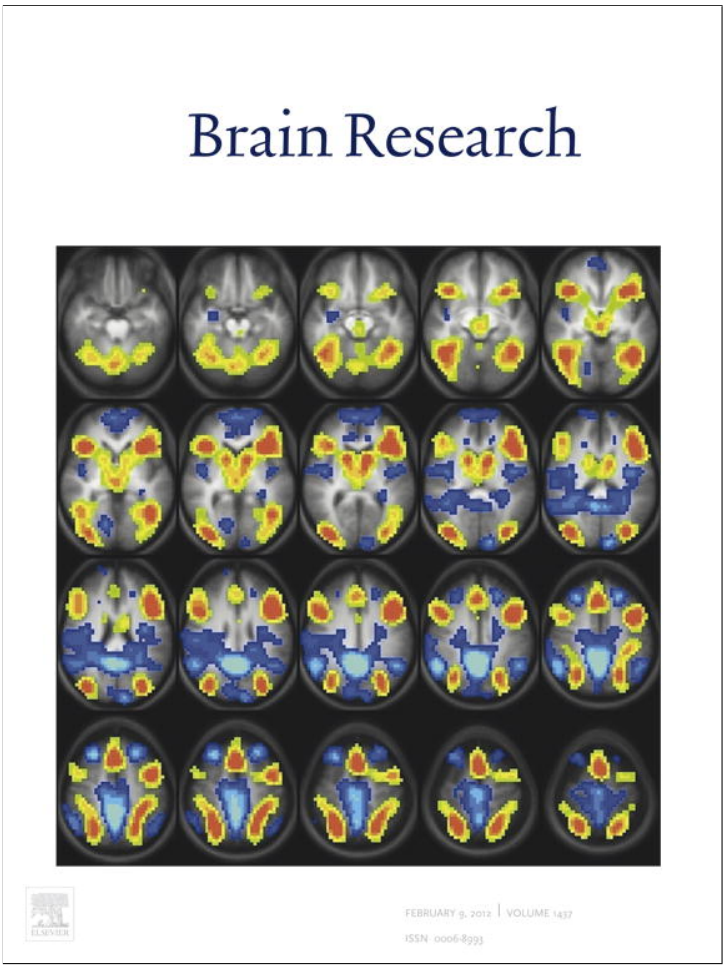

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Research Report

The enhanced processing of visual novel events in females: ERP correlates from two modified three-stimulus oddball tasks

Jiajin Yuan[a,b,*], *Shuang Xu*[b,1], *Chengqiang Li*[b], *Jiemin Yang*[b], *Hong Li*[a,c,**], *Yin Yuan*[b], *Yu Huang*[b]

[a]*Key Laboratory of Cognition and Personality (SWU), Ministry of Education, Chongqing 400715, China*
[b]*School of Psychology, Southwest University, Chongqing 400715, China*
[c]*Research Center for Psychological Development and Education, Liaoning Normal University, China*

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ABSTRACT

The ability to detect and cope with unpredictable novel events is fundamental for adapting to a rapidly changing environment and ensuring the survival of the organism. Despite knowledge of gender differences in emotional processing, little is currently known about the impact of gender on neural processing of emotion-irrelevant, novel stimuli. Using two modified three-stimulus oddball tasks and event-related potentials (ERPs), the present study investigated the impact of sex on brain processing of novel events and the associated neurophysiological correlates. With novel and non-novel control stimuli used as task-irrelevant distracters, Experiment 1 showed higher novelty rating scores and larger size of novelty effects in brain potentials at 200–300 ms and 300–430 ms time intervals in females compared to males. After excluding the contribution of stimulus probability, Experiment 2 continued to display significant novelty effects in the response times and the amplitudes of the 130–500 ms time windows. Most importantly, females displayed a sustained novelty effect in the late positive component (LPC) amplitudes of the 500–600 ms interval, which was not observed in males. Therefore, Experiment 1 and 2 demonstrated that females are equipped with enhanced brain processing of emotion-irrelevant, novel stimuli. This phenomenon is independent of the established gender difference in infrequent stimulus processing. We suggest that our findings reflect the differential adaptive demands on females and males during evolution.

1. Introduction

The processing of novel events which are unpredictable and perceptually salient from the context (Ranganath and Rainer, 2003), is biologically important for adaptive living in changing environments (Delplanque et al., 2005; Sokolov et al., 2002). Novel events are often associated with the orienting response (Halgren and Marinkovic, 1995) which, as previously indicated (Ranganath and Rainer, 2003), enables organisms to rapidly direct attention towards unusual events. In life and laboratory settings, novel events are typically infrequent but emotionally relevant, and thus linked with affective responses such as in-

* *Correspondence to:* J. Yuan, School of psychology, Southwest University, Beibei, Chongqing, 400715, China. Fax: +86 23 6825 2309.
** *Corresponding author.*
E-mail addresses: yuan_jiajin@126.com (J. Yuan), lihongwrm@vip.sina.com (H. Li).
[1] Co-first author.

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terest or surprise (Coon, 2000; Wright et al., 2008). Behavioral and neuroimaging studies have reported gender differences in brain responding to emotion-relevant infrequent stimuli (Campanella et al., 2004; Orozco and Ehlers, 1998). In an early study, Orozco and Ehlers (1998) discovered that infrequent emotional faces elicited greater amplitude and longer latency P450 brain potentials in females compared to males during a facial discrimination task. In addition, Campanella et al. (2004) observed that females are faster in detecting infrequent happy faces than males. Recently, using a non-emotional distracting task and event-related potential (ERP) measures, we observed emotion effects for mildly negative infrequent stimuli in females but not in males (Li et al., 2008). In addition to these findings indicating a gender effect in the processing of emotion-relevant infrequent stimuli, there is also evidence for gender differences in processing emotion-irrelevant infrequent stimuli. For instance, using a passive listening oddball task, Nagy et al. (2003) observed enhanced positivity in P2 and N2 components for non-emotional infrequent stimuli in females versus males. Jaušovec and Jaušovec (2009) recorded higher P3 amplitudes for both auditory and visual non-emotional infrequent stimuli in females than in males, possibly resulting from different neural substrates underlying deviance detection (Rubia et al., 2010). Recently, work in our laboratory has demonstrated enhanced startle responses to emotion-irrelevant infrequent stimuli in females versus males at both behavioral and electrophysiological levels, irrespective of whether the task required active classification or passive viewing (Yuan et al., 2010).

Nevertheless, the established gender effect in processing of infrequent stimuli does not necessarily suggest a similar gender effect in brain processing of novel events. Infrequent stimuli, as used in the above oddball studies, are inherently different to novel stimuli. Novel stimuli in natural situations are often perceptually salient distracters that are irrelevant to the current task setting, such as when you are engaged in reading (task) in the library but then interrupted by a sudden cell phone ringing (novel event). Consistent with this, novel stimuli have been defined in a considerable number of prior studies as unpredictable and rare distracters that are perceptually salient from the train of regular stimulus events (Courchesne et al., 1975; Delplanque et al., 2005; Polich, 2007). Novel events, whether emotionally salient or neutral, are biologically important, because the occurrence is sudden, with unpredictable meaning and perceptually salient from context (Ranganath and Rainer, 2003; Sokolov et al., 2002). Accordingly, it is impossible for people to evaluate the meaning of novel events in advance of their occurrence. Although females are known to show enhanced sensitivity to emotional stimuli (Lang et al., 1993; Li et al., 2008) and infrequent stimuli (both of which are biologically significant), it remains unknown whether females and males differ in their processing of emotionally neutral, novel stimuli that also share this biological significance. Exploration into this question is important in terms of clarifying whether gender differences in emotion processing exist only for emotionally laden stimuli or for biologically significant stimuli in general. Though a recent study demonstrated that negative emotion processing was impaired by novel sounds in women but not in men (Garcia-Garcia et al., 2008), it has yet to be directly investigated whether females and males are different in processing emotionally neutral, novel stimulus. It is noteworthy that recent neuroimaging evidence proposes novelty as one dimension of the affective brain, as stimulus novelty has been found to activate limbic neural networks including the amygdala and orbitofrontal cortical areas (Weierich et al., 2010). From this perspective, it could be predicted that females are more reactive to novel stimuli even when the stimuli convey no emotional charge, given that many studies have reported enhanced processing of emotionally arousing stimuli in females compared to males (Campanella et al., 2004; Orozco and Ehlers, 1998).

The present study investigated the potential effects of sex on brain processing of emotionally neutral, novel stimuli utilizing high time resolution, dense-array event-related potentials which are optimal for unraveling spatiotemporal features. We predicted that females would exhibit a novelty effect at earlier time points, and/or show greater magnitude of novelty effect measured by brain potentials, on the basis of previous findings that females are more sensitive to emotionally relevant events in comparison to males (Campanella et al., 2004; Orozco and Ehlers, 1998; Weierich et al., 2010). As novel events are accepted as unpredictably rare distracters interspersed in a train of regular stimulus events (Delplanque et al., 2005; Polich, 2007), a three-stimulus oddball paradigm was considered most suitable for investigating the novelty effect in brain potentials and the association with gender. In the classic three-stimulus oddball task, subjects are required to detect rare target presentation from a sequence of standard stimulus trials (standard and target stimuli are perceptually similar). Novel stimuli, a category of infrequent and perceptually different stimuli, are typically interspersed in the sequence of standard/target stimulus trials (Polich, 2007; Simons et al., 2001).

As novel stimuli occur unpredictably and are task-irrelevant in the three-stimulus oddball task, prior studies have often used this paradigm to study novelty processing and its relationship with emotion (Delplanque et al., 2005; Polich, 2007). However, the P3 amplitude has been shown to be larger in females than in males even in tasks without explicit instructions or in tasks irrelevant to novelty (Li et al., 2008; Steffensen et al., 2008; Yuan et al., 2010), possibly as a result of the larger callosal areas in females compared to males (Hoffman and Polich, 1999). Thus, to investigate the neural correlates of sex differences in novelty processing, it is important to control for this effect by modifying the classic three-stimulus oddball task and setting a suitable baseline. For this purpose, we designed two modified three-stimulus oddball tasks, both of which required subjects to detect a target from distracters. The distracters included a non-novel control stimulus and a set of novel stimuli. The control and novel stimuli were matched for physical attributes, different only in novelty. Using this framework, ERP differences between non-novel control and novel conditions should reflect novelty processing, free of the contamination of the larger P3 in females compared to males (Hoffman and Polich, 1999). In Experiment 1, the target stimulus (40%, a photograph of a cup) and the non-novel control stimulus (40%, a photograph of a bench) were kept constant, whereas a set of emotionally neutral, non-repeated pictures was used as the novel stimuli (20%). The novel pictures were presented less frequently than the non-novel control picture, in order to make novelty

processing in the experiment resemble that in natural settings, where novel events happen infrequently compared to regular events. Experiment 2 used the same stimulus materials, but matched non-novel control and novel stimuli in terms of onset frequency. The purpose of this manipulation was to test whether the observed sex differences in novelty processing is independent of the females' increased responding to infrequent stimuli (Yuan et al., 2010).

As females are reported to be more responsive to emotionally aversive or startling stimuli that are biologically significant (Hofer et al., 2006; Yuan et al., 2010), they are also likely to be equipped with enhanced brain processing of novel stimuli that share this biological significance. Specifically, we predicted that the size of difference between non-novel control and novel stimulus sets would differ between sexes, and would be larger in females. That is, we predicted that there would be significant stimulus type and gender interaction effects on ERP amplitudes, if males and females are indeed different in their brain processing of novel stimuli. Therefore, the present study explored stimulus (control vs. novel) and gender (male vs. female) interaction effects on ERP amplitudes rather than directly comparing novel stimuli-induced ERPs in females and in males. Furthermore, we computed novel-control difference waves (difference ERPs) which directly indexed novelty-relevant effects, and we further tested the statistical significance of gender effects in the difference ERPs in order to verify the results drawn from raw ERP analyses. We predicted that females would exhibit significantly enhanced amplitudes compared to males in the difference ERPs, reflecting enhanced brain processing of novel stimuli.

2. Results

2.1. Experiment 1

2.1.1. Behavioral results

The accuracy for target detection reached a ceiling effect (99.88%), and the independent samples *t*-test on accuracy data showed no main effect of gender ($t(30)=1.05$; $p>0.30$). In addition, the reaction times (RTs) did not significantly differ between males and females (male: 434 ms; female: 448 ms; $t(30)=0.69$, $p=0.50$). Therefore, all subjects, irrespective of gender, detected and responded to the target accurately, suggesting that the task effectively preoccupied subjects in target detection, which consequently made novelty processing happen in an unpredictable, task-irrelevant manner as that in natural situations.

2.1.2. ERP analysis

2.1.2.1. Stimulus and gender interaction effects. The repeated measures ANOVA on the P2 amplitudes in the 130–200 ms interval showed no other significant main or interaction effects, except for increased negative deflection recorded during novel than during standard conditions ($F(1, 30)=23.36$, $p<0.001$; $\eta^2=0.438$).

The ANOVA on the N2 amplitudes revealed significant main effects of stimulus ($F(1, 30)=12.31$, $p=0.001$; $\eta^2=0.291$) and electrode site ($F(8, 240)=26.28$, $p<0.001$), as well as a significant stimulus and gender interaction ($F(1, 30)=8.23$, $p<0.01$; $\eta^2=0.215$). The novel stimuli elicited larger amplitudes than the control stimulus, while the amplitudes were larger at frontal than at central sites irrespective of stimulus condition. The breakdown of the stimulus and gender interaction revealed significant amplitude differences between novel and control conditions in females ($F(1, 30)=20.34$, $p<0.001$) but not in males ($F(1, 30)=0.20$, $p>0.60$; see Table 1). Additionally, there was an interaction between stimulus and electrode site ($F(8, 240)=5.19$, $p<0.001$), with amplitude differences during novel and control conditions more pronounced at central (−1.88 μV) than at frontal sites (−1.25 μV).

The ANOVA of P3 amplitudes demonstrated greater amplitudes during control than during novel conditions, irrespective of gender ($F(1, 30)=42.87$, $p<0.001$; $\eta^2=0.588$). The amplitudes were larger at parietal sites than at anterior sites ($F(14, 420)=41.16$, $p<0.001$). More importantly, there was a significant gender by stimulus interaction in the 300–430 ms interval ($F(1, 30)=5.13$, $p<0.04$; $\eta^2=0.146$). The breakdown of this interaction showed significant amplitude differences between novel and control conditions both in females ($F(1, 30)=38.83$; $p<0.001$) and in males ($F(1, 30)=9.17$, $p<0.01$), with females exhibiting larger size of amplitude differences than males (see Table 1). The electrode site by stimulus interaction was also significant ($F(14, 420)=5.485$, $p<0.001$), with the amplitude differences between novel and control conditions larger at central and frontal sites than at parietal sites. Therefore, the stimulus and gender interaction was significant at both 200–300 ms and 300–430 ms intervals, and the amplitude differences between the novel and the control conditions were more pronounced in females than in males.

2.1.2.2. Gender effects in novel-control difference ERPs. We further analyzed the gender effect directly in the novel-control difference ERPs to confirm the results of the above analyses.

The repeated measures ANOVA of the amplitudes at 200–300 ms interval showed larger amplitudes in females than in males ($F(1, 30)=8.23$, $p<0.01$; $\eta^2=0.234$; Fig. 2). In addition, the amplitudes were significantly larger at the central sites than at the frontal sites across genders ($F(8, 240)=5.905$, $p<0.001$). Analysis of the amplitudes at 300–430 ms interval demonstrated larger amplitudes in females than in males ($F(1, 30)=5.13$, $p<0.04$; $\eta^2=0.142$), while the amplitudes were larger at frontal and central sites than at parietal sites ($F(14, 420)=3.766$, $p<0.01$). Therefore, our additional analysis of difference ERPs confirmed the results shown by the raw ERP analyses, indicating enhanced processing of novel, emotion-irrelevant stimuli in females than in males.

2.1.3. Post-experiment debriefing and novelty assessment

In the post-experiment debriefing session, all subjects ($n=32$) reported experience of a sudden, attention-arousing and novel feeling when "non-cup and non-chair" pictures were presented. The subsequent ratings of novelty using a 7-point scale demonstrated higher novelty scores in females than in males, suggesting that females may have more intense feelings of novelty during novel trials [$\text{Females}_{(M\pm SD)}$: 4.81±0.98; $\text{Males}_{(M\pm SD)}$: 3.84±1.61; $t(30)=2.06$, $p<0.05$].

2.1.4. Discussion of Experiment 1

In Experiment 1, we used an adapted three-stimulus oddball task to investigate the differences between males and females

Table 1 – Stimulus and gender interaction effects at the 200–300 ms and 300–430 ms intervals (M_1: the mean amplitude of the novel stimuli; M_2: the mean amplitude of the standers stimulus; $D(M)$: mean amplitude differences).

Gender	200–300 ms			300–430 ms		
	Novel	Standard	$D(M)=M_1-M_2$	Novel	Standard	$D(M)=M_1-M_2$
Male	−1,48±0.95	−1.18±1.83	−0.3	5.04±1.33	7.49±1.17	−2.45
Female	−4.49±0.85	−1.49±0.81	−3.3	4.68±1.33	9.74±1.33	−5.06

in novelty processing. Both novelty assessment and ERP data showed enhanced novelty relevant processing in females compared to males. In addition to higher ratings in novelty scores provided by females compared to males, ERP results demonstrated enhanced brain processing of stimulus novelty in females across both N2 and P3 time intervals (Figs. 1,2).

We observed a novelty effect, but not a significant stimulus and gender interaction in the P2 time interval (130–200 ms). Numerous studies have indicated that frontal P2 activation within 200 ms is indicative of bottom-up sensory processing involving involuntary attention (Thorpe et al., 1996), which occurs prior to the access of top-down, cognitive resources (Del Cul et al., 2007; Sergent et al., 2005). Males and females both processed novel stimuli preferentially with heavier engagement of involuntary attention and there were no significant gender differences in novelty processing at the early stage. This is possibly because novelty processing before 200 ms is a data-driven and automatic process without conscious engagement (Del Cul et al., 2007). Therefore, the gender effect in novelty processing may happen at later stages of cognitive processing.

We observed a significant stimulus and gender interaction on the N2 amplitudes in the 200–300 ms interval, and the novelty effect was significant in females but not in males. This result was confirmed by our additional analysis of the novel-control difference ERPs at 200–300 ms which revealed increased novel-related amplitudes in females compared to males (Fig. 3). The appearance of oddball N2 was indicated to represent a frontier between automatic and controlled phases of the orienting response, which is widely accepted to direct attention to novel, potentially salient stimuli (Carretié et al., 2004; Nagy et al., 2003; Sergent et al., 2005). Thus, the female-specific novelty effect in N2 amplitudes probably resulted from a significant orienting response to unpredictable novel stimuli in females. Conversely, males showed no significant attention orienting to novel stimuli, probably because males are less sensitive to unpredictable novel stimuli than females, such that novel stimuli failed to elicit increased attention orienting at this involuntary, and semi-automatic processing stage. This result is supported by previous findings of increased pre-attentive brain responding to rare stimuli in females compared to males during diverse tasks (Barrett and Fulfs, 1998; Yuan et al., 2010). Given the increased sensitivity to novel events, females are likely to be more responsive to novel stimuli than males even at later cognitive processing stages, with full access to controlled resources.

We observed a significant main effect of stimulus and a significant stimulus and gender interaction on the P3 amplitudes in the 300–430 ms interval. Both control and novel stimuli elicited pronounced P3 activity in this interval, and the P3 amplitudes were largest at the parietal scalp sites. Parietal P3, which is sensitive to the engagement of controlled cognitive resources, reflects higher-order cognitive processes, such as evaluation of stimulus meaning, and response decisional processes (Campanella et al., 2002 and 2004). Meanwhile, parietal P3 is susceptible to influences of motor relevant potentials (Verleger, 1997; Bentin et al., 1999). As both novel and control stimuli were task-irrelevant distracters and did not require behavioral responses, P3 activity in this interval was free from influences of response decision and motor execution. As such, the P3 differences between novel and control conditions resulted solely from novelty-relevant cognitive processing. Aside from the significant novelty effect in both samples, both raw and difference ERP analyses displayed larger size of novelty effect in females than in males in the P3 component. This suggests that females recruit enhanced cognitive recourses for novelty processing, particularly for evaluating the biological significance of novel events (Huang and Luo, 2006).

In summary, both behavioral (novelty assessment) and neurophysiological (N2 and P3 amplitudes) data showed enhanced processing of novel events in females compared with males in Experiment 1. As stated before, novel stimuli in natural settings are unpredictable distracters that are perceptually salient from regular events (Courchesne et al., 1975; Delplanque et al., 2005; Polich, 2007). This characteristic determines that novel events occur less frequently compared to regular events in natural settings. Accordingly, novel stimuli were presented less frequently than the control stimulus in Experiment 1, which showed a female advantage in processing novel stimuli. Despite holding ecological validity, this design met difficulties when determining whether the observed gender effect in Experiment 1 is independent (or dependent) of the enhanced sensitivity of females to infrequent stimuli, because our previous work has shown enhanced neural sensitivity of females to emotion-irrelevant infrequent stimuli relative to males (Yuan et al., 2010). Therefore, it was necessary to conduct a second experiment to reinvestigate the gender effect in novelty processing, with onset frequency equated for control and novel stimuli. If a similar gender effect was to be observed after excluding the influence of stimulus frequency then we could conclude that the observed female advantage in novelty processing is an independent phenomenon and irrelevant to the enhanced sensitivity of females to rare stimuli.

2.2. *Experiment 2*

2.2.1. *Behavioral results*

The average accuracy rates for the control and the novel stimuli reached a ceiling effect (97.65% and 98.59%, respectively). The ANOVA (stimulus as the repeated factor and gender as the between-subjects factor) on the accuracy data did not

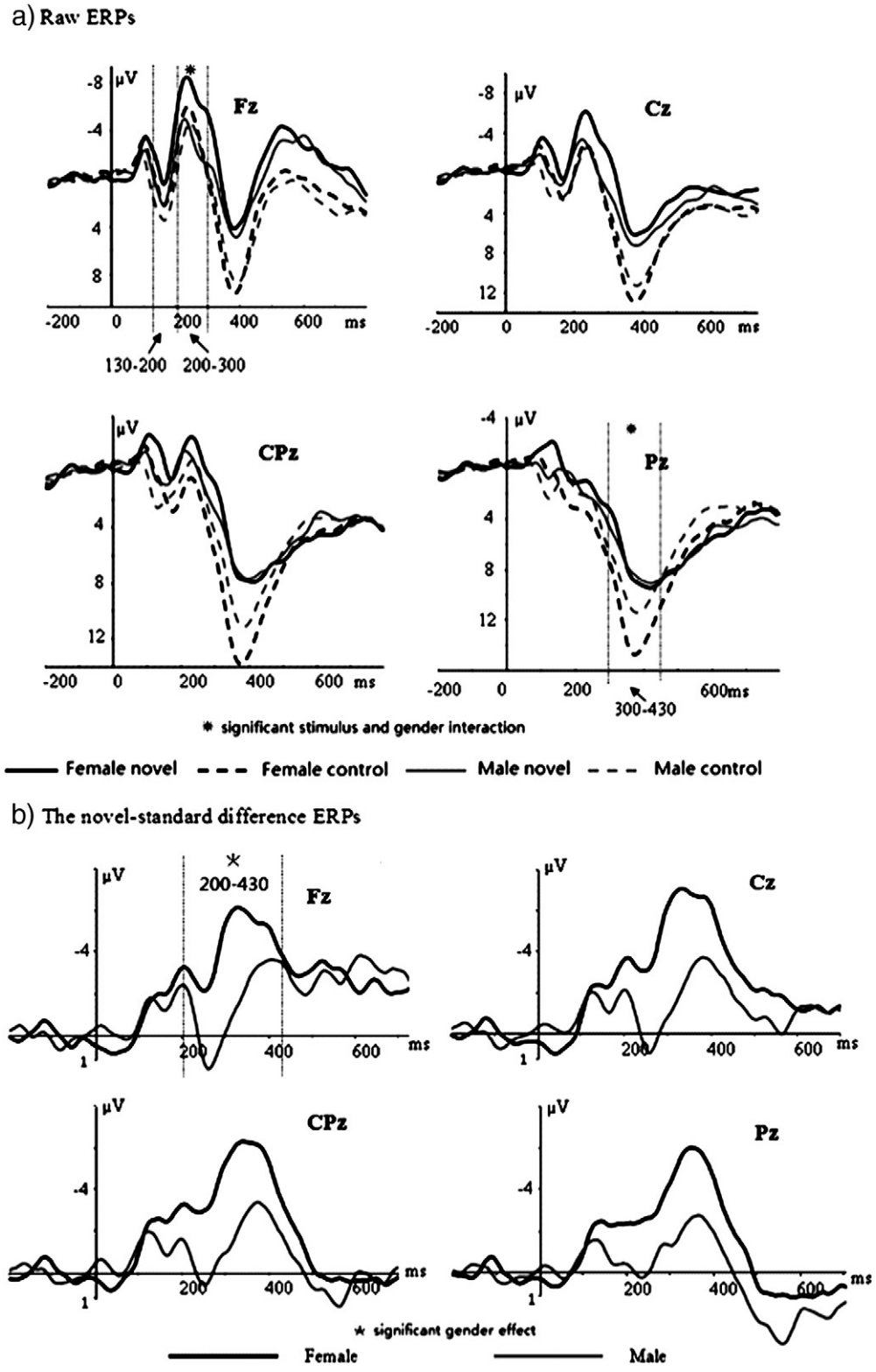

Fig. 1. Averaged ERPs in Experiment 1. Top: Raw ERPs elicited during novel and control conditions for both samples. Bottom: Novel-control difference ERPs in females and males.

show any main or interaction effects. However, the analysis of reaction times showed longer RTs for the novel (510 ms) than for the control stimuli (478 ms), indicated by a significant main effect of stimulus ($F(1, 30)=41.91$, $p<0.001$; $\eta^2=0.583$). The gender effect ($F(1, 30)=0.26$, $p>0.60$) and the gender by stimulus interaction ($F(1, 30)=1.05$, $p>0.30$) were both non-

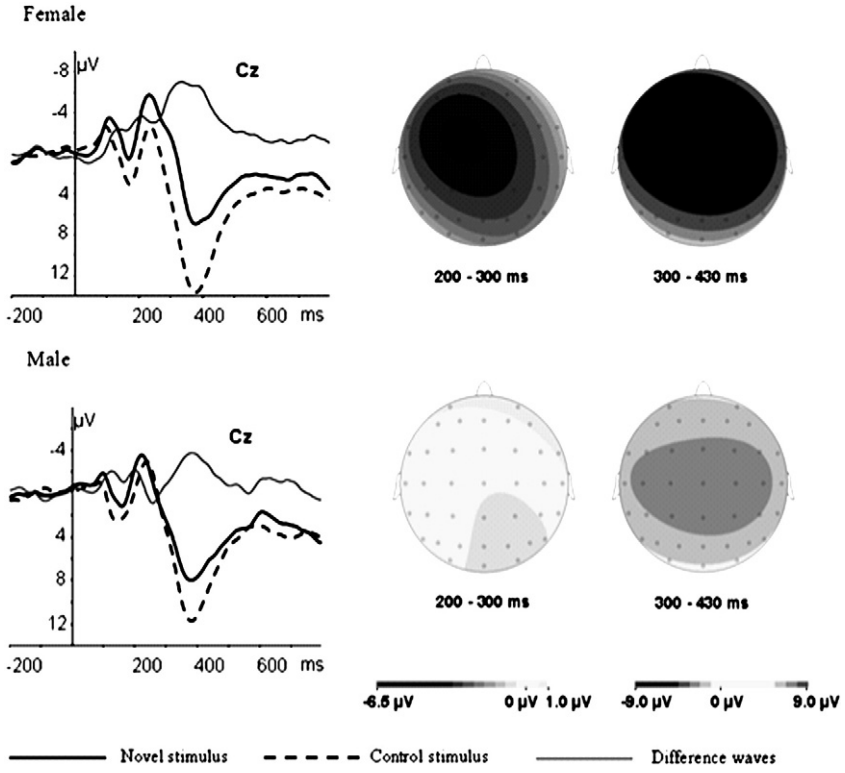

Fig. 2. The novel-control difference ERPs at Cz (left)and the topographical distribution of their voltage amplitudes (Right).

significant. This suggests that novel stimuli elicited a novelty-specific processing which interfered with the target/non-target classification in both samples.

2.2.2. *ERP results*

2.2.2.1. Early components. The ANOVA on the amplitudes of the 130–200 ms interval showed a significant main effect of stimulus ($F(1, 30)=54.73$, $p<0.001$; $\eta^2=0.646$), with the novel stimuli eliciting more negative amplitudes than the control stimulus. Additionally, the amplitudes were more pronounced at frontal than at central sites ($F(8, 240)=3.74$, $p<0.02$), while the amplitude differences between novel and control conditions were larger in the frontal than in the central sites ($F(8,240)=3.64$, $p<0.01$). There was no significant interaction effect between stimulus and gender ($F(1, 30)=0.724$, $p>0.40$; $\eta^2=0.024$).

The analysis of the amplitudes in the 200–300 ms interval showed greater negative deflections during novel relative to control conditions ($F(1, 30)=8.70$, $p<0.01$; $\eta^2=0.225$). Additionally, the amplitudes were larger at the frontal sites than the central sites ($F(8, 240)=25.61$, $p<0.001$), while women exhibited more positive amplitudes than males irrespective of stimulus condition ($F(1, 30)=11.08$, $p<0.01$; $\eta^2=0.270$). There was no significant interaction effect between stimulus and gender ($F(1, 30)=0.302$, $p>0.50$; $\eta^2=0.010$).

2.2.2.2. Late positive components: stimulus and gender interaction effects in raw ERPs. The repeated measures ANOVA on the average amplitudes of the 300–400 ms interval revealed a significant main effect of stimulus ($F(1, 30)=20.35$, $p<0.001$; $\eta^2=0.404$), with novel stimuli eliciting smaller positive amplitudes than the control stimulus. The amplitudes were larger in females than in males, shown by a significant main effect of gender ($F(1, 30)=11.66$, $p<0.01$; $\eta^2=0.280$). There was a significant main effect of electrode site ($F(18, 540)=23.744$, $p<0.001$) as well as a significant stimulus and electrode site interaction ($F(18, 540)=4.549$, $p<0.01$). The amplitudes were largest at parietal sites and decreased from central to frontal sites, while the amplitude differences between novel and control stimuli were most pronounced at central and centroparietal sites. However, the interaction between stimulus and gender did not meet statistical significance ($F(1, 30)=0.71$, $p>0.40$; $\eta^2=0.023$).

The analysis of the amplitudes in the 400–500 ms interval showed significant main effects of stimulus ($F(1, 30)=9.21$, $p<0.01$; $\eta^2=0.235$), electrode site ($F(18, 540)=33.483$, $p<0.001$) and gender ($F(1, 30)=9.667$, $p<0.01$; $\eta^2=0.244$). The amplitudes were largest at parietal sites. Novel stimuli elicited smaller positive amplitudes than the control stimulus, while the amplitudes were larger in females than in males. There was a significant stimulus and electrode site interaction ($F(18, 540)=8.14$, $p<0.001$), with the amplitude differences between novel and control stimuli being more pronounced at central than at parietal sites. However, the interaction between stimulus and gender remained non-significant ($F(1, 30)=3.47$, $p>0.07$; $\eta^2=0.104$).

The ANOVA on the average amplitudes of the 500–600 ms interval exhibited a significant main effect of electrode site ($F(18, 540)=11.15$, $p<0.001$) and a marginal effect of gender ($F(1, 30)=3.750$, $p=0.062$; $\eta^2=0.111$). The amplitudes were

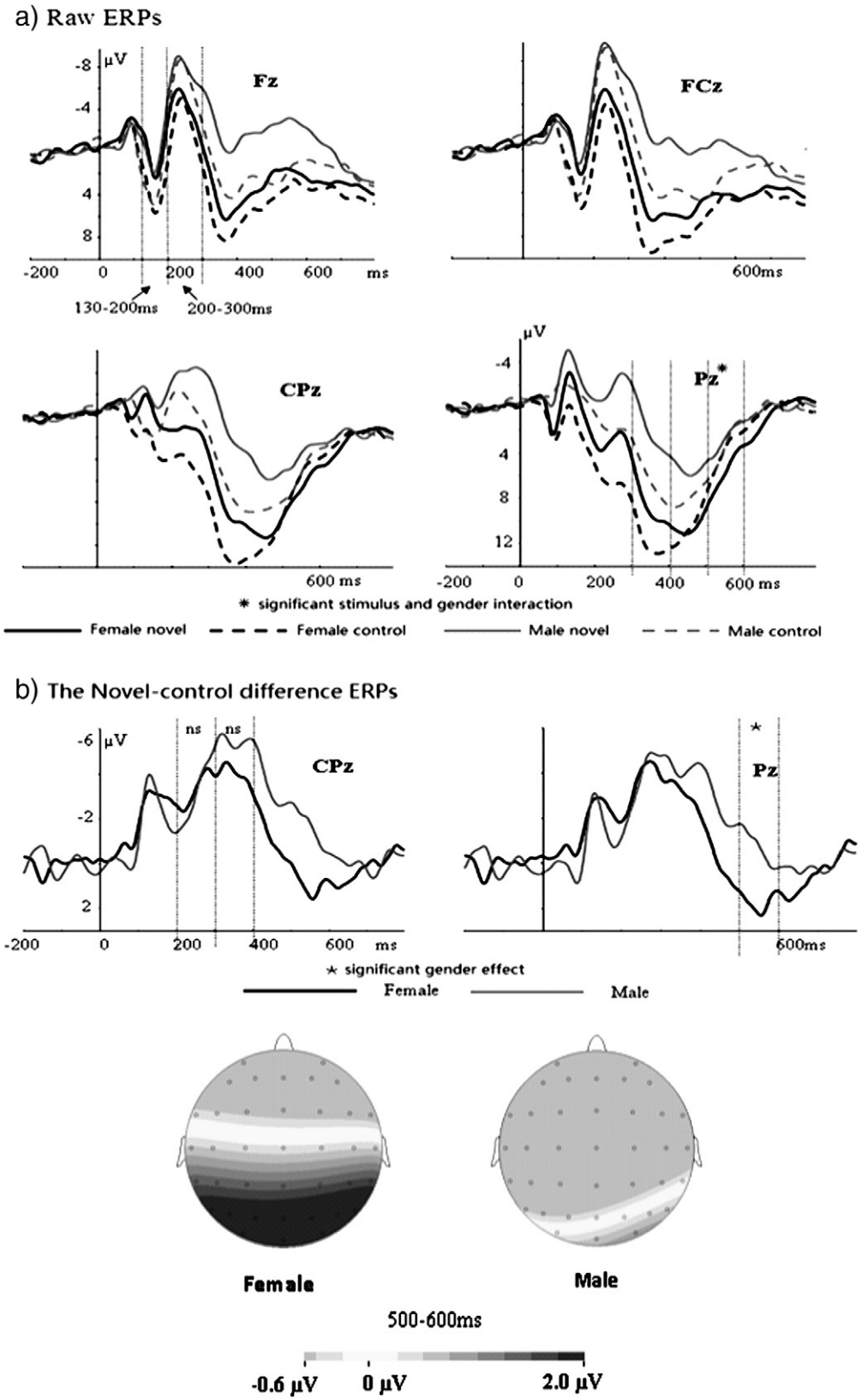

Fig. 3. Averaged ERPs in Experiment 2. Top:Raw ERPs elicited during novel and control conditions for both samples. Bottom: Novel-control difference ERPs in females and males and their topographical maps in the 500-600ms interval.

largest over parietal and central-parietal sites, and females exhibited more positive amplitudes than did males. There was a significant interaction effect between gender and stimulus ($F(1, 30) = 4.82$, $p < 0.05$; $\eta^2 = 0.139$) which interacted significantly with electrode site ($F(18, 540) = 16.11$, $p < 0.001$). In order to disentangle these interactions, we analyzed the

simple effects of the gender and stimulus interaction at the nine central-to-frontal sites, and the ten parietal sites respectively. The interaction between stimulus and gender was non-significant at the nine central-to-frontal sites ($F(1, 30)=2.863$, $p>0.1$, $\eta^2=0.087$). However, there was a significant stimulus and gender interaction across the 10 posterior-parietal sites ($F(1, 30)=5.78$, $p<0.03$; $\eta^2=0.161$). The breakdown of the interaction showed significantly more positive amplitudes during novel (M±S.E; 6.32±1.24 μV) than during control (4.32±1.36 μV) conditions in females ($F(1, 30)=8.82$, $p<0.01$), while the amplitude differences between novel (3.27±0.88 μV) and control (3.56±0.75 μV) conditions did not meet statistical significance in males ($F(1, 30)=0.18$, $p>0.60$). Lastly, the analysis of the 600–700 ms amplitudes showed largest positive amplitudes at central scalp sites, shown by a significant main effect of electrode site ($F(18, 540)=5.65$, $p<0.01$). The amplitudes tended to be larger in females than in males, shown by a marginal effect of gender ($F(1, 30)=3.97$, $p<0.06$; $\eta^2=0.117$). Nevertheless, the main effect of stimulus ($F(1, 30)=0.63$, $p>0.40$; $\eta^2=0.020$), the interaction of stimulus with gender ($F(1, 30)=0.96$, $p>0.30$; $\eta^2=0.031$), as well as the interaction amongst stimulus, gender and electrode site ($F(18, 540)=0.408$, $p>0.80$) all failed to meet statistical significance.

2.2.2.3. Gender effects in novel-control difference ERPs. As described above, the stimulus and gender interaction effect was significant in the 500–600 ms interval across centroparietal and parietal sites. Therefore, the present study further analyzed the gender effect in the novel-control difference ERPs to test the reliability of the results. The analysis of the amplitudes in the 500–600 ms interval, with gender as the between-subject factor and electrode site as the within-subject factor, demonstrated larger amplitudes in females than in males ($F(1, 30)=5.522$, $p<0.03$; $\eta^2=0.16$), while the amplitudes were larger at parietal sites than at central-parietal sites ($F(9, 270)=8.489$, $p<0.001$). Thus, the analysis of the raw and novelty-related ERPs both showed enhanced processing of stimulus novelty in females than in males in the 500–600 ms of the LPC time window (see Fig. 3).

2.2.3. Discussion of Experiment 2

In summary, after controlling the onset frequency of control and novel stimuli in Experiment 2, we still observed significant novelty effect and enhanced brain processing of novelty in females than in males. The results continued to show significant novelty effects in both response time and ERP measures. RTs were longer for the novel than for the control stimuli in both the male and female groups and novel stimuli elicited significant novelty effects at all measured components from 130 to 700 ms post-stimulus. This suggests that the task used in Experiment 2 was effective in inducing novelty processing.

In the 130–200 ms interval, novel stimuli elicited more negative deflections than the control stimulus. This suggests that participants detected the occurrence of novel events which consequently elicited enhanced early visual processing (Thorpe et al., 1996). Similarly, novel stimuli elicited more pronounced oddball N2 components than the control stimulus at the 200–300 ms interval, possibly reflecting greater attention orienting evoked by novel stimuli (Carretié et al., 2004; Yuan et al., 2007). Moreover, novel stimuli elicited smaller LPC amplitudes than the control stimulus throughout the 300–600 ms interval. This was most likely due to the involvement of a cognitive control process with which the brain inhibited task-irrelevant and distracting novel information, a higher-order process known to be associated with decreased LPC amplitudes (Chen et al., 2008; Liotti et al., 2000; Yuan et al., 2008b; 2011). Thus, the novelty effect was significant in the 130–200 ms, the 200–300 ms and the 300–500 ms intervals, which was consistent with a moderate level of "pop-out" feeling to novel stimuli reported by both samples during the post-experiment interview. On the other hand, regardless of stimulus condition, females exhibited enhanced positive amplitudes compared to males in each 100 ms of the 300–600 ms interval. This finding confirmed the previous observation showing larger P3 amplitudes in females as a result of the larger callosal areas, irrespective of the task (Hoffman and Polich, 1999; Steffensen et al., 2008).

Importantly, a significant interaction between stimulus and gender was observed in the averaged amplitudes of the 500–600 ms interval, with the LPC amplitudes enhanced during novel compared to control conditions in females, but not in males. At the same time interval, the LPC component in the novel-control difference ERPs, which served as a direct index of novelty effect, was significantly more pronounced in females than in males. Although the two samples were similar in novelty processing at earlier time stages, females, but not males, exhibited a preferential processing of novel events in the 500–600 ms interval. As LPC activity is associated with conscious cognitive evaluation of stimulus meaning (Huang and Luo, 2006; Schupp et al., 2000), the enhanced LPC responding of females in both raw and difference ERPs most likely reflects sustained cognitive processing of stimulus novelty. This is probably achieved by females allocating increased psychological resources in comparison to males for evaluating the biological significance of novel events (e.g. determining whether such events are emotionally relevant). It is apparent that females exhibited sustained and larger electrical brain activity compared to males for novel event processing in the 500–600 ms interval, even when novel and control stimuli were presented in equal frequency. This indicates that the enhanced brain processing of novel events in females is reliable and robust, irrespective of whether novel stimuli were less frequent or matched in frequency compared to the non-novel control stimulus.

3. General discussion

The two adapted three-stimulus oddball experiments consistently demonstrated enhanced brain processing of emotion-irrelevant novel stimuli in females than in males, regardless of the onset frequency of novel stimuli. In order to maximize ecological validity, Experiment 1 presented task-irrelevant novel stimuli less frequently than the task-irrelevant control stimulus. The results of this experiment showed enhanced processing of novel events in females compared to males, reflected by both the behavioral and ERP measures. To test whether this enhanced processing of novelty in females was independent of the established brain sensitivity of females to infrequent stimuli (Yuan et al., 2010), Experiment 2 matched novel and control stimuli in onset frequency. This

experiment continued to demonstrate enhanced brain processing of stimulus novelty in females versus males. Thus, the enhanced brain processing of novel events observed in the present studies is stable and robust, and is a unique phenomenon independent of the known enhanced sensitivity of females to rare stimuli (Yuan et al., 2010). Taking together the results of Experiment 1 and 2, the enhanced processing of novel events by females was primarily manifested by: 1) higher novelty assessment scores in females versus males; 2) more pronounced novelty effects in females on ERP amplitudes of the 200–430 ms (Experiment 1) and 500–600 ms (Experiment 2) intervals (Figs. 1–3). The gender differences in processing novel events were observed later in Experiment 2 (500–600 ms) than in Experiment 1 (200–430 ms). This was possibly because Experiment 2 required behavioral responses to both target and non-target stimuli, whereas Experiment 1 required only passive viewing of non-target pictures. The active classification task, which is irrelevant to novelty processing, may distract subjects to a larger extent and thus may have delayed the appearance of the gender effect in novelty processing in Experiment 2.

As previously stated, novel events are biologically important during adaptation because they are perceptually salient and often happen unpredictably in the context of regular events (Polich, 2007; Ranganath and Rainer, 2003; Sokolov et al., 2002). These features determine that it is adaptively important for the brain to respond rapidly to novel events in order for organism to increase survival probability in changing environments, although novel events are not necessarily emotionally salient. This is most likely why Experiment 1 and 2 both showed significant novelty effects from early to late time windows in both genders. This view is supported by recent evidence showing emotion neural network (e.g. amygdala, orbitofrontal cortex) activation with novel stimulation (Weierich et al., 2010). The contribution of the present study, however, is to reveal that females are equipped with enhanced brain processing of novel events that are biologically important. In consideration of the well-known fact that females, compared with males, are more sensitive to emotionally unpleasant stimuli (Hofer et al., 2006; Montagne et al., 2005; Yuan et al., 2009) and emotion-irrelevant rare stimuli (Yuan et al., 2010) (both of which are biologically important), our results suggest that females may be equipped with an advantage in processing biologically significant events, irrespective of whether the event itself contains emotional content or not. This conclusion would be more convincing, if we have controlled the subliminal states of depression/anxiety that has been reported to influence ERP responding to emotionally relevant stimuli (Rossignol et al., 2007; 2008). Though none of subjects, whether they are males or females, reported symptoms of depression/anxiety in the present study, we have to acknowledge it a limitation that our studies missed quantifiable measurement of subliminal anxiety/depression.

The female advantage in processing biologically important stimuli may be associated with a larger size of limbic cortex and better neural connection between orbital frontal and amygdala in females (Gur et al., 2002). Previous studies suggest that women have larger orbital frontal cortices and identical volumes of amygdala and hippocampus compared to men, which results in a larger ratio of orbital-frontal gray matter to amygdala volume in women (Gur et al., 2002). However, this hypothesis requires confirmation in future studies using high spatial resolution techniques, such as functional magnetic resonance imaging.

Greater sensitivity of females to novel events may be the result of evolutionary adaptation (Bjorklund and Shackelford, 1999; Geary, 1998). For example, greater sensitivity to unpredictable novel events may equip females to treat potential threats more effectively, as they are usually the primary caregivers to offspring and need to ensure the survival of offspring (Bjorklund and Shackelford, 1999). Furthermore, the advantage for processing biologically significant stimuli may be a compensation for female physiological disadvantages relative to males (Malina and Johnson, 1967; Roche and Malina, 1983; Thomas and French, 1985), such as smaller size (Espenschade and Eckert, 1980), a lesser muscle to fat ratio (Malina and Johnson, 1967) and physiological vulnerabilities resulting from pregnancy and lactation (Teperi and Rimpela, 1989). The enhanced responding to all biologically important stimuli, irrespective of whether they are emotional or neutral, may also increase female liability to startle responses and negative emotions (i.e., more false alarms about negative events), which may be one of the major factors underlying the higher rate of various affective disturbances in females compared to males (Nolen-Hoeksema, 2001; Yuan et al., 2009).

4. Conclusion

Using two modified three-stimulus oddball tasks and ERP measures, the current experiments revealed enhanced brain responding to emotion-irrelevant novel stimuli in females compared to males. There may be a female advantage in processing biologically important events, irrespective of whether the event itself is emotional or neutral, possibly as a result of the differential demands on females and males during evolution.

5. Experimental procedures

5.1. *Experiment 1*

5.1.1. *Participants*

Sixteen female (19–25 years; mean = 21.41 years) and sixteen male (18–23 years; mean = 21.25 years) college students participated in the experiment as paid volunteers. All subjects were healthy, right-handed and had normal or corrected to normal vision. No subjects reported history of affective disorder. In addition, they were free from psychiatric medication and had no symptoms of anxiety/depression. The study was approved by the local Review Board for Human Participant Research and each subject signed an informed consent form prior to the experiment.

5.1.2. *Stimuli*

This experiment employed an adapted three-stimulus oddball task. There were 2 blocks of 100 trials, with each block including 40 target, 40 non-novel control and 20 novel stimuli (40% vs. 40% vs. 20%). A photograph of a cup served as the target stimulus, a photograph of a bench as the non-novel control

stimulus and 40 non-repeated photographs of natural scenes as the novel stimuli (Bai et al., 2005). Both novel and non-novel control stimuli in this experiment were task-irrelevant distracting photographs that are emotionally neutral.[2] All pictures used in this experiment were identical in size and resolution (15×10 cm^2, 100 pixels per inch). In addition, the luminance level of the photographs was kept similar across the control and novel stimulus sets, and the contrast of the monitor was set to a constant value across subjects throughout the experiment.

5.1.3. *Behavioral procedure*

Subjects were seated in an acoustically isolated room approximately 150 cm from a computer screen; thus, the horizontal and vertical visual angles were both less than 6°. The onset sequence of the pictures was randomized for each subject. 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 from 500 to 1,500 ms was presented and was followed by the 1000 ms presentation of a picture stimulus. Subjects were instructed to detect the "cup" picture by pressing the space key, in a sequence of distracters that should be ignored. The presentation of the picture (target, control or novel) was then replaced by a blank screen for 1,000 ms. At the end of each block, an accuracy rate was presented as feedback for participant performance. The experiment started after subjects achieved 100% accuracy in the practice session. At the end of the experiment, subjects were debriefed and asked about their feelings regarding the presentation of "non-cup and non-chair" pictures. Further, they were required to rate the strength of their subjective novelty feeling for these trials using a 7-point scale (ranging from 1: no novel feeling at all; 7: has very intense novel feeling).

5.1.4. *ERP recording and analysis*

Electroencephalography (EEG) was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products), with the reference electrodes on the left and right mastoids (average mastoid reference, Luck, 2005) and a ground electrode on the medial frontal aspect. Vertical electrooculograms (EOGs) were recorded supra- and infra-orbitally at the left eye. Horizontal EOG was recorded as the left versus right orbital rim. EEG and EOG activity was amplified with a DC ~100 Hz bandpass filter and continuously sampled at 500 Hz/channel. All electrode impedances were maintained below 5 kΩ. ERP averages were computed off-line; trials with EOG artifacts (mean EOG voltage exceeding ±80 μV), amplifier clipping artifacts, or peak-to-peak deflection exceeding ±80 μV were excluded from averaging.

EEG activity during the novel and the non-novel control conditions was averaged separately. ERP waveforms were time-locked to the onset of stimuli and the average epoch was 1000 ms, including a 200 ms pre-stimulus baseline. The following 15 electrode sites were selected for statistical analysis: F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4 (9 frontal and central sites), CP3, CPz, CP4, P3, Pz, P4 (6 central-parietal and parietal sites). As shown by Fig. 1, the amplitude differences between non-novel control and novel conditions started at approximately 130 ms post-stimulus, and the gender effect on the size of these differences was mainly distributed in the 130–430 ms interval (see Fig. 1b), where we observed prominent P2 (130–200 ms), N2 (200–300 ms), and P3 (300–430 ms) components (see Fig. 1a). Thus, the present study first examined stimulus (non-novel control, novel) by gender (male, female) interaction effects for the mean amplitudes at 130–200 ms, 200–300 ms, and 300–430 ms intervals, by conducting a repeated measures analysis of variance (ANOVA) (stimuli and electrode as repeated factors and gender as the between-subjects factor). Because P2 and N2 components were observed mainly in central and frontal sites, and P3 was distributed broadly in the scalp, we analyzed the amplitudes of the P2 and N2 at the nine frontal-central sites, and selected the 15 sites for analysis of P3 component. Based on the significant stimulus by gender interaction effects that indicated gender effects in novel stimulus processing, we conducted an additional analysis of the novelty-related amplitudes at corresponding intervals of the novel-control difference ERPs, to confirm and supplement the results indicated by the raw ERP analyses. A repeated measures ANOVA was conducted on the amplitudes with electrode as the within-subject factor and gender as the between-subject factor. The degrees of freedom for the *F*-ratio were corrected according to the Greenhouse–Geisser method in all these analyses.

5.2. *Experiment 2*

5.2.1. *Participants*

Sixteen female (18–23 years; mean age=20.88 years) and sixteen male (19–24 years; mean age=21.63 years) college students participated in Experiment 2 as paid volunteers. No subjects had participated in Experiment 1. All subjects were healthy, right-handed, had normal or corrected to normal vision. No subjects reported history of affective disorder, anxiety/depression symptoms, and all subjects were free from psychiatric medication. The study was approved by the local Review Board for Human Participant Research and each subject signed an informed consent form prior to the experiment.

5.2.2. *Stimuli*

This experiment used a further adaptation of the three-stimulus oddball task in which subjects were asked to respond by pressing one key to the target stimulus (i.e., cup), and the other key for non-target stimuli (control stimulus and novel stimuli). The experiment had 2 blocks of 80 trials, with each block including 40 target, 20 control and 20 novel stimuli (50% vs. 25% vs. 25%). Thus, the frequency of target response and that of non-target response was equated in each block, in order to avoid the influence of behavioral inhibitory control when non-target stimuli occur infrequently (Yuan et

[2] The neutral photographs used in this study were taken from Chinese Affective Picture System (CAPS), a system adapted from IAPS that was developed in the Key Lab 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 directly. All the images used in this study were normatively rated as neutral, non-emotional. The contents of the selected images include furniture, utensil, craftworks, tools, animals and so on. The valence of the selected neutral photographs is around the neutral midpoint of the 9-point rating scale while the arousal was low. The averaged values of these photographs are 5.68±0.60 (M±SD) for valence, and 4.20±0.86 (M±SD) for arousal.

al., 2008a). Moreover, control and novel stimuli were equal in onset frequency, both belonging to the non-target category for each subject. The stimulus materials in Experiment 2 were the same as those in Experiment 1.

5.2.3. *Behavioral procedure*

The experimental procedure was similar to that in Experiment 1, except that subjects were instructed to press the "F" key as accurately and quickly as possible if the "cup" picture appeared, and to press the "J" key if the other pictures appeared, irrespective of stimulus contents.

5.2.4. *ERP recording and analysis*

The ERP recording and averaging was similar to that in Experiment l. EEG activity for correct responses during control and novel conditions was averaged separately. ERP waveforms were time-locked to the onset of stimuli and the average epoch was 1000 ms, including a 200 ms pre-stimulus baseline. The following 19 electrode sites were selected for statistical analysis: F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4 (9 frontal and central sites), CP1, CP3, CPz, CP2, CP4, P1, P3, Pz, P2, P4 (10 central-parietal and parietal sites).

According to the averaged ERPs (Fig. 3), there were obvious components in 130–200 ms (P2), 200–300 ms (N2) across nine frontal and central sites (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4). Thus, firstly we tested whether there were significant novelty effects and gender differences in these early time points at the nine frontal-central sites (using the same method as in Experiment 1). Amplitude differences between novel and control conditions appeared more positive in females compared to males in the late positive component (LPC, see Fig. 3) measured in the 300–600 ms time interval, particularly over posterior-parietal scalp sites (see Fig. 3). Thus, this experiment examined stimulus (control, novel) by gender (male, female) interaction effects for the averaged amplitudes in each 100 ms interval of the 300–700 ms time window, by conducting a repeated measures ANOVA (stimuli and electrode as the repeated factors while gender was the between-subjects factor). We included the 10 posterior-parietal sites (CP1, CP3, CPz, CP2, CP4, P1, P3, Pz, P2, P4) in addition to the above nine central and frontal sites for this analysis, because the averaged amplitudes were largest at parietal sites in the 300–600 ms (LPC) intervals. Similar to Experiment 1, based on the observation of significant stimulus by gender interaction effects, we conducted an additional analysis of the novelty-related amplitudes at corresponding intervals of the novel-control difference ERPs, to confirm the results indicated by the raw ERP analyses. The method of analyses was the same as that in Experiment 1.

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