Different patterns of puberty effect in neural oscillation to negative stimuli: sex differences

Jiajin Yuan · Enxia Ju · Jiemin Yang ·
Xuhai Chen · Hong Li

Received: 16 December 2013 / Revised: 4 March 2014 / Accepted: 21 March 2014 / Published online: 28 March 2014
© Springer Science+Business Media Dordrecht 2014

Abstract The present study investigated the impact of puberty on sex differences in neural sensitivity to negative stimuli. Event-related oscillation technique was used. Because girls are more vulnerable to affective disturbances than boys during adolescence, it was hypothesized that puberty exerts different influences on neural sensitivity to negative stimuli in boys and girls. EEGs were recorded for highly negative (HN), mildly negative (MN) and neutral pictures, when boys and girls distinct in pubertal status performed a non-emotional distracting task. No emotion effect and its interaction with sex and puberty were observed in response latencies. However, puberty influenced the gamma-band oscillation effect for negative stimuli differently for boys and girls: Pre-pubertal boys showed a significant emotion effect for HN stimuli, whose size was decreased in pubertal boys. By contrast, there was a significant emotion effect for HN stimuli in pubertal girls

but not in pre-pubertal girls. On the other hand, the size of the emotion effect for HN stimuli was similar for pre-pubertal boys and girls; while this effect was significantly more pronounced in pubertal girls compared to pubertal boys. Additionally, the size of the emotion effect in gamma oscillations decreased as a function of pubertal development during both HN and MN stimulation in boys. For girls, the emotion effect in gamma oscillations increased with pubertal development during HN stimulation. Thus, puberty is associated with reduced neural sensitivity in boys but increased sensitivity in girls, in reaction to negative stimuli. The implications of these results for the psychopathology during adolescence were discussed.

Keywords Pubertal transition · Emotional sensitivity · Sex differences · Event-related brain oscillations (ERO)

Introduction

Many studies indicated a higher prevalence of affective disturbances in females relative to males during adolescence (Patton and Viner 2007; Nolen-Hoeksema 2001; Kessler et al. 1993). The greater prevalence of depression in women was reported to emerge at early adolescence, approximately from 13 years of age and persists until midlife (Angold and Rutter 1992; Nolen-Hoeksema 2001). In early studies, researchers reported that the rates of depression were similar or lower in pre-pubertal girls in comparison with pre-pubertal boys (Angold and Rutter 1992; Angold et al. 1998; McGee et al. 1990; Wichstrom 1999), whereas depressive disorders began to be more prevalent in girls versus boys from pubertal transition (Angold and Rutter 1992; Ge et al. 2006; Kessler et al. 1993). Also, pubertal development is linked with a greater prevalence of other affective

J. Yuan (✉) · J. Yang
Key Laboratory of Cognition and Personality of Ministry of Education, School of Psychology, Southwest University, No. 1 of Tiansheng Road, Beibei, Chongqing 400715, China
e-mail: yuanjiajin168@126.com; yuanjiaj@swu.edu.cn

E. Ju
Chongqing Preschool Education College, Wanzhou, Chongqing 404047, China

X. Chen
Key Laboratory of Behavior and Cognitive Psychology in Shaanxi Province, School of Psychology, Shaanxi Normal University, Xi'an 710062, China

H. Li
Research Center for Psychological Development and Education, Liaoning Normal University, Dalian, Liaoning, China

disturbances in girls compared to boys, such as panic disorder, social anxiety disorder and dysthymia (Deardorff et al. 2007; Hayward et al. 1992; Patton and Viner 2007).

Nevertheless, the mechanisms underlying this sex difference are unclear. There were a number of studies suggesting that psychosocial factors, such as the girls' more concerns about body image, might interact with biological factors (e.g. more hormonal fluctuations in girls) to contribute to this phenomenon (Hankin and Abramson 2001; Angold et al. 1999). However, most of these studies relied on questionnaires and psychometric methods, such as treating psychosocial and hormonal measurements as predictors, and depressive symptoms as outcomes (Angold et al. 1998, 1999; Hayward et al. 1999; Wichstrom 1999; Nolen-Hoeksema and Girgus 1994). Accordingly, the conclusions were primarily based on regression methods (e.g. Angold et al. 1998, 1999; Wichstrom 1999; Nolen-Hoeksema and Girgus 1994), and seldom experimental evidence was available to date that directly examines this phenomenon.

To better understand why girls become more vulnerable to affective disturbances than boys during adolescence, it is necessary to use experimental methods, by which we are able to manipulate the emotionality of stressful stimuli and directly assess how sex and puberty may influence one's behavioral and physiological reactivity to stressful stimuli. The use of experimental approach is important, because previous studies suggest that individuals with greater sensitivity to emotionally stressful stimuli, are usually more vulnerable to negative emotions and affective disturbances (Hofer et al. 2006; Gohier et al. 2013). A typical example is that adult females, a population known for the enhanced brain sensitivity to negative stimuli (Hofer et al. 2006; Yuan et al. 2009), have a higher prevalence of affective disturbances than adult males (Altemus 2006; Simon et al. 2006). Additionally, it is well known that pubertal development is a land-marking event of adolescence, which significantly influences both health and social adaptation (Patton and Viner 2007). Thus, to understand the girls' vulnerability to affective disturbances during adolescence, it would be helpful to investigate the influence of puberty on brain sensitivity to negative stimuli, and how this influence varies across sexes.

As puberty is associated with higher prevalence of affective disturbances in girls versus boys, it is likely to observe that pubertal girls are more reactive to negative stimuli than pre-pubertal girls in EEGs. This likelihood should be high, considering that the feminine gender role, which stereotypes girls to be passive, less assertive and emotion-oriented, is intensified during puberty (Hankin and Abramson 2001). This puberty effect, however, may not apply to boys, as little evidence showed increasing affective disturbances with pubertal development in boys.

Particularly, pubertal development of boys is associated with intensified masculine gender identity, a trait that predisposes boys to be assertive, instrumental and less emotion-focused (Wichstrom 1999). Thus, it is likely that pubertal boys are less reactive to negative stimuli compared to pre-pubertal boys. If these hypotheses are confirmed, the sex differences in the prevalence of affective disturbances during adolescence may be explained, at least in part, by the girls' enhanced reactivity and the boys' decreased reactivity to negative stimuli during pubertal transition.

In life settings, emotional responses are often triggered by unpredictable stimuli during non-emotional activities (Delplanque et al. 2005; Yuan et al. 2007). Thus, an experimental design that presents emotional stimulus unpredictably and that does not require subjects to assess stimulus valence, may allow emotional responses in the laboratory setting to more closely resemble those in natural settings (Delplanque et al. 2005). Thus, to increase ecological validity of emotion induction, the present study used a distracting oddball task that required subjects to make a standard/deviant distinction by pressing different keys, irrespective of the emotionality of the deviants. Considering that negative stimuli of distinct valence strengths often influence cognitive functions differently (Yuan et al. 2012), we manipulated negative stimuli into two valence levels: highly or mildly negative.

On the other hand, compared to the classic event-related potential method that is restricted to low-pass filtering and phase-locked averaging, neural oscillation is able to provide richer information, such as non-phase-locked and fast rhythmic (e.g. gamma rhythm) indexes of emotion arousal (Bastiaansen and Hagoort 2006). Based on this consideration, we used event-related oscillations (ERO) to investigate the influence of puberty on brain sensitivity to negative stimuli and sex differences. Specifically, it has been reported that the power of high-frequency gamma oscillations in EEGs is sensitive to negative stimulation, and the gamma power behaves as a valid index of emotion arousal to stressful stimuli (Balconi and Lucchiari 2008; Balconi et al. 2009). Thus, we chose gamma oscillatory activities as an index of the emotional arousal effect and its interaction with puberty and sex. Lastly, we used emotional pictures, instead of facial expressions, as experimental stimuli, because pictures were better to induce direct emotional arousal compared to other materials (Britton et al. 2006).

Methods

Subjects

As paid volunteers, 24 pre-pubertal (aged 10–12; 12 boys), and 24 pubertal students (aged 12–16; 12 boys) from nine

Table 1 The means and standard deviations of ages and pubertal development scores for each group

	Pre-puberty (10–12 years, N = 24)			Puberty (12–16 years, N = 24)		
	Boys (N = 12)	Girls (N = 12)	Diff.	Boys (N = 12)	Girls (N = 12)	Diff.
Age	11.17 ± 0.83	10.92 ± 0.51	$t(22) = 0.88$, ns	14.17 ± 1.19	14.00 ± 1.21	$t(22) = 0.34$, ns
Pubertal status	5.75 ± 0.87	6.42 ± 1.08	$t(22) = 1.67$, $p > .10$	12.92 ± 2.11	13.92 ± 1.98	$t(22) = -1.20$, ns

local primary/high schools participated in the experiment. The subjects were sampled randomly and were screened by administrating the Pubertal Development Scale (PDS-Wave 3; Earls et al. 2000). The PDS is a 4-point (1: “have not begun”; 2: “barely started”; 3: “definitely underway”; and 4: “development completed”), 5-item self-report questionnaire that is widely used for pubertal status measurement (Petersen et al. 1988; Earls et al. 2000). To measure pubertal status, subjects were required to indicate the extent to which they had experienced body hair development, growth spurt, and skin changes. Moreover, boys were asked to rate their facial hair growth and voice change, and girls were asked to report on breast development and menarche (scoring pre-menarche as “1” and post-menarche as “4”).

Pre-pubertal subjects scored 1–2 in each item of the PDS (Quevedo et al. 2009). Pubertal subjects scored 2–4 in each item but had not completed physical development (total score <20), and all pubertal girls reported menarche while boys deepening of voices (Quevedo et al. 2009). The subjects’ scoring was confirmed by the parent reports. Boys and girls were matched in both age and pubertal scores in either group (Table 1). Subjects and parents were debriefed with respect to emotional stability in the past 2 weeks, by reporting whether they had the following symptoms by a yes/no fashion: irritable, uneasy, anxious and depression. Those who had no these symptoms were recruited for the experiment. The subjects were all right-handed, with normal/corrected to normal vision and no history of neurological disorders. The subject and his/her guardian both signed an informed consent form for the experiment. The study was approved by the local Review Board for Human Participant Research.

Stimuli

The present study adopted a modified oddball paradigm which consisted of five blocks of 100 trials, and each block included 70 standard pictures and three conditions of 10 deviant pictures. All deviant stimuli were pictures taken from the Chinese Affective Picture System.¹ A natural

scene of a cup served as the frequent standard picture, and 30 pictures grouped as highly negative (HN), moderately negative (MN), or Neutral served as the deviants. The pictures depicted highly unpleasant, mildly unpleasant, or neutral animals (e.g. snakes, bugs, or eagles), natural scenes (e.g. fire disaster, flood, clouds) and human activity (e.g. homicide, violence, or sports). To test the validity of the pictures selected for each emotion category (HN, MN or Neutral), we recruited another sample of college students aged 18–26 years [$n = 80$; 39 males, 41 females; Mean age: 21.07] to rate the valence and arousal of the 90 pictures using the Self-Assessment Manikin procedure (SAM; Lang et al. 1997).

Using a self-report 9-point rating scale, subjects were required to rate the emotion valence (ranging from 1 = “very unpleasant” to 9 = “very pleasant”) and arousal (ranging from 1 = “very calm” to 9 = “very excited”) they felt for each image by pressing corresponding number keys in the keyboard. The sequence of the two ratings was counterbalanced across subjects. The results showed a significant main effect of emotion category in valence rating [$F(2,158) = 584.42$, $p < .001$, $\eta^2 = 0.88$]. HN pictures ($M = 2.51$, $SD = 0.66$) were rated more unpleasant than were MN pictures [$M = 4.05$, $SD = 0.71$; $F(1,79) = 449.24$, $p < .001$; $\eta^2 = 0.85$] which, in turn, were rated unpleasant compared with the Neutral pictures [$M = 5.54$, $SD = 0.77$; $F(1,79) = 368.86$, $p < .001$, $\eta^2 = 0.82$]. Also, the main effect of emotion category was statistically significant for arousal rating [$F(2,158) = 303.69$, $p < .001$; $\eta^2 = 0.79$]. HN pictures ($M = 7.02$, $SD = 0.85$) were rated more arousing relative to MN pictures [$M = 5.62$, $SD = 0.88$; $F(1,79) = 270.17$, $p < .001$; $\eta^2 = 0.77$] which, again, were rated more arousing than were Neutral stimuli [$M = 4.39$; $SD = 1.05$; $F(1,79) = 190.00$, $p < .001$; $\eta^2 = 0.71$]. Therefore, the pictures used for HN

¹ The CAPS was developed in the Key Laboratory of Mental Health, Chinese Academy of Sciences, to avoid the cultural bias in emotion induction among Chinese when the IAPS was used directly (Huang and Luo 2004). The CAPS introduced a great number of pictures characterized by oriental scenes. The development method resembled

Footnote 1 continued

that of IAPS. For the CAPS development, originators collected over 2,000 pictures of various contents, and finally kept 852 pictures that fit Chinese culture and were simple in meanings for normative ratings. Chinese college students ($n = 156$, gender-matched) were recruited to rate the valence, arousal, and dominance by a self-report, nine-point rating scale for the 852 pictures. The pretest for this system showed that CAPS is reliable across individuals in emotional induction (the between-subjects reliability score was .982 for valence and .979 for arousal). For more details about CAPS, see Bai et al. (2005).

and MN conditions were valid in inducing corresponding intensity of negative emotion.

The sequence of standard and deviant pictures was randomized for each subject. 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 was tested and matched across the three 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. At the end of each block, 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 1,500 ms was presented and 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 picture presentation was terminated by key pressing or was terminated when it elapsed for 1,000 ms. Therefore, each subject was informed that their responses must be made under 1,000 ms. Each response was followed by 1,000 ms of a blank screen (Fig. 1). Ten practice trials were used before formal experiment in order to familiarize subjects with the procedure.

EEG recording

The electroencephalogram was continuously recorded from 64 scalp electrodes mounted on an elastic cap according to the extended 10–20 system (Brain Product, Munchen, Germany). EEG signals were referenced online to the left mastoid and a ground electrode was fitted in the medial frontal aspect. The impedance of all electrodes was kept less than 5 k Ω . Vertical electrooculograms (EOGs) were monitored with electrodes located above and below the left eye. The horizontal EOG was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG and EOG were amplified using a 0.05–100 Hz bandpass and continuously digitized at 500 Hz/channel for offline analysis. Artifact-free EEG segments to trials with correct responses were averaged separately for each emotion condition.

Preprocessing

EEG data were preprocessed using EEGLAB (Delorme and Makeig 2004), an open source toolbox running under the MATLAB environment. EEG epochs were segmented in 2,200 ms time window with pre-stimulus 800 ms, and baseline corrected using 200 ms interval prior to picture onset. EEG epochs were re-referenced offline to the average reference and high pass filter at 0.5 Hz. Epochs with large artifacts (exceeding ± 100 μ V) were removed and channels with poor signal quality were interpolated. Trials contaminated by eye blinks and movements were corrected using an independent component analysis algorithm (Delorme and Makeig 2004).

Time–frequency analysis

For ERO analysis, induced spectral EEG activity was assessed by creating event related spectral perturbations (ERSP) using a complex sinusoidal wavelet transform procedure implemented in EEGLAB (Delorme and Makeig 2004). The resulting complex signal provides an estimate of instantaneous power for each time point at frequencies of 3–100 Hz. This procedure is done on each trial, and then power values are averaged across trials. Power values were normalized with respect to a 100–0 ms prestimulus baseline and transformed into decibel scale ($10 \cdot \log_{10}$ of the signal). We used an EEG epoch window of –800 to 1,400 ms from each stimulus to ensure that edge effects did not contaminate time windows of interest. The mass-univariate approach implemented in the *statcond* function of EEGLAB toolbox was used to identify the frequency band and time window that the ERSP values significantly distinguished between negative and neutral conditions. Based on the mass-univariate analysis, there was no significant emotion effect in the theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz) and low-gamma (30–60 Hz) oscillations. However, the ERSP values within high gamma band (81–87 Hz) in the 200–550 ms time window showed significant differences between negative and neutral conditions (Fig. 1). Therefore, the ERSP data in the 81–87 Hz, 200–550 ms were averaged for each condition, and were then submitted into the Analysis of Variance (ANOVA) in the following 15 electrode sites: F3, Fz, F4 (frontal); FC3, FCz, FC4 (fronto-central); C3, Cz, C4 (central); CP3, CPz, CP4 (centroparietal); P3, Pz and P4 (parietal). A Repeated measures ANOVA was used with emotion (three levels: HN, MN, and Neutral), sagittality (five levels: frontal, frontocentral, central, centroparietal and parietal), laterality (left, midline, and right) as repeated factors, while sex (male, female) and puberty (pre-pubertal and pubertal) as the between-subjects factors. The degrees of freedom of the F-ratio were corrected according to the Greenhouse-Geisser method.

Fig. 1 *Top panel* the averaged oscillatory activities for HN, MN and Neutral conditions in each sample. *Top panel* the time–frequency map shows oscillatory activities at CPz over time (x-axis, 0 ms denotes picture onset) and frequency (y-axis). *Blue color* indicates power decrease relative to pre-stimulus baseline and *red color* indicates power increase relative to the baseline. *Middle panel* topographical maps for emotion-related oscillations for HN (HN-Neutral differences) and MN stimuli (MN-Neutral differences) in the 81–87 Hz, 200–550 ms window. *Bottom panel* the scatterplot of the correlation for pubertal scores and the gamma emotion effect during HN (*top left*) or MN (*top right*) condition in boys and girls. (Color figure online)

Behavioral results

Our task was suitable for both pre-pubertal and pubertal subjects, as false responses were rare, irrespective of sex and puberty. The ANOVA of response accuracy data showed no other effects except for higher accuracy in pubertal (98.49 %) compared to pre-pubertal (97.10 %) groups [$F(1,44) = 6.96, p < .02$]. The analysis of response time data showed no other effects except for faster responses in pubertal (560 ms) versus pre-pubertal [629 ms; $F(1,44) = 6.11, p < .02$] groups.

Time–frequency data

The analysis of 81–87 Hz gamma band activity in the 200–550 ms interval showed a significant main effect of sagittality [$F(4,176) = 13.25, p < .001$]. The gamma band oscillation was more pronounced at frontal (Mean: -2.50 dB), frontocentral (-2.69 dB) and central (-2.55 dB) regions compared to the parietal region (-2.00 dB). There were significant main effects of emotion [$F(2,88) = 10.18, p < .001$] and puberty [$F(1,44) = 6.16, p = .017$]. More importantly, there was a significant three-way interaction amongst emotion, sex and puberty [$F(2,88) = 3.71, p < .03$]. This interaction is reliable, as the Analysis of Covariance using age as a covariate did not alter its significance [$F(2,88) = 3.74, p < .03$]. Also, this interaction should not be explained by the shorter RTs in pubertal versus pre-pubertal subjects, because our additional ANCOVA showed the same interaction after controlling the influence of RT differences [$F(2,88) = 3.88, p < .03$].

To facilitate decomposing the three-way interaction, we computed the negative-neutral difference gamma power as an index of the emotion effect. Then, two steps of analyses were conducted: 1), test the significance of negative-neutral differences in each group; 2), test how the puberty effect (in the emotion index) varies across sexes, by a two-way ANOVA.

The first analysis showed significant HN-neutral differences in pre-pubertal boys [$t(11) = -2.96, p = .013$] and pubertal girls [$t(11) = -4.17, p = .002$] but not in pubertal boys [$t(11) = -0.34, ns$] and pre-pubertal girls [$t(11) = -1.62, p > .10$].

However, MN-neutral differences failed to meet significance threshold ($p < .05$) in pre-pubertal boys [$t(11) = -1.89, p = .09$], pre-pubertal girls [$t(11) = -2.25, p = .05$], pubertal girls [$t(11) = -2.08, p = .06$] and in pubertal boys [$t(11) = -0.93, ns$].

The second analysis showed a significant puberty and sex interaction in the emotion effect for HN stimuli [$F(1,44) = 7.06, p < .02$; $\eta^2_p = 0.14$]. Post hoc analyses with bonferroni correction showed a smaller emotion effect in pubertal (-0.07 dB) compared to pre-pubertal [-0.70 dB; $F(1,22) = 4.81, p < .04$; $\eta^2_p = 0.10$] boys. In contrast, the size of the emotion effect was not significantly different

between pre-pubertal (-0.32 dB) and pubertal girls [-0.76 dB; $F(1,22) = 2.45, p = .12$], despite value increases in pubertal compared to prepubertal samples. Also, we broke down this interaction by testing sex differences in pubertal and pre-pubertal groups, respectively. The results showed a similar size of the emotion effect across sexes in pre-pubertal group [$F(1,22) = 1.57, p = .22$], while the emotion-related gamma oscillatory activity was significantly more pronounced in pubertal girls than in pubertal boys [$F(1,22) = 6.77, p < .02$]. The analysis of the emotion effect for MN stimuli did not yield a significant puberty and sex interaction [$F(1,44) = 2.93, p = .09$].

Pubertal scores and gamma power effect correlations

To confirm these findings, we conducted Pearson correlations between pubertal scores and the gamma emotion effect in boys and girls, respectively. The results showed that the two variables were significantly and positively correlated for both HN ($r = 0.383, p < .04$) and MN ($r = 0.357, p < .05$) conditions in boys. This suggests that the size of the gamma emotion effect (note that this effect was expressed by negative values) decreased as a function of increasing puberty in boys, regardless of whether HN or MN stimuli were used. On the other hand, the size of the gamma emotion effect increased significantly as a function of pubertal development during HN ($r = -0.364, p = .04$), but not MN ($r = 0.101, p = .32$), condition in girls.

Discussions

The present study showed a significantly smaller size of gamma emotion effect for HN stimuli (i.e., HN-Neutral differences) in pubertal compared to pre-pubertal boys; and the magnitude of the emotion effect for negative stimuli decreased with pubertal development in boys, regardless of whether HN or MN stimuli were used. By contrast, the size of the gamma emotion effect for HN stimuli increased with pubertal development in girls. On the other hand, we observed a similar size of the emotion effect in gamma oscillations in pre-pubertal boys and girls; while this emotion effect was significantly more pronounced in pubertal girls than in pubertal boys. These results suggest that puberty is linked with reduced brain sensitivity in boys, and with increased brain sensitivity in girls, to negative stimuli, as previous studies have established that the EEG oscillations in gamma frequencies behave as a reliable index of emotion arousal to negative stimuli (Balconi and Lucchiarì 2008; Balconi et al. 2009; Keil et al. 2001).

For instance, Keil et al. (2001) observed that gamma band oscillations were sensitive to the arousal of emotional stimuli, such that the gamma power decrease compared to

the baseline (i.e. event-related desynchronization; ERD) around the 200–300 ms post stimulus was more pronounced for emotional compared to neutral pictures. This result was confirmed by Balconi and colleagues who, in a series of studies (Balconi and Lucchiari 2008; Balconi et al. 2009), observed larger gamma oscillation (e.g. ERDs) for high-arousing compared to low-arousing faces and pictures in a variety of temporal windows and scalp regions (e.g. anger vs. sadness). Similarly, we observed higher gamma oscillations, reflected by larger ERDs, for unpleasant-arousing compared to neutral pictures.

We observed decreased emotion arousal effect for HN stimuli, reflected by gamma oscillations, in pubertal relative to pre-pubertal boys. This result should be reliably attributed to puberty, as our analysis of covariance yielded the same puberty, sex and emotion interaction after controlling the age influences. Also, the reliability of this result was confirmed by our correlation analysis that showed reduced emotion effect for both HN and MN stimuli, as a function of increasing puberty in boys. These results coincided with epidemiological studies that showed a prevalence of depression before puberty (Anderson et al. 1987), and decreased rates of depression as a result of pubertal transition in boys (Angold et al. 1998). A most plausible explanation for this reduction, according to previous studies, is the intensified masculinity during puberty, which predisposes boys to be less emotion-focused, more assertive and action-oriented (Wichstrom 1999; Hyde et al. 2008). Also, there was evidence showing that the increasing testosterone levels of boys during puberty is associated with more developed top-down control of prefrontal cortices (e.g. ventromedial PFC; Stanton et al. 2009), which helps to regulate sub-cortical emotional arousal inputs (Lieberman et al. 2007). These factors might contribute to the reduction of boys' reactivity to negative stimuli with pubertal development. However, it is a limitation that we did not measure testosterone/estrogen levels in different groups that might have reinforced these inferences.

We observed significant larger gamma oscillations for HN versus neutral stimuli in pubertal girls, which was non-significant in pre-pubertal girls. This suggests that the puberty of girls is related to increased brain sensitivity to negative stimuli. This result is reinforced by our correlation analysis that showed increasing emotion effect for HN stimuli with pubertal development in girls. Also, this inference is supported by our observation that girls exhibited greater emotion-related oscillatory activity than boys in pubertal but not pre-pubertal samples. Our observation of increased reactivity to negative stimuli with the girls' pubertal development, is consistent with previous studies that reported multiple vulnerable factors of girls for negative emotion during puberty. Firstly, previous studies reported

that puberty brought challenges to girls in adapting to the intensified feminine gender and social roles (Patton and Viner 2007), which stereotype girls to be passive, emotionally expressive and using helpless coping styles (Wichstrom 1999; Hyde et al. 2008). Secondly, the start of menstrual cycle leads girls to more fluxes in reproductive hormones than boys (Angold et al. 1999), and this flux was considered to influence emotional reactivity (Altemus 2006). We need to acknowledge the weakness that we did not measure menstrual phases of pubertal girls, which would otherwise allow us to see whether controlling menstrual phases influences the current findings. Furthermore, the puberty of girls is associated with increased concerns for body image and greater rates of dissatisfaction with physical attractiveness (Hankin and Abramson 2001; Hyde et al. 2008). All these factors might play a part in mediating the enhanced sensitivity of girls to negative stimuli with pubertal development. Further studies need to directly measure psychosocial and hormonal variables (e.g. gender trait and body image; testosterone and estrogen) in addition to emotion reactivity, to explore the reasons behind these different patterns of puberty effect between sexes.

Despite these implications, several limitations should be overtly acknowledged. Firstly, the present study used a cross-sectional design instead of a longitudinal study. Thus, our finding is more a reflection of different sex differences in the pubertal and pre-pubertal samples specific to this study, not necessarily a reflection of different pubertal transition effect in emotional susceptibility to negative stimuli across sexes. Additionally, this study did not directly measure subjective emotion arousal to pictures in different groups. Thus, the neural oscillatory differences between negative and neutral stimuli may not directly reflect subjective negative emotion, which implies that caution should be taken when generalizing our findings to the mechanisms behind the girls' greater vulnerability to affective disturbances during adolescence. Future studies need to record both physiological and emotion experience data, to directly assess how different patterns of neural oscillations may account for emotion changes in different groups, which might lend further insights into the occurrence of affective disturbances in adolescent girls.

Taken together, the present study observed that puberty increased girls' neural reactivity to negative stimuli but decreased boys' reactivity to these stimuli. These different patterns of puberty effect across sexes might contribute to understanding the greater prevalence of affective disturbances in girls versus boys during adolescence.

Acknowledgments This study was supported by National Natural Science Foundation of China (NSFC31371042; 31170989), and the National Key Discipline of Basic Psychology in Southwest University (TR201207-3). The authors thank two anonymous reviewers for their helpful comments.

References

- Altemus M (2006) Sex differences in depression and anxiety disorders: potential biological determinants. *Horm Behav* 50:534–538
- Anderson JC, Williams S, McGee R, Silva PA (1987) DSM-III disorders in preadolescent children: prevalence in a large sample from the general population. *Arch Gen Psychiatry* 44:69–76
- Angold A, Rutter M (1992) The effects of age and pubertal status on depression in a large clinical sample. *Dev Psychopathol* 4:5–28
- Angold A, Costello EJ, Worthman CM (1998) Puberty and depression: the role of age, pubertal status, and pubertal timing. *Psychol Med* 28:51–61
- Angold A, Costello EJ, Erkanli A, Worthman CM (1999) Pubertal changes in hormone levels and depression in girls. *Psychol Med* 29:1043–1053
- Bai L, Ma H, Huang YX, Luo YJ (2005) The development of native Chinese affective picture system. *Chin Ment Health J* 19:719–722
- Balconi M, Lucchiari C (2008) Consciousness and arousal effects on emotional face processing as revealed by brain oscillations. A gamma band analysis. *Int J Psychophysiol* 67:41–46
- Balconi M, Brambilla E, Falbo L (2009) BIS/BAS, cortical oscillations and coherence in response to emotional cues. *Brain Res Bull* 80(3):151–157
- Bastiaansen M, Hagoort P (2006) Oscillatory neuronal dynamics during language comprehension. In: Christa N, Wolfgang K (eds) *Progress in brain research*, vol 159. Elsevier, Amsterdam, pp 179–196
- Britton JC, Taylor SF, Sudheimer KD, Liberzon I (2006) Facial expressions and complex IAPS pictures: common and differential networks. *Neuroimage* 31:906–919
- Deardorff J, Hayward C, Wilson KA, Bryson S, Hammer LD, Agras S (2007) Puberty and gender interact to predict social anxiety symptoms in early adolescence. *J Adolesc Health* 41(1):102–104
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134:9–21
- Delplanque S, Silvert L, Hot P, Sequeira H (2005) Event-related P3a and P3b in response to unpredictable emotional stimuli. *Biol Psychol* 68:107–120
- Earls FJ, Brooks-Gunn J, Raudenbush SW, Sampson RJ (2000) Project on Human Development in Chicago Neighborhoods (PHDCN): Physical Development Scale, Wave 3, 2000–2002, U.S. Department of Justice, Office of Justice Programs, National Institute of Justice, Chicago, Illinois, United States
- Ge X, Natsuaki MN, Conger RD (2006) Trajectories of depressive symptoms and stressful life events among male and female adolescents in divorced and nondivorced families. *Dev Psychopathol* 1:253–273
- Gohier B, Senior C, Brittain PJ, Lounes N, El-Hage W, Law V, Surguladze SA (2013) Gender differences in the sensitivity to negative stimuli: cross-modal affective priming study. *Eur Psychiatry* 28(2):74–80
- Hankin BL, Abramson LY (2001) Development of gender differences in depression: an elaborated cognitive vulnerability-transactional stress theory. *Psychol Bull* 127:773–796
- Hayward C, Gotlib IH, Schraedley PK, Litt IF (1999) Ethnic differences in the association between pubertal status and symptoms of depression in adolescent girls. *J Adolescent Health* 25:143–149
- Hayward C, Killen JD, Hammer LD, Litt IF, Wilson DM, Simmonds B, Taylor CB (1992) Pubertal stage and panic attack history in sixth- and seventh-grade girls. *Am J Psychiatry* 149:1239–1243
- Hofer A, Siedentopf CM, Ischebeck A, Rettenbacher MA, Verius M, Felber S, Fleischhacker W (2006) Gender differences in regional cerebral activity during the perception of emotion: a functional MRI study. *Neuroimage* 32(2):854–862
- Huang Y, Luo Y (2004) Native assessment of international affective picture system. *Chin Ment Health J* 18:631–634
- Hyde JS, Mezulis AH, Abramson LY (2008) The ABCs of depression: integrating affective, biological, and cognitive models to explain the emergence of the gender difference in depression. *Psychol Rev* 115(2):291–313
- Keil A, Müller MM, Gruber T, Wienbruch C, Stolarova M, Elbert T (2001) Effects of emotional arousal in the cerebral hemispheres: a study of oscillatory brain activity and event-related potentials. *Clin Neurophysiol* 112:2057–2068
- Kessler RC, McGonagle KA, Swartz M, Heath AC, Eaves LJ (1993) Sex and depression in the National Comorbidity Survey. I. Lifetime prevalence, chronicity and recurrence. *J Affect Disord* 29:85–96
- Lang PJ, Bradley MM, Cuthbert BN (1997) International affective picture system: technical manual and affective ratings. NIMH Center for the Study of Emotion and Attention. University of Florida, Gainesville
- Lieberman MD, Eisenberger NI, Crockett MJ, Tom SM, Pfeifer JH, Way BM (2007) Putting feelings into words: affect labeling disrupts amygdala activity to affective stimuli. *Psychol Sci* 18:421–442
- McGee ROB, Feehan M, Williams S, Partridge F, Silva PA, Kelly J (1990) DSM-III disorders in a large sample of adolescents. *J Am Acad Child Adol Psy* 29:611–619
- Nolen-Hoeksema S (2001) Gender differences in depression. *Curr Dir Psychol Sci* 10:173–176
- Nolen-Hoeksema S, Girgus JS (1994) The emergence of gender differences in depression during adolescence. *Psychol Bull* 115:424–443
- Petersen AC, Crockett L, Richards M, Boxer A (1988) A self-report measure of pubertal status: reliability, validity, and initial norms. *J Youth Adolescence* 17(2):117–133
- Patton GC, Viner R (2007) Pubertal transitions in health. *Lancet* 369:1130–1139
- Quevedo KM, Stephen DB, Gunnar MR, Dahl RE (2009) The onset of puberty: effects on the psychophysiology of defensive and appetitive motivation. *Dev Psychopathol* 21(01):27–45
- Simon NM, Zalta AK, Worthington JJ, Hoge EA, Christian KM, Stevens JC, Pollack MH (2006) Preliminary support for gender differences in response to fluoxetine for generalized anxiety disorder. *Depress Anxiety* 23:373–376
- Stanton SJ, Wirth MM, Waugh CE, Schultheiss OC (2009) Endogenous testosterone levels are associated with amygdala and ventromedial prefrontal cortex responses to anger faces in men but not women. *Biol Psychol* 81(2):118–122
- Wichstrom L (1999) The emergence of gender difference in depressed mood during adolescence. *Dev Psychol* 35:232–245
- Yuan J, Zhang Q, Chen A, Li H, Wang Q, Zhuang Z, Jia S (2007) Are we sensitive to valence differences in emotionally negative stimuli? Electrophysiological evidence from an ERP study. *Neuropsychologia* 45:2764–2771
- Yuan J, Luo Y, Yan JH, Meng X, Yu F, Li H (2009) Neural correlates of the females' susceptibility to negative emotions: an insight into gender-related prevalence of affective disturbances. *Hum Brain Mapp* 30:3676–3686
- Yuan JJ, Meng XX, Yang JM, Yao GH, Hu L, Yuan H (2012) The valence strength of unpleasant emotion modulates brain processing of behavioral inhibitory control: neural correlates. *Biol Psychol* 89:240–251