

Published online: 11 October 2011
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The present study investigated the neural mechanisms that underlie the higher levels of subjective well-being in extraverts. The impact of extraversion on the human sensitivity to pleasant and unpleasant pictures of diverse emotional intensities was examined. We recorded event-related potentials (ERPs) for highly positive (HP), moderately positive (MP), and neutral stimuli in the pleasant session, and for highly negative (HN), moderately negative (MN), and neutral stimuli in the unpleasant session, while subjects (16 extraverts and 16 ambiverts) performed a standard/deviant categorization task, irrespective of the emotionality of the deviant stimuli. The results showed significant emotion effects for HP and MP stimuli at the P2 and P3 components in extraverts, but not in ambiverts. Despite a pronounced emotion effect for HN stimuli across the P2, N2, and P3 components in both samples, ambiverts displayed a significant emotion effect for MN stimuli at the N2 and P3 components that was absent in extraverts. The posterior cingulate cortices, which connect multiple neural regions that are important in interactions of emotion and extraversion, may mediate the extravert-specific emotion effect

for pleasant stimuli. Thus, extraverts are less susceptible to unpleasant stimuli of mild intensity than are ambiverts, while extraverts have an additional enhanced sensitivity to pleasant stimuli, regardless of emotion intensity. Consequently, the decreased threshold for pleasant emotion and the increased threshold for unpleasant emotion might be essential neural mechanisms that underlie the higher levels of subjective well-being in extraverts.

Extraverts · Event-related potentials · Unpleasant resistance · Well-being · Posterior cingulate cortices (PCC)

Extraversion is a trait that describes the tendency of a person to be upbeat and optimistic and to enjoy social contact (Ashton, Lee, & Paunonen, 2002; Eysenck, 1990). Extraversion has been shown by many studies to be associated with subjective well-being and personal happiness (Cosell-bnonextraverts. Furthermore, this association proved to antedate and to be effective in predicting levels of happiness over a period of 10 years (Costa & McCrae, 1980, 1991). Consistent with this finding, it was reported that the measure of pleasant affect strongly correlated with extraversion (Watson & Clark, 1997), and that extraverts

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tended to experience pleasant affects in various reward situations, both social and nonsocial (Cunningham, 1988). Furthermore, social psychology studies have also found a correlation between extraversion and subjective well-being, with greater levels of personal happiness in people who are strong extraverts (Myers, 1992). Recently, cross-cultural studies using large samples have established the essential roles of pleasant affects and reward sensitivity in trait extraversion (Lucas & Diener, 2001; Lucas, Diener, Grob, et al., 2000).

These behavioral findings have been reinforced by a number of neuroimaging studies. In a series of functional MRI studies, Canli and colleagues (Canli, Sivers, Whitfield, et al., 2002; Canli et al., 2001) observed that the brain response to pleasant pictures increased with extraversion in a number of cortical and subcortical regions, including the temporal lobe, amygdala, and the basal ganglia. In addition, neurobiological evidence suggests that extraversion is associated with the functioning of the corticolimbic–dopaminergic system, which is critical for incentive and reward motivation (Depue & Collins, 1999). Consistent with these findings, in a recent ERP study we observed that extraverts not only were emotionally sensitive to pleasant stimuli, but also were sensitive to valence intensity changes in these stimuli (Yuan, He, Lei, Yang, & Li, 2009).

Despite knowledge of the association between extraversion and subjective well-being, the brain mechanisms that underlie the higher levels of subjective well-being in extraverts remain largely unresolved. The enhanced brain sensitivity to reward, as previously established (Canli et al., 2002; Canli et al., 2001; Yuan, He, et al., 2009), may not fully explain this phenomenon. It is unlikely that extraverts experience more rewards than do nonextraverts in natural situations, though if they have a more positive response to similar rewards, this could contribute to enhanced well-being. It is also unclear whether extraverts are less responsive to punishments, as has been suggested by some theories (Bartussek, Becker, Diedrich, Naumann, & Maier, 1996; Derryberry & Reed, 1994). More importantly, it is unknown whether extraverts are more or less sensitive to punishment than are ambiverts, a group of nonextraverted and nonintroverted individuals that are more representative of the average population than introverts are. However, the fact that extraverts experience increased levels of subjective well-being may imply that extraverts are better at regulating negative emotions or are less susceptible to negative events than are ambiverts, because less experience of negative emotion is critical for maintaining a balanced mood and subjective well-being. Some existing evidence does imply that extraverts

how different cognitive steps, indicated by different components, embody the impact of extraversion in emotional responding.

Prior studies that have used oddball tasks reported emotion valence effects for several ERP components after controlling for arousal influences, such as in early components including the frontal P2 (Delplanque, Lavoie, Hot, Silvert, & Sequeira, 2004; Yuan et al., 2007) and central N2 (Li et al., 2008; Yuan et al., 2007), and in late components including the parietal P3 (Delplanque et al., 2004; Delplanque et al., 2005; Rozenkrants & Polich, 2008; Yuan et al., 2008). Moreover, the frontal P2 and the parietal P3, two components that are accepted as indexing attentional (Carretié et al., 2001) and controlled evaluative (Ito, Larsen, Smith, & Cacioppo, 1998) processes, respectively, have been reported as early and late markers of extraversion's impact on emotion (Bartussek et al., 1996; Yuan, He, et al., 2009). Additionally, a centrally peaking N2 was known to reflect the attention orienting response to potentially important stimuli in oddball tasks (Carretié, Hinojosa, Martín-Loeches, Mercado, & Tapia, 2004). Therefore, if extraverts are indeed different from ambiverts in terms of their attentional, vigilant, and controlled cognitive processing of unpleasant and pleasant stimuli, we predict that the frontal P2, central N2, and parietal P3 components will reflect the impact of extraversion on the emotional brain effects for different processing phases. Specifically, the P2 and P3 amplitudes, which increase with greater involvements of attention and cognitive resources, respectively, may be more pronounced during pleasant stimulation in extraverts as compared to ambiverts (Bartussek et al., 1996; Yuan, He, et al., 2009). However, if extraverts are truly less susceptible to unpleasant events than are ambiverts (Carretié et al., 2004), they should exhibit less ERP differentiation between unpleasant and neutral conditions. This would particularly be the case for the N2 and P3 components, which index attention alerting to and the cognitive processing of unpleasant stimuli, respectively. Additionally, the occipital P1 component and its frontal counterpart (frontal N1), which peak at approximately 100 ms poststimulus (Spitz, Emerson, & Pedley, 1986; Wei & Luo, 2002), are considered to be indexes of early visual processing (Campanella et al., 2002; Heinze et al., 1994; Spitz et al., 1986; Yuan et al., 2007). Therefore, we measured and analyzed the occipital P1 and the frontal N1 components to examine whether extraversion modulated the early visual processing of stimulus features, and whether this potential modulation varied depending on the emotional valence intensity of the stimuli.

Moreover, because we targeted the brain mechanisms that underlie the higher levels of subjective well-being in extraverts, the present study used an extreme-group design

instead of a set of subjects whose extraversion scores would be evenly distributed in each interval of the distribution. We did so in order to create groups that differed only on the variable of interest (extraversion) and not on neuroticism. Specifically, we classified as the experimental group a set of subjects who scored highly in extraversion (extraverts), and as the control group a set of subjects who had medium levels of extraversion (ambiverts). Additionally, because emotionally evocative scenes have been found to be effective in generating an experience of emotion states (Britton, Taylor, Sudheimer, & Liberzon, 2006; Lang, Greenwald, Bradley, & Hamm, 1993), the present study used standardized emotional pictures for the induction of emotion (Bai, Ma, & Huang, 2005; Lang et al., 1997). We used pictures from the Chinese Affective Picture System (CAPS; Bai et al., 2005), which is a system adapted from IAPS (International Affective Picture System; Lang et al., 1997), since a cultural bias is present when the standard IAPS is used with Chinese subjects (Huang & Luo, 2004). In addition, a number of early studies had suggested that the fundamental organization of emotion is motivational and that the affectively motivational significance of a stimulus is determined mainly by hedonic valence (pleasant–appetitive motivation vs. unpleasant–defensive motivation) and arousal (degree of motivational activation; Cacioppo & Berntson, 1994; Dickinson & Dearing, 1979; Lang et al., 1997). Therefore, it is generally accepted that valence (ranging from -1 to 1) and arousal (ranging from 0 to 1) are the two primary dimensions that should be considered in emotional research (Lang et al., 1997). Emotional studies that address the valence effect on ERPs need to control for arousal influences across conditions (Carretié, Iglesias, & García, 1997; Corson & Verrier, 2007; Delplanque et al., 2004; Delplanque et al., 2005; Rozenkrants & Polich, 2008; Yuan et al., 2007). Thus, the present study used emotional pictures with relatively lower arousal values, and neutral pictures with medium arousal levels, in order to match the overall arousal levels across emotion conditions.

Subjects

As paid volunteers, 16 extraverted (20–29 years; $M = 22.47$ years, 8 males) and 16 nonextraverted ambivert (19–25 years; $M = 22.38$ years, 8 males) students from Southwest University in China participated in the experiment. Each subject was paid 30 RMB for their participation. The subjects were selected from a large pool of 400 college students who completed the NEO Five-Factor Inventory (NEO-FFI, Chinese version; internal consistency

than 1,000 ms. Each response was followed by 1,000 ms of blank screen (see Fig. 1 for the session designs). Pretraining with 10 practice trials was used before either session in order to familiarize the subjects with the procedure. The standard picture in pretraining was the same as that in the subsequent experiment, whereas the deviants for the pretraining were neutral pictures that were not used in the experiment. All subjects achieved 100% accuracy on the 10 practice trials prior to the formal experiment. Each subject participated in both experimental sessions, with the order of the sessions counterbalanced across subjects.

Emotion assessment

After the EEG recording session, an emotion assessment procedure that resembled the Self-Assessment Manikin (SAM) was conducted (Lang et al., 1997), in order to explore the subjective emotion induced by each set of images in both sessions. Using a self-reporting nine-point

rating scale, subjects were required to rate the emotion valence (ranging from -9 to 9) and arousal (ranging from 1 to 9) that they felt for each image by pressing the corresponding number key on the keyboard. The onset sequence of images was randomized across emotion conditions.

ERP recording and analysis

The EEG was recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Products, Munich, Germany), 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 infraorbitally at the left eye. The horizontal EOG was recorded from the left versus the right orbital rim. The EEG and EOG were amplified using a DC ~100-Hz bandpass and continuously sampled at 500 Hz/channel. All interelec-

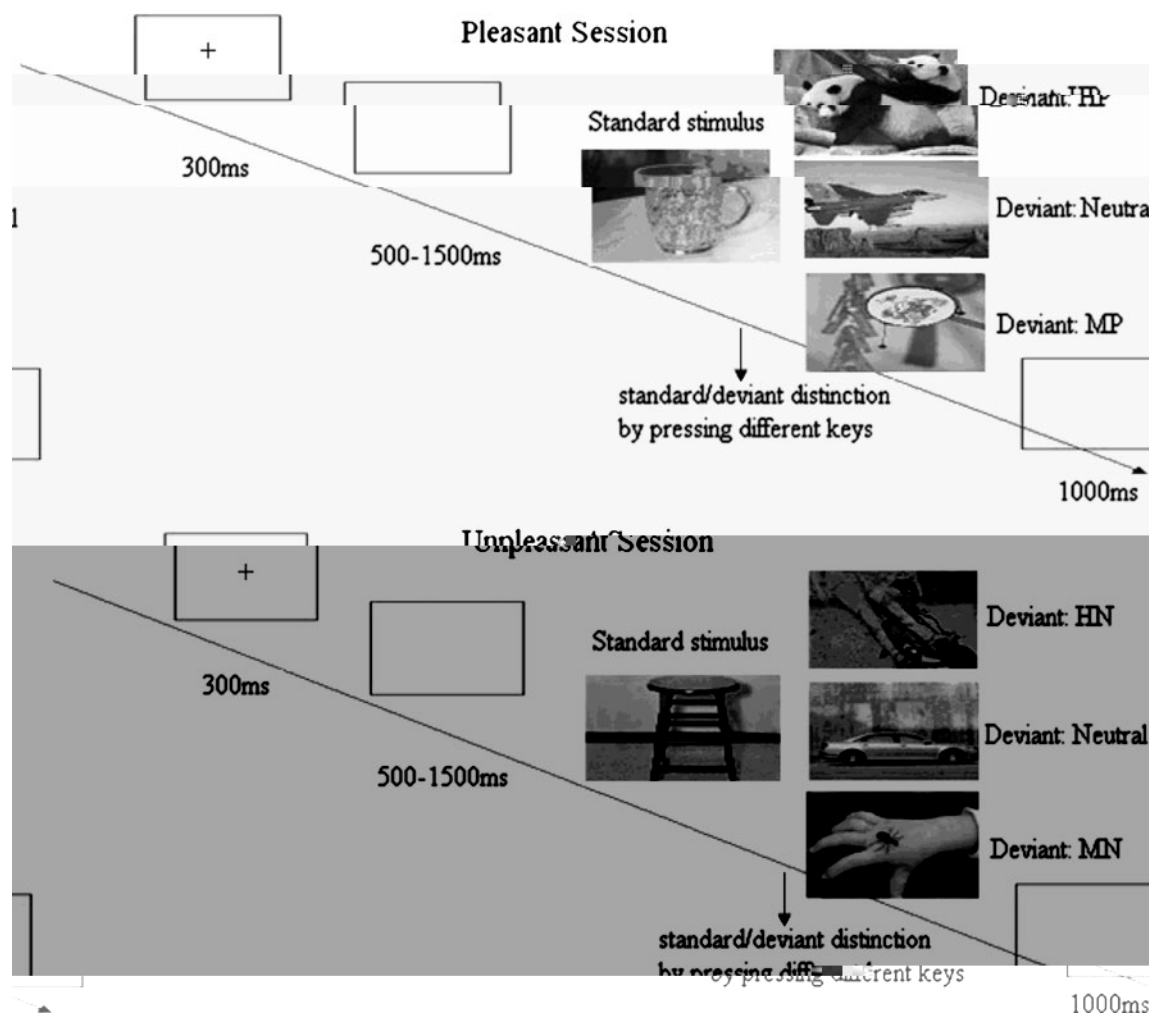


Fig. 1 Schematic illustration of the experimental procedure and the stimulus examples. Each trial presented a single stimulus. In each session, a standard stimulus was presented in 70% of the trials, while stimuli in each deviant condition were presented in 10% of trials

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 factor. Because P3 activity was maximal at the parietal sites, the analysis of the P3 component included the three parietal sites (P3, Pz, and P4), along with the 12 sites above. In addition, the occipital P1 and its frontal counterpart (frontal N1), which both peaked at approximately 100 ms poststimulus, were analyzed in the 70- to ~130-ms interval to establish whether there was an emotion effect, as well as an extraversion influence during early visual processing (Mangun, 1995).

The occipital P1 component was analyzed at the three occipital sites (O1, O2, and Oz), while the frontal N1 component

HP	498	23	511	
MP	495	26		
Neu(P)	502			14
HN			484	6
MN		29	483	7
	514	25	490	7

Neu(P), neutral condition for the pleasant session; Neu(N), neutral condition for the unpleasant session.

factors and extraversion as the between-subjects factor, showed significant main effects of emotion [$F(2, 60) = 76.04$, $< .001$, $\eta^2 = .72$], session [$F(1, 30) = 183.64$, $< .001$, $\eta^2 = .86$], and extraversion [$F(1, 30) = 12.32$, $< .01$, $\eta^2 = .29$]. The valence ratings were greater in the pleasant ($\pm E$: 6.34 ± 0.15) than in the unpleasant (4.28 ± 0.09) sessions. Moreover, there were a significant emotion \times session interaction [$F(2, 60) = 349.88$, $< .001$, $\eta^2 = .92$] and a significant session \times extraversion interaction [$F(2, 60) = 8.94$, $< .01$, $\eta^2 = .23$]. To break down these interactions, we tested the simple effect of emotion and that of extraversion in the pleasant and unpleasant experimental sessions. There were significant effects of emotion [$F(2, 60) = 124.99$; $< .001$, $\eta^2 = .81$] and extraversion [$F(1, 30) = 6.65$, $< .02$, $\eta^2 = .17$] in the pleasant session. Subjects rated HP pictures as more pleasant than MP pictures ($< .001$), which, in turn, were rated as more pleasant than neutral pictures ($< .001$), irrespective of extraversion (see Fig. 2). In addition, extraverts rated all pictures, irrespective of stimulus category, as more pleasant than did the ambiverts (see Fig. 2). On the other hand, there was a significant simple effect of emotion [$F(2, 60) = 288.20$, $< .001$, $\eta^2 = .91$], while the simple effect of extraversion was nonsignificant [$F(1, 30) = 1.46$, $= .23$, $\eta^2 = .05$] in the unpleasant session. HN pictures were rated as more unpleasant than MN pictures ($< .001$),

which, in turn, were rated as more unpleasant relative to neutral pictures ($< .001$) by both groups (see Fig. 2).

Similarly, the emotion arousal scores were averaged within each of the three picture sets in both experimental sessions. The repeated measures ANOVA of arousal scores showed a significant main effect of emotion [$F(2, 60) = 86.69$, $< .001$, $\eta^2 = .74$]. The post hoc pairwise comparison showed increased arousal ratings for the highly emotional pictures (6.71 ± 0.16) relative to the mildly emotional (5.73 ± 0.12) [$F(1, 30) = 121.51$, $< .001$, $\eta^2 = .80$] and neutral (5.55 ± 0.14) [$F(1, 30) = 140.11$, $< .001$, $\eta^2 = .82$] pictures, irrespective of extraversion and experimental session. The arousal ratings, however, were not statistically significant between the mildly emotional and neutral picture sets [$F(1, 30) = 3.58$, $= .068$, $\eta^2 = .10$]. Moreover, extraverts rated all pictures, irrespective of stimulus category and experimental session, as more arousing than did ambiverts, as shown by a significant main effect of extraversion [$F(1, 30) = 15.53$, $< .001$, $\eta^2 = .34$]. The arousal ratings were not significantly different between the pleasant and unpleasant experimental sessions in both extraverts and ambiverts, as shown by the nonsignificant main effect of session [$F(1, 30) = 0.24$, $= .63$] and by the nonsignificant interaction of session with extraversion [$F(1, 30) = 0.15$, $= .69$; see Fig. 2].



Fig. 2 A schematic illustration of the valence and arousal ratings for highly emotional, moderately emotional, and neutral picture sets during pleasant and unpleasant sessions. Error bars represent standard errors

P1 The repeated measures ANOVA for the occipital P1 component, with session and emotion as the repeated factors and extraversion as the between-subjects factor, showed no significant main or interaction effects for either peak amplitudes or latencies (see Fig. 3). Moreover, the ANOVA of the N1 data showed no other main or interaction effects except for a main effect of frontality on N1 amplitudes [$F(3, 90) = 18.60, < .001, \eta^2 = .38$] and peak latencies [$F(3, 90) = 12.10, < .001, \eta^2 = .29$], with N1 amplitudes largest at the frontal sites, while peak latencies increased from parietal to frontal sites (Figs. 4 and 5).

P2 The analysis of P2 amplitudes demonstrated larger amplitudes during pleasant sessions than during unpleasant sessions [$F(1, 30) = 4.41, < .05, \eta^2 = .13$]. In addition, the amplitudes were larger for extraverts than for ambivert subjects [$F(1, 30) = 5.97, < .03, \eta^2 = .17$]. This was probably because extraverts are more novelty-seeking, and accordingly more reactive to the novel deviant stimuli (Digman, 1990). There was a significant interaction between emotion and session [$F(2, 60) = 21.13, < .001, \eta^2 = .41$]. The breakdown of this interaction showed larger amplitudes in the HP ($6.05 \pm 0.80 \mu\text{V}$) and MP ($5.06 \pm 0.74 \mu\text{V}$) than in the neutral ($3.91 \pm 0.65 \mu\text{V}$) [$F(2, 60) = 16.86, < .01, \eta^2 = .36$] conditions in the pleasant session,

while the unpleasant session revealed smaller P2 amplitudes during HN stimuli ($2.61 \pm 0.53 \mu\text{V}$) than during MN ($3.87 \pm 0.64 \mu\text{V}$) and neutral ($3.69 \pm 0.65 \mu\text{V}$) stimuli [$F(2, 60) = 9.03, < .01, \eta^2 = .21$]. More importantly, in the present study we observed a significant three-way interaction between session, extraversion, and emotion [$F(2, 60) = 7.99, < .01, \eta^2 = .44$].

To analyze the components of this interaction, we analyzed the extraversion and emotion interaction in the pleasant and unpleasant experimental sessions. The analysis in the pleasant session showed a significant interaction of extraversion and emotion [$F(2, 60) = 5.24, < .05, \eta^2 = .22$]. The simple-effect analyses of the two-way interaction showed a significant emotion effect in extraverts [$F(2, 30) = 20.21, < .01, \eta^2 = .57$], with larger amplitudes recorded for HP ($8.19 \pm 1.14 \mu\text{V}$) than for MP ($6.53 \pm 1.05 \mu\text{V}$) stimuli [$F(1, 15) = 12.73, < .01, \eta^2 = .46$], which, in turn, elicited larger amplitudes than did neutral stimuli ($4.85 \pm 0.92 \mu\text{V}$) [$F(1, 15) = 11.57, < .01, \eta^2 = .44$]. In contrast, the emotion effect was not significant in ambivert subjects [$F(2, 30) = 1.73, = .20$]. On the other hand, the analysis conducted in the unpleasant experimental session showed no significant two-way interaction between emotion and extraversion [$F(2, 30) = 0.14, = .74$], which indicated that both extraverts and ambiverts showed less-pronounced P2 amplitudes during HN than during the MN and neutral conditions.

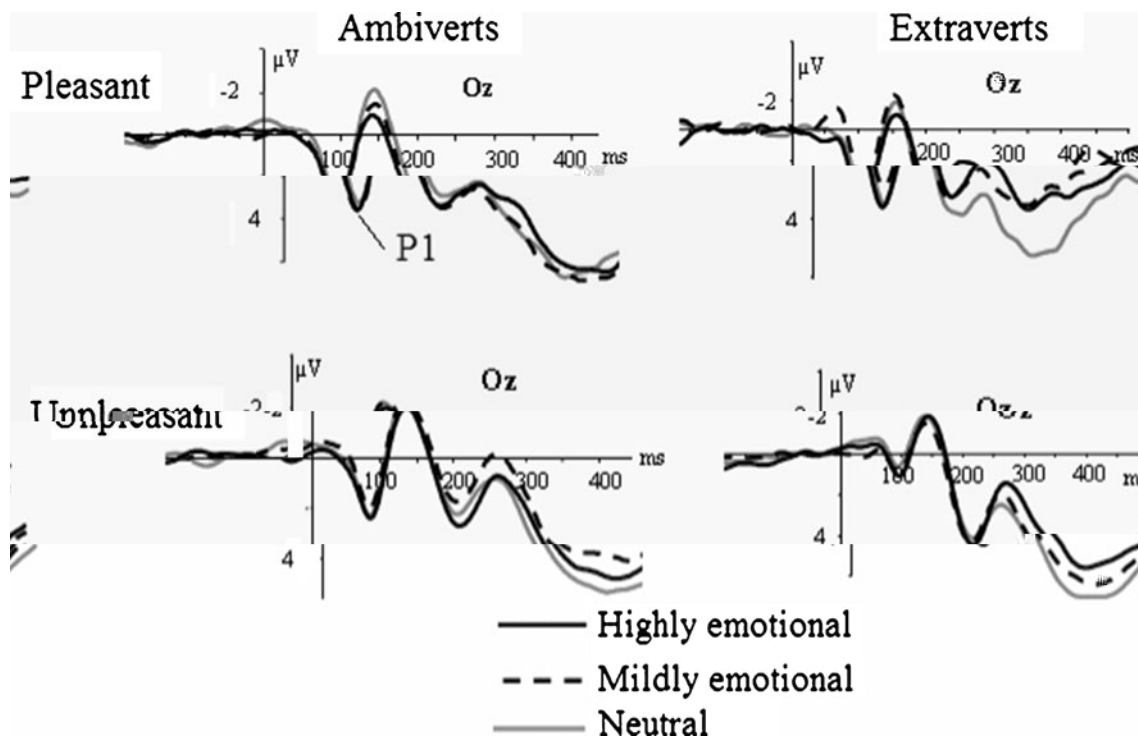


Fig. 4 Averaged ERPs at electrode Oz for the pleasant (top panels) and unpleasant (bottom panels) sessions in ambiverts (left column) and extraverts (right column)

In addition, the P2 amplitudes were more pronounced at left ($4.29 \pm 0.46 \mu\text{V}$) and midline ($4.12 \pm 0.47 \mu\text{V}$) sites than at the right-lateralized ($3.41 \pm 0.59 \mu\text{V}$) sites, as shown by a significant main effect of laterality [$F(2, 60) = 13.92, < .001, \eta^2 = .32$]. There were significant main effects of frontality [$F(3, 90) = 7.48, < .01, \eta^2 = .20$] and emotion [$F(2, 60) = 4.53, < .05, \eta^2 = .13$], while frontality significantly interacted with extraversion

[$F(3, 90) = 5.39, < .05, \eta^2 = .15$]. The effect of larger amplitudes for extraverts relative to ambiverts was pronounced at both the central and frontal scalp regions, but not at the parietal sites (

1.7 ms) elicited shorter latencies than did moderately emotional (158.7 ± 1.6 ms) and neutral (160.8 ± 1.9 ms) stimuli, regardless of the experimental session type. In addition, P2 peaked faster at central-to-frontal sites (157.3 ± 1.8 ms) than at parietal sites (161.6 ± 2.0 ms).

N2 The ANOVA of *N2* amplitudes displayed a significant main effect of emotion [$F(2, 60) = 5.68, < .01, \eta^2 = .17$] and an emotion \times frontality interaction [$F(6, 180) = 4.98,$

$< .01, \eta^2 = .15$], with the amplitude differences across the highly emotional, mildly emotional, and neutral conditions more pronounced at the central and frontal sites.

significant session \times emotion interaction [$F(2, 60) = 11.64$, $< .001$, $\eta^2 = .26$], as well as a significant three-way interaction between session, emotion, and extraversion [$F(2, 60) = 5.33$, $< .01$, $\eta^2 = .16$]. The breakdown of the session by emotion interactions showed a significant emotion effect that was only present in the unpleasant experimental session [$F(2, 60) = 20.57$, $< .001$, $\eta^2 = .42$].

In order to subanalyze the interaction between session, emotion, and extraversion, the present study analyzed the interaction effects between extraversion and emotion in the pleasant and unpleasant experimental sessions. While the extraversion \times emotion interaction failed to reach statistical significance in the pleasant experimental session [$F(2, 60) = 2.07$, $> .10$, $\eta^2 = .06$], the analysis showed a significant extraversion \times emotion interaction [$F(2, 60) = 3.69$, $< .05$, $\eta^2 = .11$] in the unpleasant experiment session. The simple-effect analyses for this interaction showed a significant emotion effect in ambivert subjects [$F(2, 30) = 17.99$, $< .001$, $\eta^2 = .55$], with N2 amplitudes more pronounced for both the HN ($-7.21 \pm 1.30 \mu\text{V}$) [$F(1, 15) = 34.60$, $< .001$, $\eta^2 = .64$] and MN ($-6.65 \pm 1.41 \mu\text{V}$) [$F(1, 15) = 26.47$, $< .001$, $\eta^2 = .64$] stimuli, as compared to the neutral stimuli ($-4.76 \pm 1.48 \mu\text{V}$). Also, the emotion effect was significant in extraverts [$F(2, 30) = 9.68$, $< .01$, $\eta^2 = .39$]: While their amplitudes remained larger during HN ($-7.10 \pm 1.30 \mu\text{V}$) than during neutral ($-4.78 \pm 1.41 \mu\text{V}$) conditions [$F(1, 15) = 13.05$, $< .01$, η^2

than the left ($9.40 \pm 0.52 \mu\text{V}$) and the right ($10.98 \pm 0.55 \mu\text{V}$) lateralized sites. On the other hand, the analysis of P3 latencies showed no other main or interaction effects, except for the main effects of frontality [$F(4, 124) = 6.48$, $< .01$, $\eta^2 = .17$] and laterality [$F(3, 90) = 9.76$; $< .01$; $\eta^2 = .24$]. P3 latencies were delayed at parietal relative to anterior sites, and were longer at the left ($412.2 \pm 5.22 \text{ ms}$) and midline ($411.3 \pm 5.5 \text{ ms}$) sites than at the right ($401.0 \pm 5.1 \text{ ms}$) scalp sites.

the role of parietal P3 in reflecting conscious processing that involves the cognitive evaluation of stimulus meaning (Campanella et al., 2002; Campanella et al., 2004; Ito et al., 1998). With the use of top-down cognitive resources (Del Cul et al., 2007; Delplanque et al., 2005), extraverts continually displayed prominent emotion effects for HP stimuli and, with smaller-size effects, for MP stimuli in this study. This was possibly because they evaluated all positive stimuli, irrespective of emotion intensity, as pleasant at the conscious level. This coincided with the results of the emotion assessment, which showed that extraverts rated all stimuli as more pleasant than did the ambiverts, irrespective of category. Distinct from our prior finding of similar P3 amplitudes for MP and neutral stimuli (Yuan, He, et al., 2009), extraverted subjects in the present study exhibited more pronounced P3 amplitudes for MP versus neutral stimuli, probably because the extravert sample in the present study scored higher in the measure of extraversion than did those in the previous study. This fact, again, verified that extraversion was associated with enhanced reward sensitivity. Conversely, despite pleasant feelings for MP and HP stimuli in the emotion assessment, ambivert subjects showed no significant emotion effect in P3 amplitudes with either picture set, possibly because we used a distracting task that was associated with decreased late positive potential responses to emotional stimuli (Carretié, Iglesias, García, & Ballesteros, 1997; Delplanque et al., 2004). This argument, however, should be interpreted cautiously, as behavioral data showed ceiling accuracy in the distinction of the standard/deviant images. To conclude, whether at early or late time points, extraverts elicited significant emotion effects for both sets of pleasant stimuli that were absent in ambiverts.

Reduced sensitivity of extraverts to mildly negative stimuli

In the unpleasant session, although early visual processing was not influenced by emotion, HN stimuli elicited a significant emotion effect in P2 amplitudes and latencies in both samples. This suggested that extraverts and ambiverts were both emotionally reactive to HN stimuli at time points before 200 ms (Smith et al., 2003; Yuan et al., 2007). Despite a significant interaction of emotion, session, and extraversion in P2 amplitudes, there was no significant emotion \times extraversion interaction in the unpleasant session. This suggested that both samples were similar in their processing of unpleasant pictures of diverse emotional intensities at this stage. Thus, the impact of extraversion on unpleasant emotion sensitivity may occur at later stages.

In addition, there was a significant emotion \times extraversion interaction in the N2 amplitudes. Consistent with the account of negative bias, both samples elicited a significant emotion effect for HN stimuli that were biologically important

(Bradley et al., 2001). However, ambiverts, but not extraverts, exhibited enlarged N2 amplitudes for MN relative to neutral stimuli. This suggested that ambivert subjects detected the emotional negativity of MN stimuli and accordingly, allocated more attention resources to them relative to neutral stimuli (Nagy et al., 2003). In contrast, extraverts responded similarly to MN and neutral stimuli at this component, which implied that extraverts exhibited little attention bias for MN stimuli, whose unpleasantness was less salient than that of HN stimuli (Fig. 5).

Moreover, there was a significant interaction of emotion with extraversion for P3 amplitudes in the unpleasant session. Both samples exhibited a significant emotion effect for HN stimuli, as shown by the clear differences between the HN and neutral conditions (Fig. 5). This was consistent with the results of the emotion assessment, which showed similarly intense unpleasant ratings for HN stimuli in extraverts and ambiverts (Fig. 2). The enhanced susceptibility of the human subjects, irrespective of extraversion, to HN stimuli may have resulted from the biological significance of reacting intensely to salient negative events (Bradley et al., 2001; Cacioppo & Berntson, 1994). More importantly, while ambiverts exhibited a significant emotion effect for MN stimuli that were less emotionally salient than HN stimuli, extraverted individuals displayed no significant emotion effect for MN stimuli at the P3 stage, which involved conscious and evaluative processing (Ito et al., 1998; Yuan et al., 2007). Cognitive evaluation has been shown to be important in generating emotion and in modulating its strength (Ellis, 1991; Gross, 2007). It is likely that extraverts are more habitual in using emotion regulation strategies, such as cognitive reappraisal or inhibitory control, to dampen unpleasant emotions elicited by mildly negative stimuli, thus leading to reduced brain susceptibility to such stimuli. Evidently, this hypothesis requires future study that will directly test the impact of extraversion on the regulation of unpleasant emotions. Therefore, although human beings, irrespective of extraversion, are susceptible to highly negative events, extraverted individuals are less susceptible to mildly negative events than are ambiverts.

Our observation of smaller P3 amplitudes for unpleasant versus neutral stimuli appeared to be inconsistent with the abundant literature that has shown enlarged P3 or late positive potential amplitudes for emotionally salient as compared to neutral stimuli in emotional assessment tasks (Ito et al., 1998; Schupp et al., 2000; Schupp, Fleisch, Stockburger, & Junghöfer, 2006; Schupp et al., 2003). As has been established, unpleasant stimuli convey information that is significant for survival and adaptation (Cacioppo & Berntson, 1994), and higher-order cognitive processes (e.g., evaluation and categorization) are reflected mainly by the late positive components in brain potentials

(Donchin, 1981; Ito et al., 1998). In emotion assessment tasks, subjects are required to evaluate the emotionality of the stimuli and to categorize them according to valence (Ito et al., 1998; Schupp et al., 2003). Therefore, unpleasant stimuli, which are known to be important for biased processing in the brain, should be evaluated as more biologically significant, and consequently should elicit enhanced physiological and psychological resources, relative to other stimuli. This biased evaluative process probably contributes to the higher P3 amplitudes during unpleasant versus neutral conditions in emotion assessment tasks (Ito et al., 1998). However, in covert emotional studies, subjects are required to perform a cognitive task that is irrelevant to emotion evaluation. This determines that subjects have to inhibit all task-irrelevant information, especially that associated with prepotent, biased processing (for discussions, see Yuan, Lu, Yang, & Li, 2011; Yuan et al., 2007). Accordingly, unpleasant trials may involve a process of cognitive control that is absent in neutral trials, which probably contributed to the smaller P3 amplitudes during negative versus neutral conditions in this study. This explanation is consistent with the established findings in cognitive control studies, whereby the cognitive control of task-irrelevant information results in smaller P3 or late positive potential amplitudes (Liotti, Woldorff, Perez, & Mayberg, 2000; Markela-Lerenc et al., 2004; Yuan, Xu, et al., 2011). The involvement of cognitive control might explain why covert emotional studies have consistently yielded smaller P3 amplitudes for negative than for neutral stimuli, in addition to the present findings (Carretié et al., 1997; Delplanque et al., 2004; Li et al., 2008; Yuan et al., 2007).

Neural bases underlying the sensitivity of extraverts to pleasant events

Neuroimaging studies have shown the roles of wide regions of frontal temporal lobes and of subcortical structures (e.g., the basal ganglia, amygdala, and nucleus accumbens) in pleasant emotion processing and in its interaction with extraversion (Canli et al., 2002; Canli et al., 2001; Cohen, Young, Baek, Kessler, & Ranganath, 2005). It is worth noting that the cingulate cortex (particularly the posterior cingulate cortex [PCC]), a limbic structure located between the neocortices and subcortical structures, has neural projections with wide areas of the neocortices (e.g., temporal and orbitofrontal cortices) and with subcortical areas (e.g., hippocampus and amygdala), which are important in emotion processing (Bromm, 2004; Fredrikson, Wik, Fischer, & Andersson, 1995; Northoff & Berman, 2004). Moreover, several studies have indicated that the PCC is important in generating, evaluating, maintaining, and integrating pleasant emotions (Bromm, 2004; Cohen et

al., 2005; Damasio et al., 2000; Esslen, Pascual-Marqui, Hell, Kochi, & Lehmann, 2004; Maddock & Buonocore, 1996; Maddock, 1999). Consequently, patients who are incapable of identifying emotional states show less PCC activation than do normal subjects when to induce pleasant affects (Mantani, Okamoto, Shirao, Okada, & Yamawaki, 2005), and depressive individuals have been associated with a significant volume reduction of the PCC (Caetano et al., 2006). In line with these data, our source modeling of the emotional effect of extraverts for MP stimuli indicated generators in the bilateral posterior cingulate cortices (see the supplementary materials). Thus, the bilateral PCCs and their collected regions—including the fusiform gyrus, amygdala, and basal ganglia, which are critical for the interaction of pleasant emotion and extraversion (Amin et al., 2004; Canli et al., 2002; Canli et al., 2001)—might jointly mediate the brain sensitivity of extraverts to pleasant stimuli of even mild intensities. Due to the inherent limitations of source modeling, which relies on an inverse solution and significant ERP differences, the results of source modeling should be considered as tentative, and other techniques with better localization (e.g., functional MRI) will be needed to clarify the neural bases that underlie the enhanced sensitivity of extraverts to pleasant stimuli with mild intensities.

Implications

In the present study, subjects were engaged in a distracting task that required a standard/deviant distinction, irrespective of the emotion of the deviant stimuli. Moreover, the onset sequence of standard and deviant pictures was randomized in both experimental sessions. Additionally, deviant pictures in the conditions to be presented were determined randomly throughout the experiment. Thus, the presentation of emotional stimuli in each condition (HP and MP in the pleasant session, HN and MN in the unpleasant session) was unpredictable before stimulus onset. However, rare deviant stimuli (30%) were composed of three conditions in either session, which determined that the occurrence of events of each emotional type was rare in each condition (10%). These manipulations made the emotional responses in the present experiment closely resemble those in natural settings, where emotion reactions are triggered by accidental, unexpected events during activity that is irrelevant to the affective assessment (Delplanque et al., 2005; Yuan, Luo, et al., 2009).

Therefore, using a task in which emotion closely resembles that in natural settings, we observed that extraverts were more reactive to both highly and mildly pleasant stimuli, and were less susceptible to mildly unpleasant stimuli, relative to ambiverts. Evidently, most negative life events are moderately rather than highly

negative. For instance, daily stresses are more frequent than serious traffic accidents in a real-life situation (Yuan, Luo, et al., 2009). Therefore, based on our findings, extraverted individuals are more resistant to unpleasant affects and find it easier to maintain a pleasant affect throughout life. They gain pleasure from more events and develop negative emotions from fewer events than do ambiverts. This correlates with prior reports that have shown that extraversion was associated with a shift of attention away from the location of punishment and an attention bias for the location of reward (Amin et al., 2004; Derryberry & Reed, 1994). Therefore, a greater experience of pleasant emotions and less involvement in unpleasant emotions are likely to lead to higher levels of subjective well-being in extraverts throughout life. This may be associated with the neural sensitivity of the reward circuit to pleasant events in extraverts. However, the lack of direct measurement of subjective well-being was a weakness in the present study, although extraverts are known for higher levels of personal happiness (Costa & McCrae, 1980, 1991).

It has to be noted that the present study was able to unravel how extraverts are different from ambiverts in terms of their brains' susceptibility to emotional events of diverse valences and intensities and of how these features relate to their increased levels of subjective well-being. This study does not suggest that introverts, who are another extreme group in the measure of extraversion, are lower or higher than extraverts in their brain sensitivity to emotional stimuli. The characteristics of introverts in sensitivity to pleasant or unpleasant stimuli of diverse intensities, and how these sensitivities relate to the health and well-being of introverts, remain open questions that are worthy of further investigation. However, the present findings are likely to be dependent on the experimental paradigm. It has been established that processing resource availability significantly modulates emotion processing, such that attention shortage leads to the decrease or disappearance of emotional brain activation (Dollo, Holguin, & Cadaveira, 2006; Pessoa, Padmala, & Morland, 2005). Despite its better ecological validity in emotion induction, the distracting cognitive task in our study was likely to divert attention away from emotional processing, consequently decreasing the strength of emotional effects in brain potentials (Dollo et al., 2006). Thus, despite giving an insight into the neural mechanisms that underlie the increased subjective well-being of extraverts, the present results are likely to be specific to the covert emotional paradigm. Accordingly, caution should be taken when concluding that there are emotional sensitivity differences between extraverts and ambiverts, especially in concluding that the brain sensitivity of ambiverts to pleasant stimuli was nonsignificant in the present study.

By varying the valence intensity of emotional stimuli systematically, in the present study we observed that extraverts were more reactive than ambiverts to pleasant stimuli, regardless of emotion intensity. Extraverts were less susceptible to mildly unpleasant stimuli as compared to an ambivert population. Enhanced brain sensitivity to pleasant events and resistance to the impact of unpleasant events might be important neural mechanisms that underlie the higher levels of subjective well-being found in extraverts.

This study was supported by the National Natural Science Foundation of China (Grants NSFC31170989 and 30770727), the Fundamental Research Funds for the Central Universities (Grant XDJK2009B038), and the National Key Discipline of Basic Psychology in Southwest University (Grant NSKD08015). We thank Hong Yuan, Shuang Xu (School of Psychology, Southwest University), and two anonymous reviewers for their kind help and suggestions on the manuscript. Supplemental materials may be downloaded along with this article from www.springerlink.com.

Pleasant session

Highly positive (HP): 4, 7, 10, 11, 12, 13, 14, 16, 18, 20, 28, 29, 45, 40, 52, 72, 73, 77, 78, 88, 94, 84, 39, 57, 32, 98, 27, 65, 663, 819.

Moderately positive (MP): 1, 2, 5, 6, 8, 9, 21, 23, 24, 25, 33, 34, 36, 38, 41, 44, 46, 49, 50, 53, 56, 59, 60, 66, 79, 82, 83, 85, 87, 99.

Neutral (positive): 840, 841, 843, 547, 89,306, 454, 482, 538, 521, 523, 614, 722, 848, 308, 321, 326, 328, 377, 402, 634, 645, 810, 363, 300, 291, 816, 818, 838, 839.

Unpleasant session

Highly negative (HN): 173, 185, 191, 194, 196, 205, 206, 232, 240, 243, 244, 246, 248, 254, 255, 256, 270, 273, 280, 284, 471, 533, 541, 569, 573, 577, 580, 629, 583, 584.

Moderately negat,

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