Neural correlates underlying humans' differential sensitivity to emotionally negative stimuli of varying valences: an ERP study*

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Abstract The present study aims to investigate the neural correlates underlying humans' sensitivity to valence differences in negative stimuli. Event-related potentials (ERPs) for highly negative (HN), moderately negative (MN), and Neutral pictures were recorded while subjects perform a standard/deviant categorization task, irrespective of the emotional valence of the deviants. The results show more negative ERP deflections during HN condition than during MN condition at each 50 ms interval from 350 to 650 ms after stimulus onset (at P3 and slow negative wave (SNW) components). Moreover, emotional effect was also observed for MN stimuli at P3 component (350—450 ms interval). Dipole analyses on the HN-MN difference wave during 350—450 ms interval (P3 component) and that during 450—650 ms interval (SNW component) were both localized to the right medial temporal lobe. Thus, the present study confirmed the human sensitivity to valence variations in emotionally negative stimuli, and further showed that the right medial temporal lobe, in particular, the right hippocampus/amygdala complex, may be the critical neural substrates underlying humans' differential sensitivity to emotionally negative stimuli of varying valences.

Keywords: ERP, valence variations, sensitivity, medial temporal lobe, emotional negativity bias.

As has been well established, the human brain has a processing bias for emotionally negative events due to their enhanced adaptive or evolutionary values[1—3]. Behavioral studies have shown that negative events recruit attentional resources more rapidly, or automatically, compared with positive events[4—6]. When subjects are asked to respond to the emotional properties of the stimuli, the negative stimuli often facilitate the task more than the other stimuli. In contrast, subjects' performance is often obstructed more heavily by negative stimuli than by other stimuli if the task is to respond to non-emotional aspects of the stimuli[4,5]. Moreover, a body of ERP studies have revealed that emotional negativity bias occurs at each stage of information processing stream, from early visual processing and attention allocation to later higher cognitive processing and reaction readiness[1,2]. Neural substrates mediating the processing of negative emotions, however, is rather complex, with distinct emotions and different tasks implicating different neural bases. Often, multiple neural structures are involved in processing a given negative event[1]. Nevertheless, some cerebral structures are typically involved in processing affectively arousing events in a given experiment. For instance, activations in rostal anterior cingulate cortex (rostal ACC) are often elicited by emotionally negative words during an emotional stroop task[7], and orbitofrontal cortex is evidenced to mediate humans' gambling behavior and the experience of regret[8]. More prominently, the medial temporal lobe, particularly the amygdala/ hippocampus complex, is closely related to the processing of fearful information[9—12].

In addition to the preferential processing towards negative events over neutral and positive events, a recent study by Yuan et al. furthered our understanding of emotional negativity bias by showing greater sensitivity of the human brain to valence differences in emotionally negative stimuli than to that in positive stimuli[2]. During this study, subjects were required to make a standard/deviant distinction by pressing different keys, and the results revealed that highly negative pictures elicited more negative ERP deflections than moderately negative pictures throughout the information processing stream whereas no significant amplitude or latency differences were observed during the two positive conditions[2,13]. Thus, negative stimuli of varying valences are processed differentially probably due to their differential adaptive values, with highly negative events signifying greater

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threats than moderately negative events doing[2]. Given this discovery, however, one issue remains regarding neural basis underlying this automatic differential processing of negative events varying in valence. More specifically, as mentioned before, neural substrates mediating emotional processing are complex, such that several neural substrates are engaged during a negative mood induction task[14], and the processing of a certain facial affect (e.g. sadness) would engage multiple neocortical and sub-cortical neural structures[11]. Moreover, neural structures within Papez Circuit, typically the hippocampus, amygdale, mamillary body, anterior and medial nuclei of the thalamus, and ACC (anterior cingulate cortex), are all thought to play a part in the emotional experience, expression and regulation. Despite the possibility of complex neural bases engaged in emotional processing, there are often some given structures, however, of primary importance in emotional processing during a given task. For instance, amygdala is more important than other neural substrates in the fast processing of salient threatening events[9], whereas hippocampus, in particular, the right hippocampus, plays a critical role in humans' habituation to the fearful stimuli[10]. A more noticeable example is the particular function of ventro-medial prefrontal cortex in the reward/punishment processing[15,16]. As for the present study, although multiple neural structures are likely to be related to the processing of valence differences in negative stimuli, it is predictable that some neural structures are of central importance in processing valence differences relative to others. On the other hand, a further study may be necessary to confirm the validity of the finding that humans are sensitive to valence variations in emotionally negative stimuli. Based on these considerations, the present study employs the similar design to that of Yuan et al.[2], and further employs ERP dipole analyses measures (BESA.5.0) to investigate the neural bases underlying the differential sensitivity to negative events of varying valences.

The present study used a modified oddball paradigm that required subjects to make a standard/deviant distinction by pressing different keys, irrespective of the emotional valence of the deviants. Rather than requiring a single response for the deviants, we designed two responses to mask the true purpose of the experiment, so as to avoid a "relevance-for-task" effect that was repeatedly reported to obscure the effect of valence on ERPs[17,18]. Because a cultural bias for the International Affective Picture System (IAPS) has been reported in Chinese subjects[19], the pictures used to elicit emotional responses in current study were from the native Chinese Affective Picture System (CAPS)[2,13]. In addition, as previous studies have shown that arousal can non-specifically mask the influence of valence on ERPs[17,20], in the present study the arousal was matched across the three valence conditions, in particular, between the neutral pictures and the two negatively-valenced image groups.

1 Materials and methods

1.1 Subjects

As paid volunteers, 12 undergraduate students (6 women, 6 men) aging 19—25 years (mean age, 22.5 years) participated in the study. All subjects were healthy, right-handed, with normal or corrected to normal vision, and reported no history of affective disorder. Each subject signed an informed consent form for the experiment. The experimental procedure was in accordance with the ethical principles of the 1964 Declaration of Helsinki.

1.2 Stimuli

The present experiment consisted of 6 blocks of 100 trials, with each block including 70 standard and 30 deviant (grouped into 3 conditions) pictures. All deviant pictures were taken from the CAPS. During the experiment, a natural scene of cup served as the frequent standard picture and 30 pictures grouped as either highly negative (HN), moderately negative (MN), or neutral served as the deviants. Moreover, The sequence of standard and deviant pictures was randomized. The three groups of deviant pictures differed significantly in valence from one another [Mean: HN = 1.85, MN = 3.52, Neutral = 5.46; $F(2,87) = 266.19$, $P < 0.0001$; Max (HN) = 2.20, Min (MN) = 2.98] but were similar in arousal (mean: HN = 6.08, MN = 5.88, Neutral = 5.86; $F(2,87) = 1.49$, $P = 0.23$). All pictures were identical in size and resolution (15 cm × 10 cm, 100 pixels per inch), and the luminance and contrast were also matched across the three valence conditions.

1.3 Behavioral procedures

Subjects were seated in a quiet room at approxi-

mately 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 response selection and to inhibit the prepotent response to the frequent stimulus when the deviant is present within a short time. At the end of each of the six blocks, accuracy rates for both standard and deviant stimuli were given to the subjects as 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 with the duration varying randomly between 500 and 1500 ms was presented and was followed by the onset of picture stimulus. Each subject was instructed to press the "F" key on the keyboard (as accurately and quickly as possible) if the standard picture appeared, and to press the "J" key if the deviant picture appeared. The stimulus picture was terminated by a key pressing, or was terminated when it elapsed for 1000 ms. Therefore, each subject was informed that their responses must be made under 1000 ms. Each response was followed by 1000 ms of a blank screen. Pre-training with 10 practice trials was used before formal experiment in order to familiarize subjects with the procedure, and the standard picture in pre-training was the same as that in the subsequent formal experiment whereas the deviants for pre-training were neutral pictures that were not selected for the formal experiment. All subjects achieved 100% accuracy on 10 practice trials prior to the formal experiment.

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 references on the left and right mastoids and a grounded 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 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 for correct response in each valence condition was overlapped and averaged separately. ERP waveforms were time-locked to the onset of stimuli and the average epoch was 900 ms, including a 200 ms pre-stimulus baseline. As shown by ERPs' grand average map and topographic map, the ERPs elicited by HN and MN conditions show prominent differences, and these differences are largest at the central and frontal electrode sites (Fig. 1). Moreover, the HN minus MN difference waveforms reach their maximal amplitudes approximately during 350—700 interval (Fig. 1(b)). In addition, as shown in Fig. 1 (a), prominent P3 and slow negative wave (SNW) components are also elicited by each valence condition during the 350—700 ms interval, with the P3 observed approximately at 350—450 ms interval and SNW at 450—650 ms interval. Therefore, the following 16 electrode sites were selected for statistical analysis: Fz, FC3, FC4, FCz, FPz, FC1, FC2, C1, C2, Cz, C3, C4 (12 anterior sites), CP1, CP2, CPz, and Pz (4 posterior sites); and the average amplitudes at each 50 ms interval from 350 to 700 ms were measured and analyzed with a two-way repeated measures analysis of variance (ANOVA). ANOVA factors were valence condition (three levels: HN, MN, and Neutral) and electrode site (16 sites). The P-value was corrected according to the Greenhouse-Geisser method.

1.5 Dipole analysis

The brain electrical source analysis program (BESA, Version 5.0, Software) was used to perform dipole source analysis, so as to explore the neural bases underlying the assumed sensitivity of the human brain to valence variations in emotionally negative stimuli. For dipole source analysis, four-shell ellipsoidal head model was used. In order to focus on the scalp electrical activity related to the processing of valence differences in emotionally negative stimuli, the averaged ERPs evoked by the MN condition were subtracted from the ERPs evoked by the HN condition. When the dipole points were determined, the software automatically determined the dipoles' location. The relevant residual variance criterion was used.

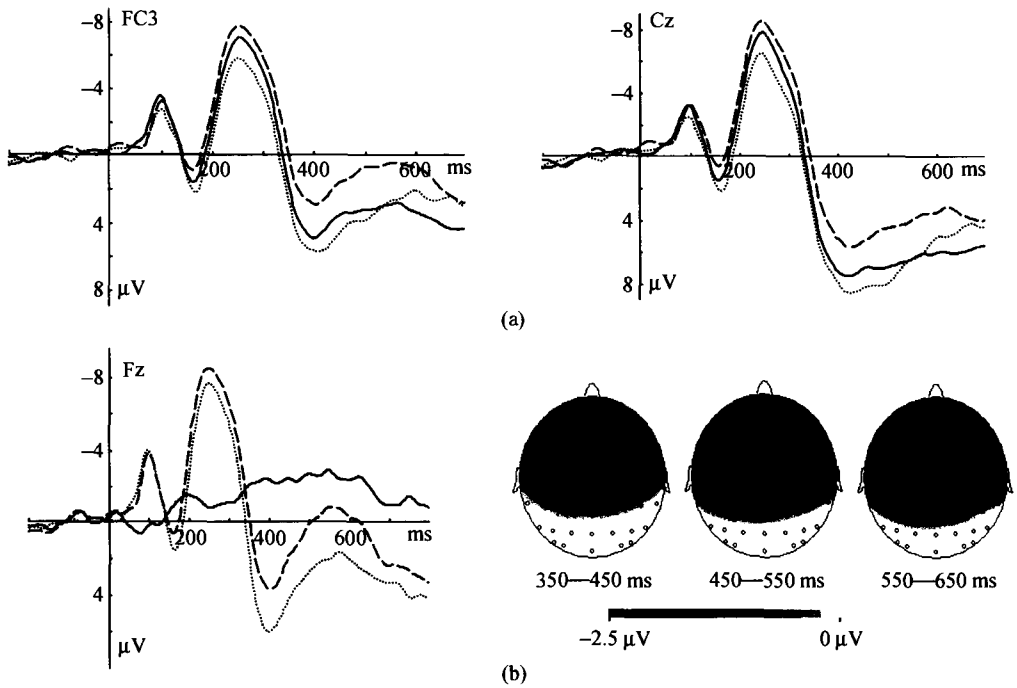

Fig. 1. The average ERPs for the three valence conditions and the scalp distribution of HN minus MN difference wave. (a) Average ERPs at FC3 and Cz for HN (dashed line), MN (solid line), and Neutral (dotted line) conditions. (b) Left: the average ERPs for the HN (dashed line) and MN (dotted line) conditions, and the HN minus MN difference waveform (HN-MN) at Fz(bold line); right: topographical maps of voltage amplitudes for the HN-MN difference waveform at 350—450, 450—550, and 550—650 ms intervals.

2 Results

A two-way repeated measures ANOVA was conducted on the average amplitudes at each 50 ms interval during 350—700 ms time window. A significant valence main effect was observed during each 50 ms interval from 350 to 650 ms, whereas the valence main effect during 650—700 ms interval was not significant. In addition, significant valence by electrode interaction effect was observed during 350—400 ms, 450—450 ms, 500—550 ms and 550—600 ms intervals. Central and frontal sites revealed larger amplitude differences between HN and MN conditions than posterior sites in both P3 and SNW components [Fig.1(b)]. The subsequent pairwise comparison for the valence main effect during 350—650 ms interval demonstrated significant amplitude differences between HN and MN conditions in each 50 ms interval, with the HN condition eliciting more negative ERP deflections than MN condition. In addition, significant amplitude differences between MN and Neutral conditions were also observed during the 350—400 ms interval, and the emotional effect for the MN stimuli was marginal during the 400—450 ms interval. All these results show that valence does not need to be categorized by subjects for the human brain to process valence differences along the information processing stream. Thus, it is reliable to conclude that the human brain is sensitive to valence variations in emotionally negative stimuli.

Thus, the present study confirmed the human sensitivity to valence differences in emotionally negative stimuli, such that valence-distinct negative stimuli are processed differentially even during a task irrelevant to valence assessment. In order to investigate the neural substrates underlying the human sensitivity to valence differences in emotionally negative stimuli, source analysis using BESA software was performed on the ERP difference wave of HN and MN conditions. Because different information processing stages often involve the operations of distinct cerebral structures[11,21], and 350—650 ms interval, when significant amplitude differences were observed between HN and MN conditions, covers both P3 (350—450 ms) and SNW (450—650 ms) stages, the present study conducted source analysis at 350—450 ms interval and the 450—650 ms interval. First, principal component analyses (PCA) was conducted on the HN minus MN difference waveform at 350—450 ms interval to determine the neural substrates responsible for the difference during this higher cognitive processing stage[1,2]. PCA indicated that only one principal component was needed to explain 99.4% of the vari-

ance in the data for this interval. Therefore, one dipole was fitted with no restriction to the direction or location of the dipole. The results indicat that the dipole is located in the right medial temporal lobe (approximately at the right hippocampus; talairach coordinate values: $x = 21.3$, $y = -35.4$, $z = 2.4$) and that the maximal strength of the dipole occurs at approximately 370 ms. This model best explains the data and accounts for most of the variance with a residual variance (RV) of 7.13% at the peak activity of the dipole (Fig. 2).

Fig. 2. Results of dipole source analysis of the HN minus MN difference waveform at the 350—450 ms time window. The left side shows the source activity waveforms and the right shows the mean dipole location. The dipole is approximately located in the right hippocampus ($x = 21.3$, $y = -35.4$, $z = 2.4$).

Similarly, principal component analyses were conducted on the HN minus MN difference waveform at 450—650 ms interval to determine the neural substrates responsible for the difference during this memory-related stage[1,2,22]. PCA of the 450—650 ms interval indicated that only one principal component was needed to explain 99.1% of the variance in the data. Therefore, one dipole was fitted with no restriction to the direction or location of the dipole. The results indicate that the dipole is also located in the right medial temporal lobe (approximately at hippocampus; talairach coordinate values: $x = 17.7$, $y = -38.0$, $z = 5.8$) and that the maximal strength of the dipole occurs at approximately 540 ms. This model best explains the data and accounts for most of the variance with a residual variance (RV) of 9.72% at the peak activity of the dipole (Fig. 3).

Fig. 3. Results of dipole source analysis of the HN minus MN difference waveform at the 450—650 ms time window. The left side shows the source activity waveforms and the right side shows the mean dipole location. This dipole is also approximately located in the right hippocampus ($x = 17.7$, $y = -38.0$, $z = 5.8$).

3 Discussion

The present study replicated the previous discovery that the human brain is sensitive to valence differences in emotionally negative stimuli. As shown in Fig. 1, ERPs evoked by HN and MN conditions showed obvious differences from about 200 ms onwards after stimulus onset, and these differences were prominent during 350—650 ms interval and were largest over central and frontal sites. All these findings lend further credibility to the differential sensitivity of the human brain to emotionally negative events of varying valences.

The finding of greater importance in the present study, however, is that the dipole analyses localize the HN-MN difference wave for the 350—450 ms interval (P3), and for the 450—650 ms (SNW) interval both to the right medial temporal lobe (MTL). This finding suggests that the right MTL plays an important role in processing valence differences in emotionally negative events, and in the subsequent

memory effects evoked by HN stimuli. That is, differential physiological and psychological resources are recruited during the cognitive processing stage for the human brain to process emotionally negative stimuli of varying valences, and the right MTL is the most likely neural substrate mediating the automatical processing of valence differences in emotionally negative stimuli, with greater cerebral activations elicited by HN stimuli than by MN stimuli at this neural structure. Moreover, the later memory effect, as indexed by SNW component, was much larger during HN condition than during MN condition, suggesting that richer associations with emotional negativity from long term memory were evoked by HN stimuli than MN stimuli[2,28]. HN minus MN difference waveform at SNW time interval was also localized to the right MTL. With regards to the well established role of MTL in memory encoding, consolidation and recollection, and the famous role of the right hemisphere in processing negative emotions[9,10,23], the result of dipole analyses during 450—650 ms interval supported the memory-arousing interpretation of the increased SNW negativity elicited by HN stimuli in the present study.

The present discovery that the right medial temporal lobe, most probably, the right hippocampus/amgydala complex mediating the valence processing of emotionally negative stimuli, agrees with the previous evidence demonstrating the involvement of the right MTL in processing the negatively-vaelnced stimuli. Early studies have demonstrated a direct short-latency pathway from the thalamus to the amygdala, an important medial temporal lobe structure, which enables the amygdala to respond to emotional events in the environment rapidly, or even subconsciously[24]. In fact, a more recent study has demonstrated that even when the emotional facial expressions were rapidly presented with a backward masking procedure and subjects reported that they had not seen these facial expressions, blood oxygen level-dependent (BOLD) fMRI signal in the right amygdala was significantly higher during the viewing of masked fearful faces than during the viewing of masked happy faces, indicating a critical role of the right amygdala in subconsciously processing threatening information[25]. Additionally, it has been well established that the amgydala is crucial for the acquisition and expression of fear conditioning, and that the right amgydala plays an important role in processing threatening information[9,25,26]. On the other hand, fMRI studies of fearful habituation have revealed that the right hippocampus/amgydala complex is preferentially activated by the presentation of fearful faces over happy faces, and the right-sided lesions of the anterior MTL impair recognition of negative facial expressions to a greater extent than left-sided lesions[10,27]. In addition, animal experiments have indicated that the hippocampus is involved in the generation of emotional fear, and there is evidence demonstrating the important function of hippocampus / amygdale complex in the formation of emotional memory[9,10].

Based on abundant literature as for the role of the right MTL, particularly the right amygdala and hippocampus complex in processing negatively-valenced stimuli, the present study suggests that, the right medial temporal lobe, especially the right amygdala and hippocampus complex, is the most likely neural bases underlying humans' sensitivity to valence differences in emotionally negative stimuli, or rather, the right hippocampus/amygdale complex may be the very neural structure sensitive to valence variations in emotionally negative stimuli. Probably, the right hippocampus/amygdale complex conducts a fast evaluation of the valence intensity of the incoming negative stimulus, and responds differentially to emotionally negative events of varying valences even in the absence of subjective awareness[24,25]. On the other hand, it could be assumed that, emotionally negative images, irrespective of their valence intensity, could evoke the activations in the right MTL as well as some other likely neural substrates. However, the activation level of the right MTL, more than that of other emotion-related neural structures, varies delicately as a function of the stimulus valence intensity. HN stimuli, which is higher in saliency, would elicit greater right MTL activations relative to MN stimuli. Thus, the activation subtraction during HN and MN conditions would implicate the right MTL, instead of other emotion-related neural structures, in processing valence differences in emotionally negative stimuli, as was shown by the present dipole source analyses. This hypothesis, of course, requires further examination of its validity in future studies employing high spatial resolution measures.

4 Conclusions

The present study has confirmed the human sensitivity to valence variations in negative stimuli all along the information processing stream, and suggested an important role of the right MTL(the right hip-

pocampus/amygdala complex) in processing valence differences in emotionally negative events, and in the subsequent memory effects evoked by HN stimuli. Future studies should aim to clarify which neural structure(s) within the right MTL mediates the processing of valence intensity with high spatial resolution technique (e.g. fMRI). In particular, whether there is a functional dissociation between hippocampus and amygdale regarding their roles in valence processing should be predicted, with the right amygdala preferentially activated during the evaluation-related P3 stage whereas the right hippocampus activated specifically during more later memory-related SNW stage[1,2,22]. Moreover, it is also worth studying whether the patients with the right MTL lesions show less sensitivity to valence differences in emotionally negative stimuli.

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