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Three Stages of Facial Expression Processing: ERP Study with Rapid Serial Visual Presentation

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Abstract

Electrophysiological correlates of the processing facial expressions were investigated in subjects performing the rapid serial visual presentation (RSVP) task. The peak latencies of the event-related potential (ERP) components P1, vertex positive potential (VPP), and N170 were 165, 240 and 240 ms, respectively. The early anterior N100 and posterior P1 amplitudes elicited by fearful faces were larger than those elicited by happy or neutral faces, a finding which is consistent with the presence of a 'negativity bias'. The amplitude of the anterior VPP was larger when subjects were processing fearful and happy faces than when they were processing neutral faces; it was similar in response to fearful and happy faces. The late N300 and P300 not only distinguished emotional faces from neutral faces but also differentiated between fearful and happy expressions in lag2. The amplitudes of the N100, VPP, N170, N300, and P300 components and the latency of the P1 component were modulated by attentional resources. Deficient attentional resources resulted in decreased amplitude and increased latency of ERP components. In light of these results, we present a hypothetical model involving three stages of facial expression processing.

Keywords

faces; attentional blink; three stages of facial expressions processing

Introduction

As a fundamental emotional stimulus, facial expression conveys important information in social exchanges. Numerous event related potential (ERP) and magnetoencephalography (MEG) studies (Bentin et al.. 1996; Jeffreys, 1996; Eimer and McCarthy, 1999; Eimer, 2000; Liu et al., 2000, 2002; Itier and Taylor, 2004; Xu et al., 2005; Itier et al., 2006) have investigated the time course of face visual processing. In these studies, face-sensitive P1, N170 (their magnetic equivalent, the M100 and M170) and vertex positive potential (VPP)

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components have displayed differential activity when different facial expressions were being viewed, especially when faces with a fearful expression were being viewed.

P1 is a positive-direction component detected at the parieto-occipital electrode with an onset latency between 60 and 80 ms that peaks at around 100–130 ms post-stimulus. It is thought to reflect processing of the low-level features of stimuli. However, MEG and electrophysiological studies (Linkenkaer-Hansen et al., 1998; Liu et al., 2000, 2002; Pizzagalli et al., 2002) have indicated that this component correlates with processing of face categorization. While effects of facial expression on P1 have been reported previously (Halgren et al., 2000; Batty and Taylor 2003; Eger et al., 2003), differences related to distinct emotions have not been described (Batty and Taylor 2003; Esslen et al., 2004). However, Pourtois et al (2004) demonstrated that a lateral occipital P1 component was selectively increased when replacing a fearful face with a bar compared with replacing a neutral face with the same bar. Vuilleumier and Pourtois (2007) have thus suggested that there may be a rapid extraction of information related to emotion or salience that occurs before more fine-grained perceptual processes are complete.

N170 is a negative-going component detected at the lateral occipito-temporal electrode with a waveform observed in the 120 to 220 ms range that peaks around 170 ms post-stimulus. This component clearly distinguishes faces from non-face visual stimuli and is therefore considered to be an index of the configural processing of the face (Bentin et al., 1996; Rossion et al., 1999; Bentin and Deouell, 2000; Rossion et al., 2003; Itier and Taylor, 2004). N170 tends to have a shorter latency and larger amplitude in the right hemisphere than the left hemisphere (Bentin et al., 1996). Source-localization studies have localized the generators of the N170 to the fusiform gyrus and the superior temporal sulcus; the implicated fusiform gyrus has been termed the “fusiform face area”. (Itier and Taylor, 2002, 2004; Schweinberger et al., 2002a, 2002b; Caldara et al., 2003) There is conflicting evidence regarding whether N170 is responsive to emotional expression. Some researchers have found that N170 does not discriminate emotional expression (M¨unte et al., 1998; Herrmann et al., 2002; Eimer et al., 2003), while others have found that expression modulates N170 amplitude (Batty and Taylor, 2003; Miyoshi et al., 2004; Caharel et al., 2005), noting a larger amplitude for fearful relative to neutral faces (Batty and Taylor, 2003; Stekelenburg and de Gelder, 2004; Pourtois et al., 2005; Leppänen et al., 2007).

The VPP is a positive deflection detected at the fronto-central electrode with a latency similar to that of the N170. Previous research has shown that, like the N170, the VPP is sensitive to configural processing of the face (Rossion et al., 1999; Eimer, 2000; Jemel et al., 2003). Some source localization studies concluded that the VPP and N170 components are derived from the same neural dipole located in or near the fusiform gyrus (Rossion et al., 1999; Itier and Taylor, 2002; Joyce and Rossion, 2005), while other studies suggested that there are two independent neural generators (Botzel, et al., 1995; Bentin et al., 1996; Eimer, 2000; George et al., 2005). Recent findings have indicated that facial expression modulates VPP amplitude and that its amplitude is larger in response to fearful faces relative to happy and neutral faces. This effect could be attributed, at least in part, to a significant difference in recognition accuracy for these expressions, which planned contrasts showed was due to lesser accuracy for fear relative to neutral faces, but greater accuracy for happy relative to neutral and fear faces (Williams et al., 2006).

Previous studies examining the effect of attention during emotional perception on ERPs have shown that correlates of facial expression processing are modulated by spatial attention (Pessoa et al., 2002; Eimer et al., 2003; Holmes et al., 2003). In this study, we investigate how the time dimension of attention and attentional resources modulate facial expression processing. If the processing of fearful facial expression is a spontaneous process, not

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significantly affected by a competitive stimulus and not requiring attentional resources, then it should not be hindered by an experimentally controlled temporary deficit in attention, referred to as an ‘attentional blink’ (Raymond; 1992). Different facial expressions may be subject to differing attentional blink effects, such that the processing of emotional (fearful and happy) facial expressions would be less affected by an attentional blink than that of neutral facial expressions, and detectivity of fearful facial expression may be less impaired than that of happy faces.

Previous studies have demonstrated that N100, P1, VPP and N170 are significantly affected by affect in the early phase of perception and attention processing (Eimer and Holmes, 2002; Batty and Taylor, 2003; Eger et al., 2003; Ashley et al., 2004; Carretié et al., 2004; Miyoshi et al., 2004; Bar-Haim et al., 2005; Caharel et al., 2005; Huang and Luo, 2006). N300 largely reflects the dimensionality of affective valence (Carretié et al., 2001). The same is true with P300 in higher-level phases of cognitive process, such as those reflecting stimulus evaluation and selection (Campanella et al., 2002; Miltner et al., 2005). The present study hypothesizes that ERP components, such as N100, P1, VPP, N170, N300 and P300, will be sensitive to facial expression in the Rapid Serial Visual Presentation (RSVP) paradigm.

According to Lang's theory of emotional dimensions, valence and arousal are the two primary dimensions of emotion (Lang, 1995). Accordingly, arousal should be controlled for when studying the valence of emotion. In order to control for the effects of arousal on emotional valence in this study, pictures of standardized facial expressions were adopted with valence and arousal subjected to a standardized appraisal. To remove the potential for a race effect, pictures of facial expressions in the Chinese Facial Affective Picture System (CFAPS)[1] were used.

Materials and Methods

Subjects

As paid volunteers, 15 junior undergraduates (eight women, seven men, aged 19–26 years, mean age, 22.6 years) from Southwest University in China participated in the experiment. All participants were healthy, right-handed and had normal or corrected to normal vision.

Stimuli

Materials consisted of 30 face pictures and 3 upright house stimuli. Face pictures from the native Chinese Facial Affective Picture System (CFAPS) were used to elicit emotional responses, including 18 pictures of an upright face and 12 of an inverted neutral face. Upright face pictures were selected in such a way that they differed significantly in valence from one another $F_{2,15} = 338.03$, $P<0.001$ ($M \pm SD$, happy: 6.90±0.22 neutral: 4.70±0.31, fearful: 2.75±0.29); but were similar in arousal $F_{2,15} = 0.66$, $P>0.5$ (happy: 5.55±0.40, neutral: 5.28±0.44, fearful: 5.28±0.57). Males and females were represented equally in the pictures. They were similar to one another in size, background, spatial frequency, contrast grade, brightness, and other physical properties. All of the male faces were shaved, with merely interior characteristics of them being retained. Every picture was cropped into the shape of an ellipse using Adobe Photoshop 8.0® software. The viewing angle was 5.7×4.6°,

[1]The standardized CFAPS was developed at the National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University. This was done in order to avoid the race effect (people are better at recognizing faces from their own race relative to faces from other races). The CFAPS includes 600 pictures of fearful, happy, sad, angry, disgusted, surprised, and neutral faces of oriental female and male subjects. These images are rated by both Chinese college students (gender-matched) with respect to the valence category (unpleasant to pleasant) and arousal level (low to high) of the images on a nine-point scale. ANOVAs revealed that there were significant differences in the valence and arousal levels across seven facial expressions ($F_{6,593} = 333.18$, $P < 0.001$; $F_{6,593} = 82.26$, $P < 0.001$). The pretest for this system showed that CFAPS is reliable across individuals in emotional inducement (the between-subjects reliability scores were 0.986 for valence and 0.978 for arousal).

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and the screen resolution was 72 pixels per inch. The experiment was conducted in a sound-proof room. Subjects were seated in a quiet room with their eyes approximately 100 cm from a 17-in screen. All stimuli were displayed in the center of the screen.

Procedure

The RSVP paradigm chosen for the present study can be used to investigate the character of the time-based attention. In the dual task mode of this paradigm, when the stimulus onset asynchrony (SOA) between the first target (T1) and the second target (T2) is approximately 200–500 ms, the correct detection of T1 impaired T2 detction; this effect is called attentional blink. The acute lack of attentional resources during this time window provides an opportunity to investigate the effect of attentional resources on facial expression.

The experimental procedure was programmed with E-Prime 1.2 (Psychology Software Tools Inc., Pittsburgh, Pennsylvania, USA). At the beginning of the formal experiment, a white fixation point and a blue fixation point appeared successively in the middle of the screen and lasted for 500 ms and 300 ms, respectively. Shortly thereafter, 14 pictures of distracting and target stimuli were displayed, with each being visible for 119 ms. Distractive stimuli consisted of 12 inverted neutral faces; the T1 stimulus was one of three upright pictures of a house, with the probability of the occurrence of each being the same; the T2 stimulus was one of the three kinds of faces, with the probability of the occurrence of each being the same. T1 appeared randomly and equiprobably in the third, fourth, or fifth position in the picture series, while T2 appeared randomly and equiprobably in the positions of the second (lag2) or the sixth (lag6) picture after the T1 stimulus (see Fig. 1 for examples). After presentation of T2 stimuli, the screen remained black and blank for 600 ms.

This task can be done in single task or dual task mode. Subjects were presented with a question about T2 in the single task. In the dual task, they were presented with a question about T1 and a question about T2. Subjects were asked to make as accurate of a judgment as possible. There was no time limit for subjects to indicate their responses. The pictures disappeared when the subject indicated his or her response by pressing a button. The subject would be led into the next picture series after a 500 ms period during which the screen remained black and blank. The single task mode serves as a control condition during which the subject is required to respond only to T2 (faces), but not to T1 (houses).

In the formal experiment, the dual task and single task were divided into eight blocks which appeared at random, with corresponding cues being revealed before the occurrence of each type of block. The subject was allowed rest between consecutive blocks. In order to get rid of the superposition of front and rear electroencephalograms and to obtain ERP components elicited purely by T2, corresponding baseline tasks were designed based on the methods of previous studies (Vogel et al., 1998; Sergent et al., 2005). In baseline tasks, facial expressions at T2 were absent and replaced with a black and blank screen, with other conditions remaining unchanged. Each subject completed a total of 960 trials. The study includes sixteen conditions (three facial expressions and ‘T2 absent’ × two lags × two tasks) and 60 trials were presented for each condition.

ERP recording

Brain electrical activity was recorded from 64 scalp sites using tin electrodes mounted on an elastic cap (Brain Product), with the reference on the left and right mastoids. The vertical electrooculogram (EOG) was recorded with electrodes placed above and below the left eye. All interelectrode impedance was maintained below 5 kΩ. The electroencephalogram (EEG) and EOG were amplified using a 0.01–100 Hz bandpass and continuously sampled at 500 Hz/channel. Averaging of ERPs was computed off-line; trials with EOG artifacts (mean

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EOG voltage exceeding ±80μV) and those contaminated with artifacts because of amplifier clipping, where peak-to-peak deflection exceeding ±80μV, were excluded from averaging.

Data measure and analysis

We mainly analyzed ERP elicited by happy, neutral and fearful faces. The averaged epoch for ERP was 1200 ms including a 200 ms prestimulus baseline. In this study, N100, P1, VPP, N170, N300 and P300 components were measured and analyzed the peak latencies (from stimulus onset to the peak of each component) and amplitudes (N100 and P1: baseline to peak; VPP, N170, N300, and P300: peak to peak). On the basis of the topographical distribution of grand-averaged ERP activity and previous studies (e.g. Righart and de Gelder, 2007; Williams et al., 2006), we chose a different set of electrodes for these components. The following 15 electrode sites (FCz, FC3, FC4, Cz, C3, C4, CPz, CP3, CP4, Pz, P3, P4, POz, PO7, PO8) were selected for statistical analysis of the P300 component (350~500 ms), Pz, P3, P4, POz, PO3, PO4 were selected for statistical analysis of the P1 component (130–200 ms), N100 (60–140 ms) and VPP (200–280 ms) were analyzed at the Fz, F3, F4, FCz, FC3, FC4 electrode sites, N170 (200–280 ms) was analyzed at the P7, P8, PO7, PO8 electrode sites, N300 (250–350 ms) was analyzed at the T7, T8, FT7, FT8 electrode sites. A four-way repeated measures analyses of variance (ANOVA) on the amplitude and latency of each component was conducted with task (two levels: single, dual), lag (two levels: lag2, lag6), expression (three levels: happiness, neutral, fear) and electrode site as within-subjects factors. P values were corrected by Greenhouse-Geisser correction.

Dipole source analysis

The Brain Electrical Source Analysis programme (BESA, Version 5.0, Software; MEGIS Software GmbH, Munich, Bavaria, Germany) was used to perform dipole source analysis. For dipole source analysis, the four-shell ellipsoidal head model was used. To focus on the scalp electrical activity related to the processing of the face, the averaged ERPs evoked by the baseline task was subtracted from the ERPs evoked by the neutral faces, and one difference wave was obtained. Principal Component Analysis (PCA) was employed in the interval of 200–280 ms for the N170 and VPP in order to estimate the number of dipoles needed to explain the difference wave. When the number of dipoles was determined with PCA, software automatically determined the dipoles' location. The relevant residual variance criterion was used to evaluate whether this model explained the data best and accounted for most of the variance.

Results

Behavioral performance

ANOVAs revealed that response accuracy was significantly affected by task, lag, and facial expression ($F_{1,14}=15.93$, $P<0.001$; $F_{1,14}=26.70$, $P<0.001$; $F_{2,28} = 54.79$, $P<0.001$). Subjects performed at a higher correct rate in the single task condition (94.93±2.84%) than in the dual task (92.43±4.76%), and performed better in lag6 (94.64±3.06%) than in lag2 (92.72±4.75%). Pairwise comparison of the main effect of facial expression showed that the accuracy of fearful faces (96.31±2.40%) was higher than that of happy (93.60±3.29%, $P<0.01$) and neutral faces (91.13±4.56%, $P<0.001$). The task × facial expression interaction ($F_{2,28} = 25.17$, $P<0.001$) indicated that accuracy was significantly higher in the single task than in the dual task when happy ($P<0.011$) and neutral faces ($P<0.001$) were presented, but no task effect on accuracy was observed when fearful faces ($P>0.7$) were presented. The lag × facial expression interaction ($F_{2,28} = 7.08$, $P<0.006$) indicated that the accuracy at lag6 was significant higher than that at lag2 when happy ($P<0.002$) and neutral faces ($P<0.001$) were shown, but not when fearful faces were shown ($p>0.6$). Moreover, the task × lag interaction ($F_{1,14}=9.77$, $P<0.007$) revealed that the accuracy of lag6 was greater than that of

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lag2 in the dual task ($P<0.001$), but accuracy did not differ between lags in the single task ($P>0.7$).

ERP data analysis

N100—N100 amplitudes showed significant main effect at facial expression (see Fig. 2) and lag ($F_{2,28} = 20.69$, $P<0.001$; $F_{1,14} = 10.34$, $P<0.006$). Fearful faces (−2.60 μV) elicited larger N100 amplitudes than happy (−1.58 μV; $P<0.001$) and neutral faces (−1.66 μV; $P<0.001$), while the latter two emotional conditions did not show significant amplitude differences ($P>0.7$). Larger amplitudes were elicited in lag6 condition (−2.77 μV) than in lag2 (−1.13 μV) condition (Fig. 3).

P1—P1 amplitudes showed significant main effect at facial expression (Fig. 2) and electrode ($F_{2,28}=9.75$, $P<0.002$; $F_{5,70}=3.61$, $P<0.031$). Fearful faces (4.79 μV) elicited larger P1 amplitudes than happy (3.60 μV; $P<0.008$) and neutral faces (3.48 μV; $P<0.002$) while the latter two emotional conditions did not show significant amplitude differences ($P>0.5$). Larger amplitudes were elicited at the P4 (4.02 μV) electrode sites and the PO4 (4.06 μV) electrode than at the P3 (2.57 μV, $P<0.01$) sites and the PO3 (3.41 μV, $P<0.05$) electrode. P1 latency showed significant main effect at lag ($F_{1,14} = 6.89$, $P<0.02$), longer latency elicited in lag2 (169.76 ms) than in lag6 (159.74 ms).

N170—Task (Fig. 4), lag (Fig. 3), facial expression (Fig. 2) and electrode each had an effect on N170 amplitude ($F_{1,14}=16.50$, $P<0.001$; $F_{1,14}=27.47$, $P<0.001$; $F_{2,28}=6.53$, $P<0.009$; $F_{3,42}=7.43$, $P<0.002$). The single task (−7.25 μV) elicited larger N170 amplitudes than dual task (−6.20 μV), and the lag6 condition (−7.98 μV) elicited larger amplitudes than lag2 condition (−5.47 μV). The pairwise comparison showed that happy (−6.90 μV; $P<0.014$) and fearful faces (−6.94 μV; $P<0.015$) elicited larger N170 amplitudes than neutral faces (−6.33 μV), while the former two emotional conditions did not show significant amplitude differences ($P>0.7$). Larger amplitudes were elicited at the P8 (−7.11 μV) electrode sites and the PO8 (−8.72 μV) electrode than at the P7 (−4.82 μV, $P<0.005$) sites and the PO7 (−6.24 μV, $P<0.05$) electrode. The lag × expression interaction ($F_{2,28}=6.45$, $P<0.01$) revealed that larger amplitudes were elicited by fearful faces (−5.97 μV) than happy (−5.36 μV; $P<0.026$) and neutral faces (−5.08 μV; $P<0.011$) in the lag2 condition, but no significant difference between the happy and neutral faces was observed ($P>0.11$); happy faces (−8.44 μV) elicited larger amplitudes than fearful (−7.91 μV; $P<0.029$) and neutral faces (−7.58 μV; $P<0.010$) in the lag6 condition, while the latter two conditions did not show significant amplitude differences ($P>0.17$).

Facial expression affected N170 latency ($F_{2,28}=11.09$, $P<0.001$). The pairwise comparison showed that fearful (239.68 ms, $P<0.002$) and happy faces (239.14 ms, $P<0.002$) elicited shorter N170 latencies than neutral faces (246.97 ms). Meanwhile, N170 latency did not differ between happy and fearful faces ($P>0.7$).

VPP—VPP amplitudes showed significant main effect at task (Fig. 4), lag (Fig. 3), facial expression (Fig. 2) and electrode ($F_{1,14}=19.45$, $P<0.001$, $F_{1,14}=39.07$, $P<0.001$, $F_{2,28}=13.06$, $P<0.001$, $F_{5,70}=12.79$, $P<0.001$). VPP amplitudes elicited by single task (9.67 μV) were considerably larger than that elicited by dual task (8.01 μV), and that elicited by lag6 (10.34 μV) larger than by lag2 (7.33 μV). Happy (9.59 μV; $P<0.001$) and fearful (9.12 μV; $P>0.001$) expression elicited larger VPP amplitudes than neutral faces (7.81 μV), with the difference between the former two emotional conditions not significant ($P>0.11$). Amplitudes of Fz (9.93 μV, $P>0.001$) and FCz (9.71 μV, $P>0.005$) electrodes were significantly larger than the other sites. There was significant interaction between task and lag ($F_{1,14}=8.44$, $P<0.012$). The simple effects analyses demonstrated that VPP amplitudes

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elicited by single task (8.68 μV) were significantly larger than dual task (5.99 μV; $P<0.001$) in lag2 condition. By contrast, there were not significant differences between amplitudes elicited by single task (10.67 μV) and dual task (10.02 μV; $P>0.23$) in lag6 condition.

Main effects of facial expression in VPP latency were significant ($F_{2,28}=12.77$, $P<0.001$). The pairwise comparison revealed that fearful facial expression (232.57 ms) elicited shorter VPP latency than happy (244.17 ms; $P<0.001$) and neutral ones (244.02 ms; $P<0.001$), the happy and neutral facial expressions were not significant ($P>0.9$).

N300—N300 amplitudes showed significant main effect at lag(Fig. 3), facial expression (Fig. 2) and electrode ($F_{1,14}=30.39$, $P<0.001$, $F_{2,28}=7.97$, $P<0.007$, $F_{3,42}=6.16$, $P<0.007$), lag6 (−8.14 μV) condition elicited larger amplitudes than lag2 (−5.97 μV) condition; the pairwise comparison showed that fearful faces (−7.80 μV) elicited significant larger amplitudes than happy (−6.92 μV; $P<0.023$) and neutral faces (−6.45 μV; $P<0.008$), and the happy facial expression elicited larger amplitudes than neutral faces ($P<0.047$); FT8 (−8.01 μV, $P<0.05$) elicited the larger amplitudes than other electrode sites. The lag by facial expression interaction effect was significant ($F_{2,28}=4.29$, $P<0.027$), The simple effects analyses revealed larger amplitudes elicited by fearful faces (−6.83 μV) than happy (−5.99 μV; $P<0.027$) and neutral faces (−5.09 μV; $P<0.003$), and happy elicited larger amplitudes than neutral faces ($P<0.013$) in the lag2 condition; fearful faces (−8.78 μV) elicited larger amplitudes than neutral faces (−7.81 μV; $P<0.043$), the difference of fearful and happy (−7.84 μV) faces is closely approached significance ($P<0.051$), while the happy and neutral faces did not show significant amplitude differences ($P>0.8$) in the lag6 condition.

N300 latency showed significant main effect at facial expression and electrode ($F_{2,28}=4.13$, $P<0.04$, $F_{3,42}=5.34$, $P<0.015$), the pairwise comparison showed that fearful faces (314.88 ms) elicited significantly shorter latency than happy (320.43 ms; $P<0.004$) and neutral faces (319.26 ms; $P<0.035$); whereas the happy and neutral faces ($P>0.6$) did not show significant latency differences. T7 (311ms) electrode elicited shorter latency than FT7 (325 ms, $P<0.002$) site and T8 (314ms) electrode elicited shorter latency than FT8 (321 ms, $P<0.007$) site. The main effect of task is marginally significant ($F_{1,14}=4.36$, $P<0.056$), single task (314.06 ms) elicited shorter latency than dual task (322.32 ms),

P300—P300 amplitudes showed significant main effect at task (Fig. 4), lag (Fig. 3), facial expression (Fig. 2) and electrode ($F_{1,14}=48.26$, $P<0.001$, $F_{1,14}=24.54$, $P<0.001$, $F_{2,28}=14.35$, $P<0.001$, $F_{14,196}=4.475$, $P<0.003$). Single task (13.16 μV) elicited larger P300 amplitudes than dual task (10.57 μV), lag6 (13.89 μV) condition elicited larger amplitudes than lag2 (9.84 μV) condition. The pairwise comparison showed that fearful faces (12.99 μV) elicited larger P300 amplitudes than happy (12.22 μV; $P<0.02$) and neutral (10.39 μV; $P<0.001$), and happy elicited larger amplitudes than neutral faces ($P<0.005$). P4 (13.38 μV) elicited the largest amplitudes of P300, FCz, FC4, Cz, C4, CPz, CP4, Pz and P4 electrodes elicited larger amplitudes than other electrode sites ($P<0.05$). The lag by facial expression interaction effect was significant ($F_{2,28}=6.94$, $P<0.005$). The further simple effects analyses revealed that larger amplitudes elicited by fearful faces (11.42 μV) than happy (10.16 μV; $P<0.009$) and neutral faces (7.94 μV; $P<0.001$), and happy elicited larger amplitudes than neutral faces ($P<0.001$) in the lag2 condition; fearful faces (14.55 μV) elicited larger amplitudes than neutral faces (12.84 μV; $P<0.009$), the difference of fearful and happy (14.27 μV) faces is not significance ($P>0.4$), while the happy and neutral faces show marginally significant amplitude differences ($P<0.057$) in the lag6 condition.

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Source localization

PCA indicated that a single principal component could explain 98.1% of the variance in the data in the 200–280 ms time window. Therefore, only one dipole was fitted with no restriction as to the direction or location of the dipole. The results indicated that the dipole was located approximately in the right fusiform gyrus region (Talairach coordinates x=33.9, y= −35.8, z= −11.2) and that the maximal strength of the dipole occurred at about 240 ms. This model explained the data best and accounted for most of the variance with a residual variance of 10.74% at the peak activity of this dipole (Fig. 5). The validity of this model was tested through the following steps. First, the display of the residual maps in the time window showed no further dipolar activity; second, no other dipoles could be fitted in the investigated time window by comparing the solution with other plausible alternatives (e.g. bilaterally symmetric dipoles). These tests suggest that the model explained the data in the best manner for the time window.

Discussion

Response accuracy was better with fearful face stimuli than with happy and neutral face stimuli. However, responses to happy facial expression stimuli were less impaired by the presence of an attentional blink than responses to neutral ones. These findings are consistent with the hypothesis that processing of emotional, especially potentially threatening stimuli, may occur without substantial attentional involvement. This distinction would be expected to provide a highly valuable biological adaptation.

The hypothesis of three stages of facial expression processing

In light of the present results, we propose hypothetical model involving three stages of processing of emotion facial expression. In this model, the first stage allows automatic processing for negative-valence facial expressions. Emotionally charged facial expressions are distinguished from neutral faces in the second stage and different emotion facial expressions are differentiated in the third stage.

The first stage: automatic processing

The first stage mainly distinguishes potentially threatening facial expression (i.e., fear or anger) from the other expressions. The processing is very fast, automatic, and coarse. Previous studies have found responses to negatively valenced stimuli to be enhanced relative to positive or neutral stimuli, reflecting a negativity bias (Smith et al., 2003). Some ERP studies have also found that negatively valenced picture stimuli elicited comparatively larger ERPs, demonstrating electrophysiological evidence of a negativity bias (Ito et al., 1998; Smith et al., 2003). The negativity bias may be attributed to processing in this stage.

Processing fearful facial expression can elicit a more pronounced negative N100 component than happy and neutral faces (Fig. 2). The amplitude recorded at the frontal site was larger than those elicited at other electrode sites. This finding is consistent with the hypothesis that the orbitofrontal cortex serves as a rapid detector and predictor of potential information based on coarse aspects of input. This detection is valuable for recognizing and analyzing threatening information, especially if this information is modulated by the amygdala (Bar et al., 2006). The amygdala can modulate extrastriate cortex responses to fearful faces (Morris et al., 1996). Santos (2008) et al. further suggested that coarse information quickly analyzed by the orbitofrontal cortex could modulate extrastriate activity through the amygdala as part of a top-down alerting mechanism that aims to generate rapid responses to potentially threatening stimuli.

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Relative to happy and neutral faces, fearful faces elicited an enhanced positive P1 amplitude (Fig. 2). Facial expression stimuli have previously been shown to enhance positive components at 160 ms post-stimulus (Eimer 2002, 2003 ; Holmes et al., 2003). Meeren et al. (2005) reported that the P1 component was not affected by emotion expressed in isolated faces and bodies; however, the study compared only two negative emotional expressions, namely fear and anger.

The second stage: distinguishing emotional and neutral facial expressions

There is dominance for processing emotional facial expressions in the second stage of our model. During this stage, the brain can distinguish emotional from neutral facial stimuli, but cannot distinguish among different emotions. VPP and N170 may reflect processing in this stage. The presently observed N170 and VPP latencies (~240 ms) were about 70 ms later than those typically reported. Nevertheless, we believe they were not atypical for several reasons. Firstly, they had a similar latency and reversed polarity relative to each other (Jeffreys, 1989; Rossion et al., 1999; Eimer, 2000; Jemel et al., 2003). Secondly, they were distributed in the expected parietal-occipital (N170) and frontal-central (VPP) sites. Additionally, dipole source localization indicated that within the 200–280 ms window the dipole was located in the region of the right fusiform face area (Fig. 5), which is in accord with prior studies that indicated that the VPP and N170 components are located in or near the fusiform gyrus (Kanwisher et al., 1997; Rossion et al., 1999; Itier and Taylor, 2002; Joyce and Rossion, 2005).

Most studies find that N170 does not discriminate emotional expression (M¨unte et al., 1998; Herrmann et al., 2002; Eimer et al., 2003) or find that N170 distinguishes only fearful expression from the other expressions (Batty and Taylor, 2003; Stekelenburg and de Gelder, 2004; Pourtois et al., 2005; Leppa¨nen et al., 2007). However, Boucsein et al (2001) found that N170 is sensitive to facial emotional expression in general but cannot discriminate between different emotions. Some studies further suggested that fearful, disgust, and happy faces elicited a larger N170 amplitude than neutral faces (Williams et al., 2006; Wild-Wall et al., 2008), while fearful faces elicited a larger VPP amplitude than happy and neutral faces in the 120–220 ms post-stimulus period (Williams et al., 2006).

In the present study, N170 and VPP were affected by emotion expression. Specifically, happy and fearful facial expressions elicited larger VPP amplitude than neutral faces. Hence VPP distinguished emotional faces from neutral faces, but did not discriminate between different emotions. N170 amplitude was enhanced during the processing of only fearful face stimuli in the lag2 condition, but enhanced during the processing of happy face stimuli in the lag6 condition. Lag2 occurs during a deficit of attentional resources while lag6 occurs beyond the attentional blink. Unhindered processing of stimuli that may indicate the presence of a threat, such as a fearful expression, during times of strained attention (i.e. lag2) would be advantageous. Meanwhile, the processing of a happy face stimuli may not be suppressed because vigilance for detecting potential threats may be ample under abundant attentional resource conditions.

The third stage: differentiate various emotion facial expressions

The brain distinguishes among emotional facial expressions in the third stage. N300 and P300 amplitude probably reflects further evaluation of information related the affective valence of a face. Carretié et al. (2001) have highlighted N300's role of distinct stimulus in affection process. Bar-Haim et al. (2005) found that fearful facial expressions can elicit a larger N300 amplitude than the happy faces; and Schutter et al. (2004) also found that fearful facial expression can elicit enhanced negative N300 in the anterior sector relative to that observed with happy and neutral faces. Previous studies have also demonstrated that

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P300 amplitude reflects the essentiality of affective stimulus, which will elicit larger P300 amplitude than neutral stimulus (Campanella et al., 2002; Miltner et al., 2005). Williams et al. (2006) found an enhanced P300 (280 –450 ms) for fearful facial expression, suggesting that signals of potential danger serve to enhance ongoing stimulus elaboration and context evaluation. In this study, the lag × expression interaction effects indicated that fearful facial expressions elicited larger N300 and P300 amplitudes than happy or neutral faces, and happy facial expressions elicited larger amplitudes than neutral faces only in the lag2 condition. It seems that facial expressions can be processed more quickly (within ~300 ms) in the lag2 condition than in the lag6 condition. When one encounters stimuli in rapid succession, such as in the lag2 condition, processing must be completed more quickly in order for emotional valance to be judged accurately.

Attentional resource effect

Attentional processes can be examined experimentally through the use of different tasks and lags. Attentional resources are relatively abundant when a single task mode or long lag is used, and they are relatively deficient when a dual task mode or short lag is used. Mcarthur et al. (1999) found that P300 magnitude is related to the intensity of attentional blink. Under conditions of deficient attentional resources, tasks become more difficult and the P300 amplitude is decreased (Hagen et al., 2006; Kok, 2001). Similar to the findings of ERP stuhy performed by Vogel et al. (1998) and Kranczioch et al. (2003), this study has found that the P300 amplitude in the single task mode and at lag6 is larger than in the dual task and at lag2, respectively. N170 and VPP also present with a larger amplitude at lag6 than at lag2 as well as a larger amplitude in single task mode than in dual task mode. N100 and N300 similarly showed a larger amplitude at lag6 than at lag2. And the latency of P1 is shorter at lag6 than at lag2. Hence larger component amplitudes and shorter latencies are observed when attentional resources are plentiful. Processing in the second and third stages are sensitive to attentional resource availability while processing in the first stage remains relatively independent.

Laterality

We found that positive P1 amplitudes elicited in the right hemisphere parietal and parietal-occipital regions were greater than those elicited in the left hemisphere. N170 with higher amplitudes over the right hemisphere were observed in both real and schematic faces (Bentin et al., 1996; Sagiv and Bentin, 2001; Krombholz et al., 2007), the present data found that there is right hemisphere dominance for the amplitude of N170. N300 and P300 also showed right hemisphere dominance (Fig. 6). Prior studies have indicated that right hemisphere ERP amplitudes can be strengthened under emotional conditions; neurons in the superior temporal gyrus respond selectively to facial expressions and the processing of facial expression is attributed predominantly to the superior temporal sulcus in the right hemisphere (Adolphs, 2002b; Adolphs et al., 1996; Narumoto et al., 2001). Neurophysiology and neuroimaging data also suggest that the right hemisphere may be privileged when it comes to processing within 200 ms of stimulus presentation (Halgren et al., 1995; Kawasaki et al., 2001; Pizzagalli et al., 2002).

Conclusions

The amplitudes of the N100, VPP, N170, N300, and P300 components and the latency of the P1 component elicited by viewing of emotionally expressive faces can be modulated by attentional resources. Component amplitudes and latencies tend to be larger and shorter, respectively, when attentional resources are plentiful. Furthermore, the ERP components have differential preferences for different emotional expressions in a manner consistent with multi-stage processing of emotional facial expressions. Processing in the second and third

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stages of the presently proposed model are sensitive to attentional resource availability while processing in the first stage remains relatively independent.

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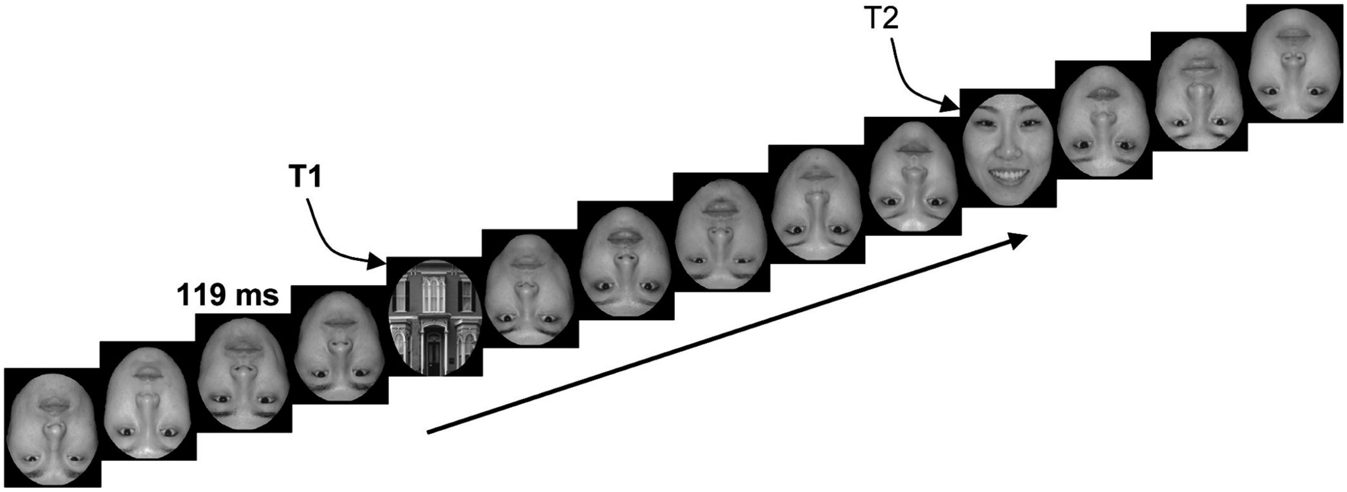

Figure 1.
Overview of a representative experimental trial.

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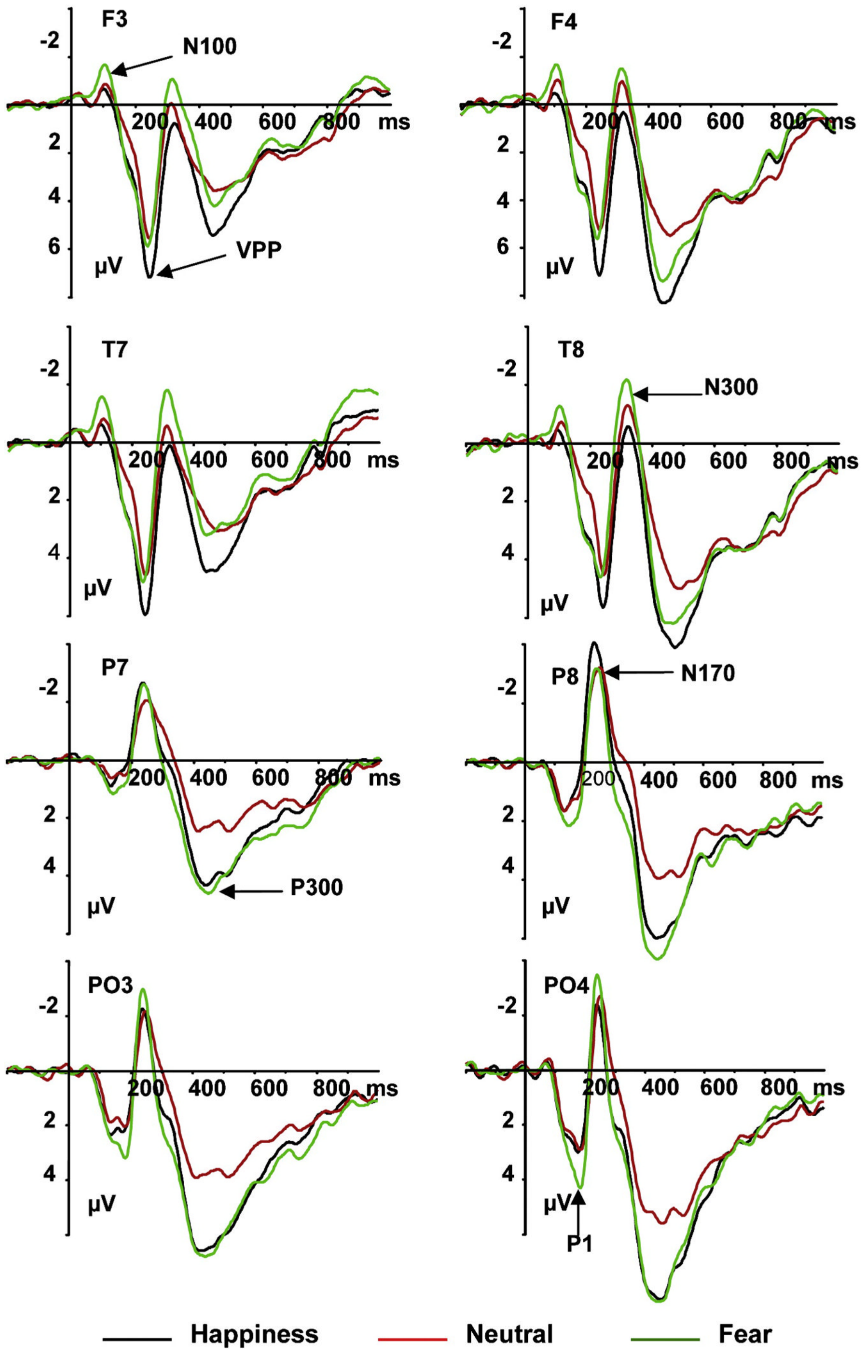

Figure 2.

Grand average ERPs for happiness (black lines), neutral (red lines), and fear (green lines) conditions recorded at the indicated electrode sites.

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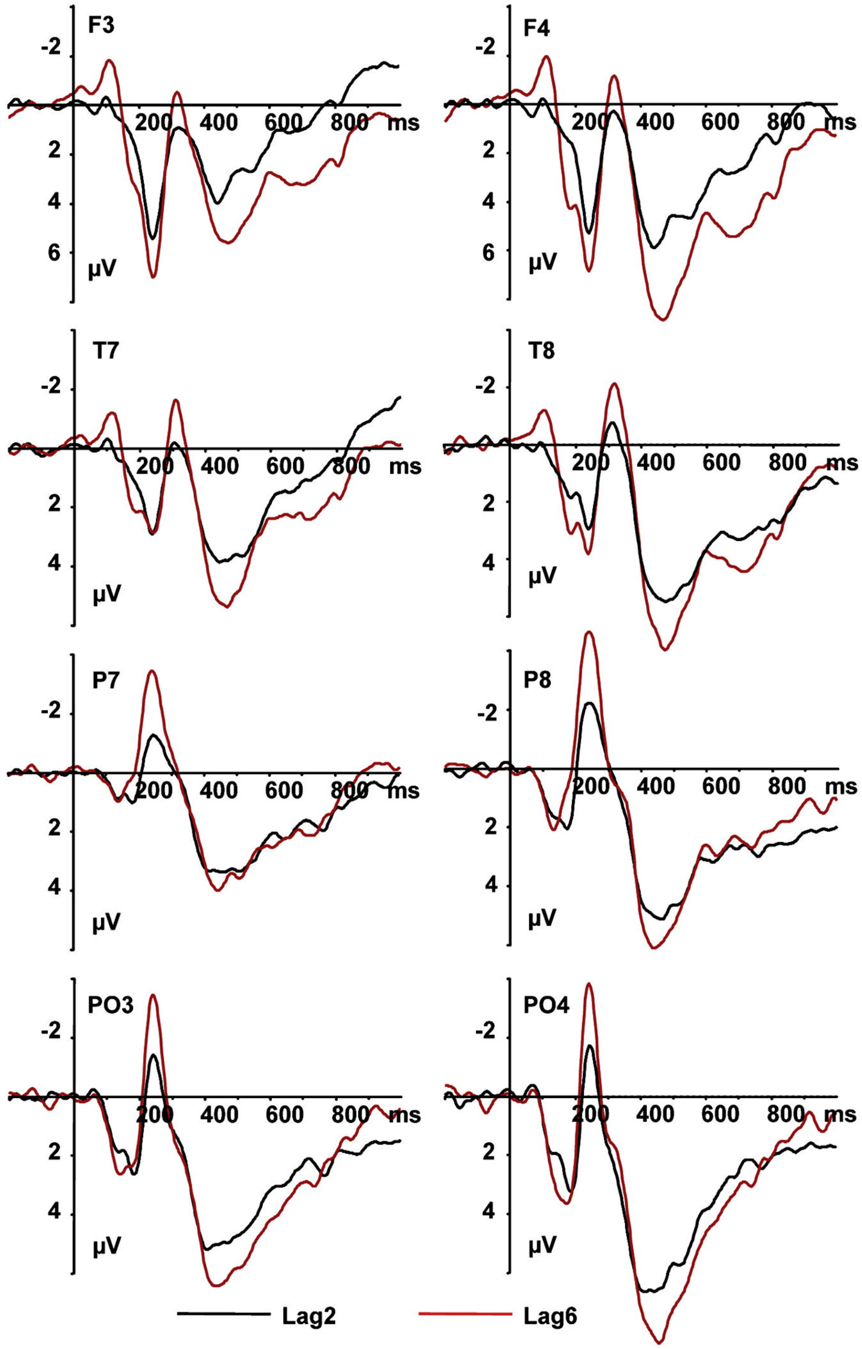

Figure 3.
Grand average ERPs at lag2 (black lines) and lag6 (red lines) recorded at the indicated electrode sites.

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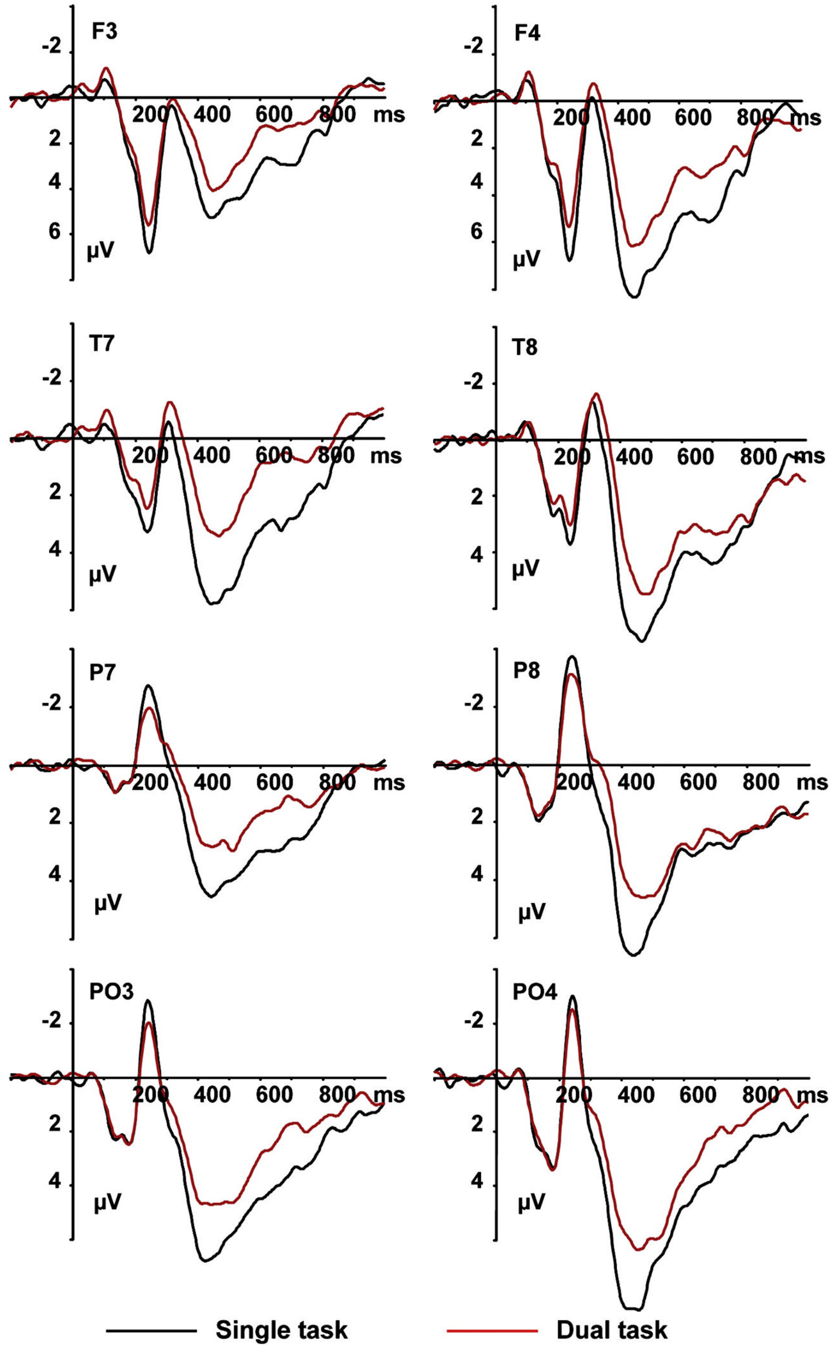

Figure 4.

Grand average ERPs for single (black lines) and dual (red lines) task modes recorded at the indicated electrode sites.

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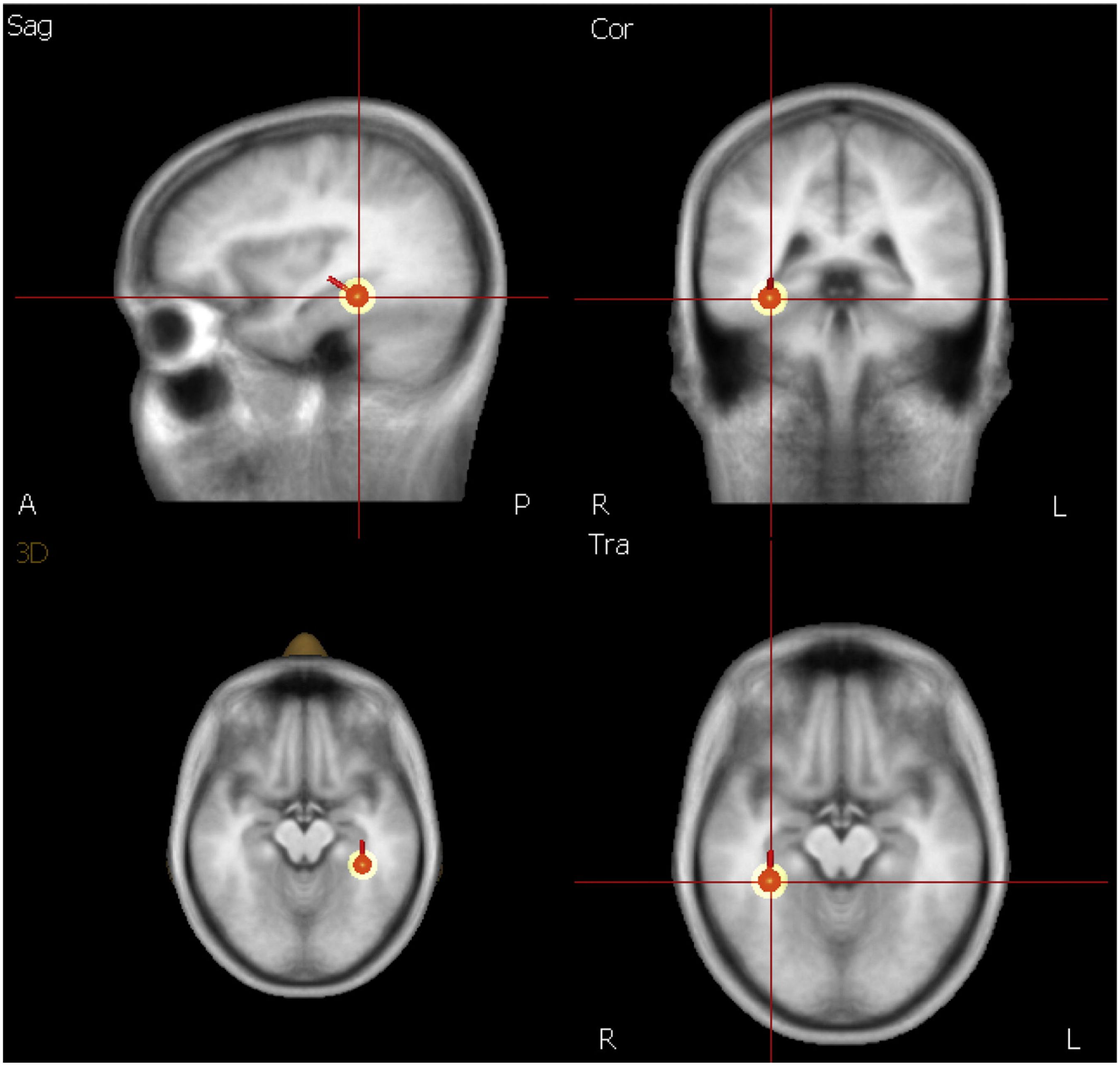

Figure 5.
Dipole source localization images of the neutral face *versus* baseline difference wave for VPP and N170 peak latencies. The panels show data for the fitted dipole 200–280 ms after stimulus presentation window presented in the sagittal, coronal, and transverse planes and a three-dimensional (3D) image. The dipole is located in the region of the right fusiform gyrus (Talairach coordinates x=33.9, y= −35.8, z=−11.2).

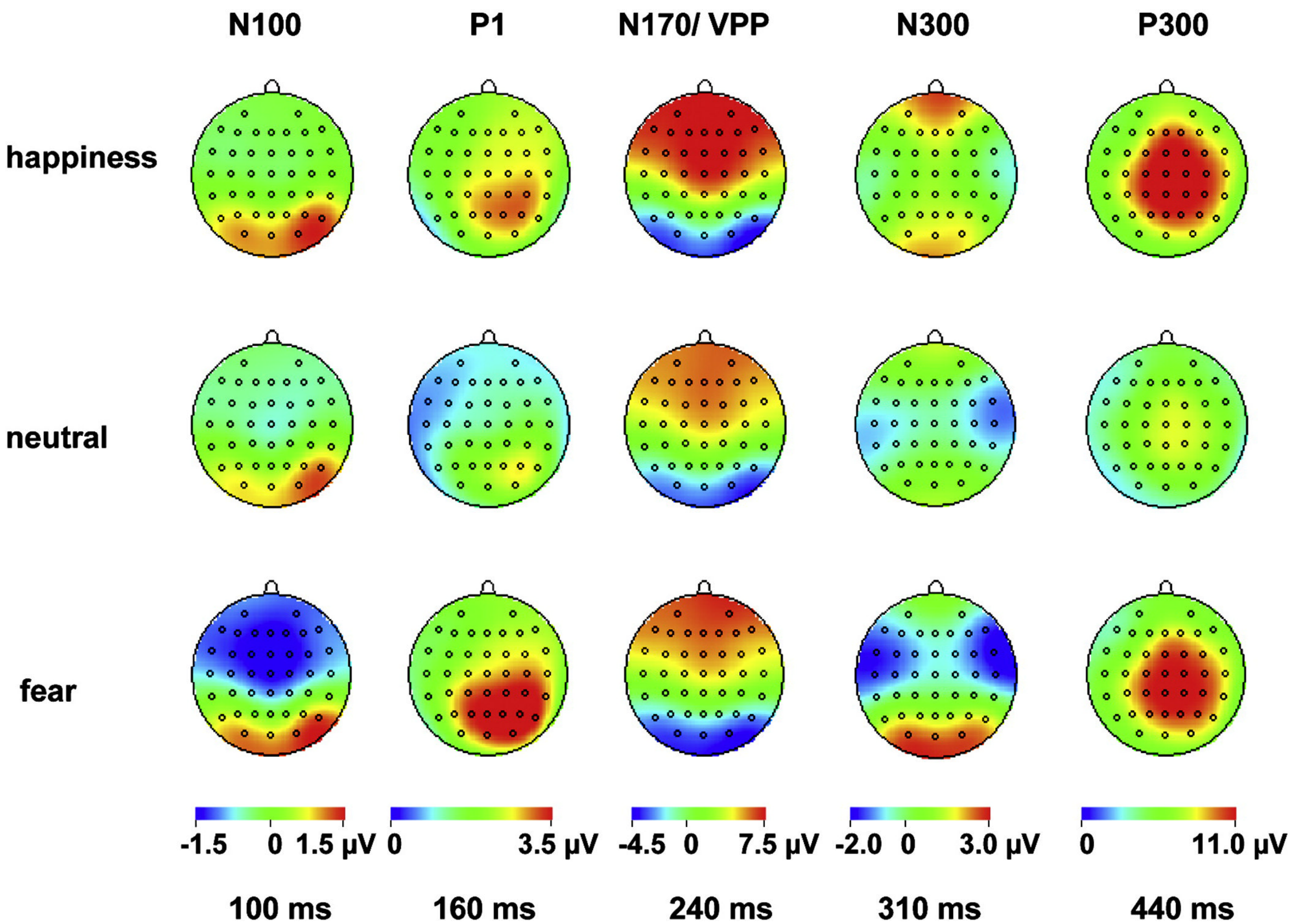

Figure 6.
Scalp topography of ERPs generated by happy, neutral, and fearful faces at100, 160, 240, 310, and 440 ms.

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