Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions

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Abstract

Previous studies have shown differential event-related potentials (ERPs) to fearful and happy/neutral facial expressions. To investigate whether the brain systems underlying these ERP differences are sensitive to the intensity of fear and happiness, behavioral recognition accuracy and reaction times as well as ERPs were measured while observers categorized low-intensity (50%), prototypical (100%), and caricatured (150%) fearful and happy facial expressions. The speed and accuracy of emotion categorization improved with increasing levels of expression intensity, and 100% and 150% expressions were consistently classified as expressions of the intended emotions. Comparison of ERPs to 100% and 150% expressions revealed a differential pattern of ERPs to 100% and 150% fear expressions over occipital-temporal electrodes 190-290 ms post-stimulus (a negative shift in ERP activity for high-intensity fearful expressions). Similar ERP differences were not observed for 100% and 150% happy expressions, ruling out the possibility that the ERPs to high-intensity fear reflected a response to increased expression intensity per se. Together, these results suggest that differential electrocortical responses to fearful facial expressions over posterior electrodes are generated by a neural system that responds to the intensity of negative but not positive emotional expressions.

Section: Cognitive and Behavioral Neuroscience

Keywords: Event-Related Potential, Emotion Intensity, Facial Expression

1. Introduction

Other people's facial expressions convey important emotional and social information such as information about readiness for friendly interaction (e.g., expressions of happiness) or information about potentially harmful objects or situations in the environment (e.g., expressions of fear). Given their impetus to very different behavioral responses, it is not surprising that the processing of different facial expressions is associated with dissociable patterns of brain activity (Williams et al., 2006), autonomic activity (Critchley et al., 2005), and attention (Georgiou et al., 2005).

Recording of event-related potentials (ERPs) provides one tool to examine the neural correlates of different facial expressions. Threat-related (fearful/angry) and positive/neutral facial expressions are associated with differential patterns of ERP activity starting from components associated with the early stages of visual processing (P100, N170) and extending to postperceptual attention-sensitive components (P300). The P100 (Kolassa and Miltner, 2006 and Pourtois et al., 2005) and the face-sensitive N170 components over occipital-temporal scalp regions (Batty and Taylor, 2003, Caharel et al., 2005, Leppänen et al., 2007, Stekelenburg and de Gelder, 2004 and Williams et al., 2006) have been shown to be of larger amplitude and, perhaps surprisingly, the N170 also of longer latency (Batty and Taylor, 2003) for fearful relative to neutral faces. Other studies have found no effects in the P100 and N170 components but have reported a negative shift in ERP activity for fearful/angry relative to neutral/happy expressions over lateral temporal sites, starting approximately 200 ms after stimulus onset and lasting for 100 ms or more (Eimer et al., 2003, Eimer and Kiss, 2007 and Schupp et al., 2004). This negative shift may reflect enhanced processing of emotional stimuli in perceptual representation areas (Schupp et al., 2004). Similar negative shift is observed for task-relevant target stimuli relative to task-irrelevant distractors in studies using non-emotional material such as colors or geometric shapes (Hillyard and Anllo-Vento, 1998).

Important differences in the processing of threat-related and positive/non-threatening facial expression may also occur in later, postperceptual processing stages. Several studies have shown larger centroparietal positivity (P300) to angry/fearful than neutral/happy facial expressions (Schupp et al., 2004 and Williams et al., 2006). The differences in ERPs to threat- and safety-related facial expressions during the early and late stages of cortical processing are typically interpreted to reflect enhanced allocation of attentional resources to emotionally salient stimuli. Fearful and angry expressions may be more potent than happy or neutral expressions in engaging emotion-related brain structures (i.e., the amygdala), and the activation of these structures, in turn, may modulate and enhance cortical information processing and guide limited processing resources to emotionally significant stimuli (Vuilleumier, 2005).

To further examine the ERP effects to threat- and safety-related facial expressions, we investigated whether the brain systems underlying these effects are sensitive to the intensity of fearful and happy facial expressions. The intensity of the displayed expression may convey important information about the immediacy of the event eliciting the expression (e.g., more intense expressions of fear may signal more imminent danger). Neuroimaging data show that activity in the amygdala, a key structure in the brain network processing emotional and especially threat-related information, *increases* in response to increasing intensity of fearful expressions and *decreases* in response to increasing intensity of happy expressions (Morris et al., 1996). It is unlikely that the scalp-recorded ERPs reflect amygdala activity directly given the closed-field organization of neurons in the amygdala and the deep position of the amygdala with respect to scalp surface (Eimer and Holmes, 2007). However, there are anatomical connections between the amygdala and sensory representation areas in the ventral visual pathway (Amaral et al., 2003), and the amygdala exerts a modulatory influence on face-sensitive areas in the occipital-temporal cortex (Vuilleumier, 2005). The amygdala and visual cortical areas may, therefore, form an interconnected network that processes emotional information from faces (Adolphs, 2002) and is sensitive to the intensity of facial expressions. A recent study (Sprengelmeyer and Jentzsch, 2006) showed that a sustained ERP negativity over lateral temporal regions, which was most pronounced 200-600 ms post-stimulus and had its generators within the inferior occipital-temporal lobe, differentiated between varying intensities of angry, disgusted, and fearful facial expressions. The size of the negative deflection increased linearly with the intensity of facial expression. However, because that study employed only negative facial expressions, it left open the question of whether a different pattern of ERPs could be observed in response to negative and positive facial expressions.

We measured behavioral recognition accuracy and reaction times (RTs) as well as ERPs to low-intensity (50%), prototypical (100%), and caricatured (150%) fearful and happy facial expressions. The caricatured expressions were generated by using computer-based morphing and caricaturing procedures (Calder et al., 1997, see Figure 1 for examples of the stimuli). We hypothesized that the recognition of facial expressions improves as the intensity of the expressions is increased from 50% to 100% and from 100% to 150%. We also hypothesized that a negative shift in ERP activity over lateral temporal scalp regions, starting approximately 200 ms post-stimulus, increases in response to increasing intensity of fearful expressions (Sprengelmeyer and Jentzsch, 2006). The hypotheses were less clear cut regarding the ERPs to increasing intensities of happy expressions. On the one hand, emotion-related brain systems show an opposite pattern of responses to increasing intensities of fear and happiness (Morris et al., 1996), predicting differential patterns of modulations of the scalp recorded ERPs to fearful and happy facial expressions. On the other hand, it is possible that the scalp-recorded ERP negativity reflects a response to emotional salience per se (irrespective of the valence of the expressions) and, hence, responses to varying intensity of fear and happiness conform to a similar pattern. In addition to recording posterior ERP negativity, we examined late positive potential (P300) over central scalp region. Based on previous data (Williams et al., 2006), we predicted that the P300 component is larger for fearful than happy expressions. However, as the sensitivity of this component to emotion intensity has not been examined in previous studies, no specific predictions regarding its sensitivity to fear and happiness intensity were made.

2. Results

2.1. Behavioral Data

Mean percentages of correct responses and RTs to fearful and happy expressions as a function of expression intensity are shown in Figure 2. A 2 (Emotion) × 3 (Intensity) repeated measures analysis of variance (ANOVA) on the percentage of correct responses yielded a significant main effect of expression intensity, $F(2, 36) = 99.7$, $p < .001$, $\eta^2 = .85$. The main effect of intensity resulted from higher percentage of correct responses for prototypical as compared to low-intensity facial expressions, $F(1, 18) = 103.2$, $p < .001$, $\eta^2 = .85$, and for caricatured as compared to prototypical facial expressions, $F(1, 18) = 7.5$, $p < .02$, $\eta^2 = .29$ (see Figure 2). There was no main effect of Emotion or Emotion x Intensity interaction effect on the percentage of correct responses.

Figures 1-2

A main effect of intensity was also observed on RT data, $F(2, 36) = 41.1$, $p < .001$, $\eta^2 = .70$. This main effect reflected faster RTs to prototypical than low-intensity expressions, $F(1, 18) = 44.5$, $p < .001$, $\eta^2 = .71$, and a non-significant trend towards faster RTs to caricatured than prototypical facial expressions, $F(1, 18) = 3.6$, $p = .07$, $\eta^2 = .17$. There was also a significant main effect of emotion, $F(1, 18) = 5.2$, $p < .05$, $\eta^2 = .23$, and a significant Emotion × Intensity interaction, $F(2, 36) = 9.5$, $p < .001$, $\eta^2 = .35$. There was no difference in RTs to fearful and happy facial expressions for the low-intensity expressions, but longer RTs were observed for fearful than happy facial expressions for the prototypical and caricatured expressions, *F*s(1, 18) > 10.2, *p*s < .006, $\eta^2 > .36$.

2.2. ERPs

The low-intensity expressions were not included in the ERP analyses because of the low percentages of correct responses to these expressions (< 55%). The majority (87%) of incorrect responses to the low-intensity facial expressions were missing responses, suggesting that these expressions were not consistently discriminated from neutral no-go expressions. Investigation of ERPs to emotion intensity changes was, therefore, based on comparison of ERPs to prototypical and caricatured facial expressions. For prototypical and caricatured expressions, an average of 14% trials was rejected as incorrect responses or due to containing artefact. There was no significant difference in the rejection rate across conditions, *p* > .60.

Figure 3

2.2.1. Early effects at posterior recording sites

Over occipital-temporal recording sites, all stimuli elicited a positive deflection (P100) at 102 ± 10 ms and a prominent negative deflection (N170) at a mean latency of 160 ± 13 ms (Figure 3). A 2 (Emotion) × 2 (Intensity) × 2 (Hemisphere) ANOVA showed no effects involving factors Emotion or Intensity on the peak amplitude or latency of the P100 component. Also, no main or interaction effects involving Emotion or Intensity were observed on the peak amplitude of the N170 component. A significant Emotion x Intensity interaction was observed on the peak latency of the N170, $F(1, 18) = 7.2$, $p < .03$, $\eta^2 = .29$. Follow-up tests showed that there was no effect of intensity on the peak latency of the N170 for happy expressions, whereas, for fearful expressions, significantly longer N170 peak latencies were observed for caricatured ($M = 164$ ms) relative to prototypical ($M = 159$ ms) fearful expressions, $F(1, 18) = 5.5, p < .05, \eta^2 = .23$.

The first clear amplitude differences for prototypical and caricatured expressions emerged at the trailing slope of the N170 component. A 2 (Emotion) × 2 (Intensity) × 2 (Hemisphere) × 2 (Time: two 50-ms time windows) ANOVA on the mean amplitude of the ERPs from 190 to 290 ms post-stimulus yielded a significant Emotion × Intensity interaction, $F(1, 18) = 7.0$, $p < .02, \eta^2 = .28$. This interaction was broken down by analyzing intensity-effects for fearful and happy expressions separately. A significant effect of Intensity was observed for fearful expressions, $F(1, 18) = 4.7, p < .05, \eta^2 = .21$, reflecting a negative shift in ERP activity for caricatured relative to prototypical fearful expressions (Figure 3). This negative shift lasted approximately 120 ms over the left hemisphere and 200 ms over the right hemisphere. The effect of expression intensity was not significant for happy facial expressions, $p > .10$.

In addition to the effect by expression intensity, significant Emotion × Time, $F(1, 18) = 8.5, p < .01, \eta^2 = .32$, and Emotion × Hemisphere, $F(1, 18) = 11.8, p < .004, \eta^2 = .40$, interactions were observed on the mean amplitude of the ERP activity between 190 and 290 ms after stimulus onset. The Emotion x Time interaction reflected smaller mean ERPs for fearful relative to happy expressions in the 190 to 240 ms time period, $F(1, 18) = 10.4, p < .006, \eta^2 = .37$, but not in the subsequent (240-290 ms time period). The Emotion x Hemisphere interaction, in turn, reflected the fact that the main effect of Emotion was significant over the right, $F(1, 18) = 7.4, p < .02, \eta^2 = .29$, but not over the left hemisphere.

Figure 4

2.2.2. Late positive potential

At Cz, a prominent positive potential was observed for all stimuli (Figure 4). This positivity emerged approximately 300 ms after stimulus onset lasting for several hundred milliseconds. A 2 (Emotion) x 2 (Intensity) x 4 (Time: 50-ms windows) on the mean ERP activity from 400 to 600 ms post-stimulus revealed a significant main effect of Emotion, $F(1, 18) = 9.9$, $p < .007$, $\eta^2 = .36$, and a significant Emotion x Time interaction, $F(3, 54) = 8.1$, $p < .001$, $\eta^2 = .31$. As shown in Figure 4, fearful expressions elicited a larger positivity than did happy expressions. Analyses of Emotion effects within each 50-ms time interval separately revealed that the emotion effects emerged between 450 and 500 ms, $F(1, 18) = 7.5$, $p < .02$, $\eta^2 = .30$, and remained significant for the remaining two time segments, Fs(1, 18) > 12.0, ps <.005, $\eta^2 > .40$. The main effect of Intensity and interactions involving Intensity factor were not significant, ps > .05.

Given the close association of the late positive potential (or P300) and behavioral responses (Nieuwenhuis et al., 2005), it was of interest to examine whether the ERPs to fearful and happy expressions are linked with behavioral RTs to fearful and happy faces. In particular, we were interested in examining whether the size of the P300 enhancement for fearful expressions 450-600 ms post-stimulus (i.e., P300 amplitude for fear minus P300 amplitude for happy within each time window) correlated positively with the RT cost for fearful relative to happy facial expressions (i.e., RT fear minus RT happiness). Correlation coefficients (Spearman's rho) for the three time windows were all positive (.40-.51, ps = 09-.03), indicating that the larger the ERP effect in response to fear, the larger the behavioral delay in responding to fearful relative to happy facial expressions.

3. Discussion

The present results replicated earlier findings in showing that caricaturing facilitates the recognition of emotion form facial expressions (Calder et al., 1997). Specifically, high-intensity expression caricatures were recognized more accurately (and marginally faster) than prototypical expressions. It is plausible that caricaturing increases the salience of the characteristic features of facial expressions and, therefore, heightens the perceived intensity of the expressions (Calder et al., 2000).

The present study sought to test the hypothesis that ERPs over occipital-temporal scalp regions, reflecting activity in cortical higher-level visual areas (Sprengelmeyer and Jentzsch, 2006), are sensitive to the intensity of fearful and happy facial expressions. Previous studies have shown that fearful expressions delay the peak latency of the N170 component (Batty and Taylor, 2003) and elicit a negative shift in ERP activity starting ~200 ms post-stimulus (e.g., Eimer and Kiss, 2007). The present results add to these data by showing that ERPs are also sensitive to the intensity of fearful but not to the intensity of happy expressions. Relative to prototypical expressions of fear, high-intensity expressions of fear elicited a delayed N170 component and a negative shift in ERP activity starting after the N170 component and extending 120 ms over the left temporal region and 200 ms over the right temporal region. A comparison between prototypical and high-intensity happy expressions did not reveal a similar pattern of results (in fact, a positive rather than negative shift of ERP activity for caricatured happy expressions was suggested by the grand average waveforms in Figure 3, but this effect was not significant). Together, these results are consistent with the hypothesis that the ERP effects over occipito-temporal scalp regions (i.e., delayed N170 and ERP negativity 200-300 ms post-stimulus) are generated by a neural system that is sensitive to the intensity of negative emotional expressions rather than expression intensity or salience per se. The amygdala (a structure linked with emotional processing) and higher-level visual areas in the ventral stream (areas associated with face processing and generation of the scalp-recorded ERPs) may form the key components of this interconnected neural system.

In a recent study, Sprengelmeyer and Jentzsch (2006) reported an enhanced occipital-temporal negativity for caricatured compared to prototypical and low-intensity (50%) facial expressions. This negativity started from the peak of the N170 component and was most pronounced 200-600 ms post-stimulus. The negativity in Sprengelmeyer's and Jentzsch's study, hence, started somewhat earlier and lasted longer than the negativity observed in the present and other previous studies comparing response to threat-related and neutral facial expressions (Eimer et al., 2003, Eimer and Kiss, 2007 and Schupp et al., 2004). There are several possible explanations for the discrepancy in the results regarding the time course, including task differences (emotion categorization vs. gender discrimination) and recording technique (average vs. common reference). Sprengelmeyer and Jentzsch (2006) suggested that the enhanced ERP negativity to high-intensity facial expressions in their study reflected a general response to the intensity or salience of facial expressions. It is of note, however, that only negative emotional expressions were used as stimuli in that study. Responses to different negative facial expressions may be, to some extent, indiscriminable but differ sharply from responses to positive facial expressions. Distinction between positive and negative expressions may pose a more fundamental categorization task for the perceiver than discrimination between discrete negative expressions since discrete negative expressions may call for a similar initial response (autonomic activation, flight etc, see Johnston et al., 2001). In light of these considerations and the present data, it seems more plausible that the negative shift in ERP amplitude for high-intensity negative expressions reflect a specific response to the intensity of negative emotions.

The positive component at central sites, reflecting later stages of stimulus processing, did not differentiate between caricatured and prototypical facial expressions. However, consistent with previous studies (Schupp et al., 2004 and Williams et al., 2006) and our hypothesis, this component was larger for fearful than happy expressions. The data also showed that the magnitude of the positivity for fearful relative to happy expressions correlated positively with the RT cost for fearful facial expressions. The enhanced ERPs and delayed RTs may reflect an enhanced allocation of processing resources and more extensive cognitive analysis of negative relative to positive stimuli during late stages of stimulus processing (Leppänen and

Hietanen, 2004, Schupp et al., 2004 and Taylor, 1991). A response to threat-related stimuli may also involve a subtle cognitive form of a freezing response that interferes with generation of an overt response to the stimulus (Fox et al., 2001, Georgiou et al., 2005 and Purcell et al., 1998). An alternative to these affective-motivational explanations is that the enhanced P300 and delayed RTs are affected by differential complexity of fearful and happy expressions (Johnson, 1986). Negative expressions are, for example, more ambiguous than positive expressions because a particular negative expression typically shares features with other negative facial expressions (Johnston et al., 2001). There are, however, other aspects of the present data that speak against the possibility that stimulus ambiguity contributed to the P300 amplitude in a systematic way in this study. Specifically, the behavioral data showed that recognition accuracy improved (and stimulus ambiguity decreased) as the intensity of the expressions was increased from 100% to 150%. Yet, the intensity increases were not associated with systematic decreases in P300 amplitude.

An important question concerns the stimulus features that underlie the differential ERPs to fearful and happy facial expressions. One possibility is that the discrimination is based on some relatively simple facial features that are “diagnostic” for particular categories of facial expressions. Facial expressions of fear are characterized by several appearance changes in the face including wide open eyes, furrowed and raised eyebrows, and stretched mouth (Kohler et al., 2004). There are, however, indications that the eyes may be particularly relevant for discrimination of fearful and non-fearful expressions. The amygdala, for example, is sensitive to the amount of white sclera exposed above and on sides of the dark pupil (Whalen et al., 2004). Future work is required to determine whether the ERP differences between 100% and 150% fearful expressions and between fearful and happy expressions are driven by the differential salience of the eyes in these expressions.

The amplitude of the P100 and N170 components did not vary as a function of the emotional content or intensity of facial expressions. These result are consistent with several earlier findings showing that the early posterior components are not sensitive to facial expressions (Krolak-Salmon et al., 2001 and Schupp et al., 2004). The results are also consistent with a view that the early components (N170) may reflect a global categorization of visual stimuli (e.g., differentiation between face and non-face objects), whereas more fined-grained within-category discriminations between facial expressions emerge only at later stages of processing (cf. Sugase et al., 1999). This view is challenged, however, by recent studies showing expression-related effects on the amplitude of the P100 (Kolassa and Miltner, 2006 and Pourtois et al., 2005) and N170 components (Batty and Taylor, 2003, Caharel et al., 2005, Kolassa and Miltner, 2006, Leppänen et al., 2007 and Stekelenburg and de Gelder, 2004). The critical factors underlying these effects and the discrepancy in results across studies are not known and require further investigation.

In sum, the present data show that ERPs over lateral temporal scalp regions known to be sensitive to threat and safety related facial expressions are sensitive to the increasing intensity of fearful but not happy facial expressions. These findings are consistent with the idea that differences in ERPs may reflect an influence of an underlying (possibly amygdala-centered) system that responds to negative emotions and exerts a modulatory influence on occipital-temporal cortical areas (i.e., areas generating the early ERPs to faces). The present result also show that increased ERPs to fearful relative to happy faces during the late stages of processing (enhanced P300 for fear) are associated with delayed behavioral responses to fearful faces, providing an important link between emotion-expression effects observed at neural and behavioral level.

4. Experimental Procedure

4.1. Participants

The participants were 19 young adults (Mean age = 23 years, range = 21-28; 10 females; 9 males). An informed, written consent was obtained from each participant. One additional participant was tested but was excluded due to excessive artifact. The participants were students at biomedical engineering laboratory course at the Tampere University of Technology.

4.2. Stimuli and Task Procedure

Participants viewed grayscale pictures of mild (50% of a prototypical expression), prototypical (100%), and caricatured (150%) facial expressions of fear and happiness of three male and three female models from Facial Expressions of Emotions – Stimuli and Tests (Young et al., 2002). In addition to fearful and happy expressions, pictures of neutral faces of each model were included from the same stimulus set. The face models (identities) were the same across expression conditions. In the 50% expressions, the original prototypical expressions from the Ekman and Friesen series (100% expressions) have been morphed with a neutral expression in proportion of 50:50 (50% happy, 50% neutral expression) to produce images in which the intensity of the expression is reduced to only half of its original intensity. The exaggerated (150%) expressions have been created by using computer caricaturing tools and neutral faces as a reference norm to increase the intensity of the prototypical expression by 50% (Young et al., 2002). All images were framed by an oval-shaped frame, masking out the models' hair and other non-facial features. Stimulus presentation was controlled by Neuroscan Stimsoftware running on a desktop computer, and the stimuli subtended approximately 8° x 11° when viewed from a distance of 75 cm. Behavioral responses were registered by a NeuroScan Stim response pad.

The stimuli were presented for 500 ms followed by a 1500-ms interstimulus interval. Subjects were asked to identify the emotion signaled by the face (i.e., is it fearful/neutral/happy?), and to press one of the choice buttons by either the left or right hand in the case of fearful or happy faces, and not to respond when a neutral face was presented. Neutral faces were included as no-go signals to avoid the possibility that observers perform the task by classifying the faces as "happy" and "not happy" without necessarily processing the other emotion (i.e., fear) at all. The index fingers of both hands were placed on the leftmost and rightmost choice buttons on the response pad at the beginning of each block, and subjects were asked to react as quickly as possible while avoiding incorrect responses to the best of their ability. The experiment was started with 12 practice trials, followed by 420 test trials: 60 × 2 (emotion) × 3 (intensity), plus 60 neutral faces. All different stimulus types were presented in a random order and the left and right arrangement of the response buttons (i.e., fearful-happy/happy-fearful) was counterbalanced across subjects.

4.3. Acquisition of EEG

Continuous EEG was recorded from selected central (Cz) and lateral temporal (T5/T6) and occipital (O1/OZ/O2) sites using electrodes mounted in an electrode cap (Electrocap), and referenced to nosetip. EEG recordings were confined to the selected scalp sites given the substantial earlier data showing that the electrophysiological effects related to the present interests are observed in these or nearby electrode sites (Eimer and Kiss, 2007, Krolak-Salmon et al., 2001, Schupp et al., 2004 and Sprengelmeyer and Jentzsch, 2006). Vertical (VEOG) and horizontal (HEOG) electro-oculogram was recorded with bipolar channels from sites above and below the midpoint of the left eye and beside the outer canthi of each eye. Mild skin abrasion was used to reduce the electrode impedances below 5kΩ. The EEG was band-pass filtered from 0.1 to 100 Hz and amplified with a gain of 5000 before storing on a computer disk at the sample rate of 500 Hz (Neuroscan/Synamps).

4.4. Data Analyses

Percentages of correct responses and mean RTs were calculated for behavioral responses occurring in a time window extending from 150 to 1200 ms post-stimulus. The EEG signal was digitally filtered off-line using a 30 Hz lowpass filter and segmented to 800-ms periods starting 100 ms prior to stimulus presentation. The segments were baseline-corrected against the mean voltage during the 100-ms prestimulus period. Segments with eye movements and blinks were detected by using ±70 μV thresholds for the EOG channels and rejected from further analyses. Segments with incorrect behavioral response were also excluded from the analyses. Based on the accepted trials, average waveforms for each individual participant in each experimental condition were calculated. To examine emotion-related ERP effects over posterior scalp regions, the peak amplitude and latency of the P100 (80-120 ms) and N170 (120-200 ms) components were determined for occipital (P100) and temporal (N170) electrodes using an automatic peak detection algorithm. In addition, the mean amplitude of the ERP activity beyond the N170 component was calculated starting from the trailing slope of the N170 component (i.e., from 190 ms post-stimulus) and extending to 290 ms post-stimulus in two 50-ms time windows for lateral temporal electrodes (T5/T6). To examine emotion effects during late stages of processing, the mean amplitude of the ERP activity at Cz was determined in 50-ms time windows from 400 to 600 ms post-stimulus. The analysis periods were selected on the basis of visual inspection of grand average waveforms and previous studies examining ERPs to emotional facial expressions (Eimer and Kiss, 2007, Krolak-Salmon et al., 2001, Schupp et al., 2004 and Sprengelmeyer and Jentzsch, 2006). Comparability of emotion expression effects across studies is complicated by the fact that the latency and spatial loci of these effects may depend on the EEG reference (Junghöfer et al., 2006). It is of note, however, that the effects of interest in the present study have been reported in studies using various reference types, including average reference (Schupp et al., 2004 and Sprengelmeyer and Jentzsch, 2006) and conventional references such as linked ears or the nosetip (Eimer and Kiss, 2007, Krolak-Salmon et al., 2001).

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Figure Captions

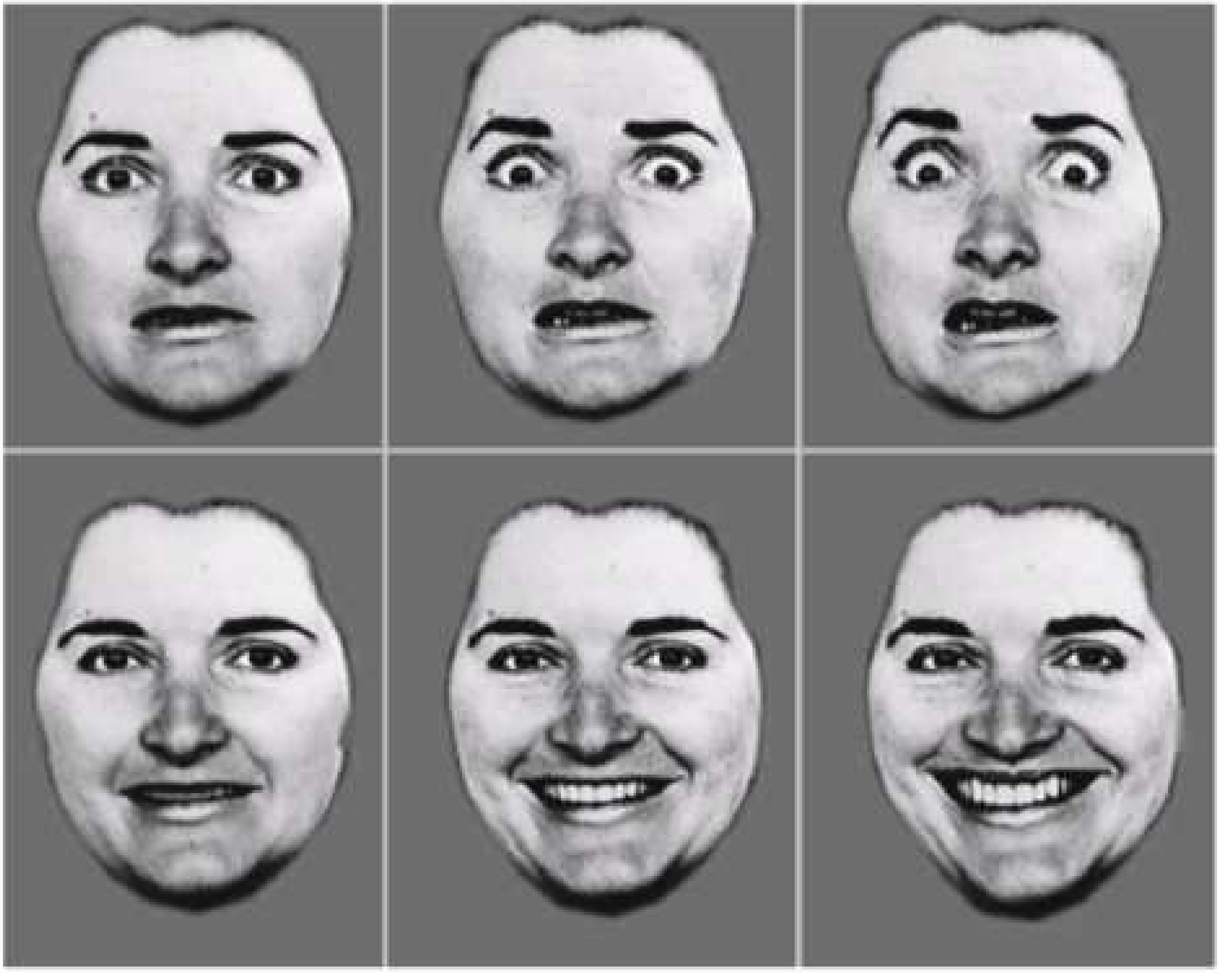
Figure 1. Examples of emotional expressions used in the study. The stimuli varied as a function of emotion (fear/happiness) and expression intensity (50%/100%/150%).

Figure 2. Recognition accuracy (%) and Reaction times (RT) for fearful (closed squares) and happy (open squares) expressions at different levels of expression intensity.

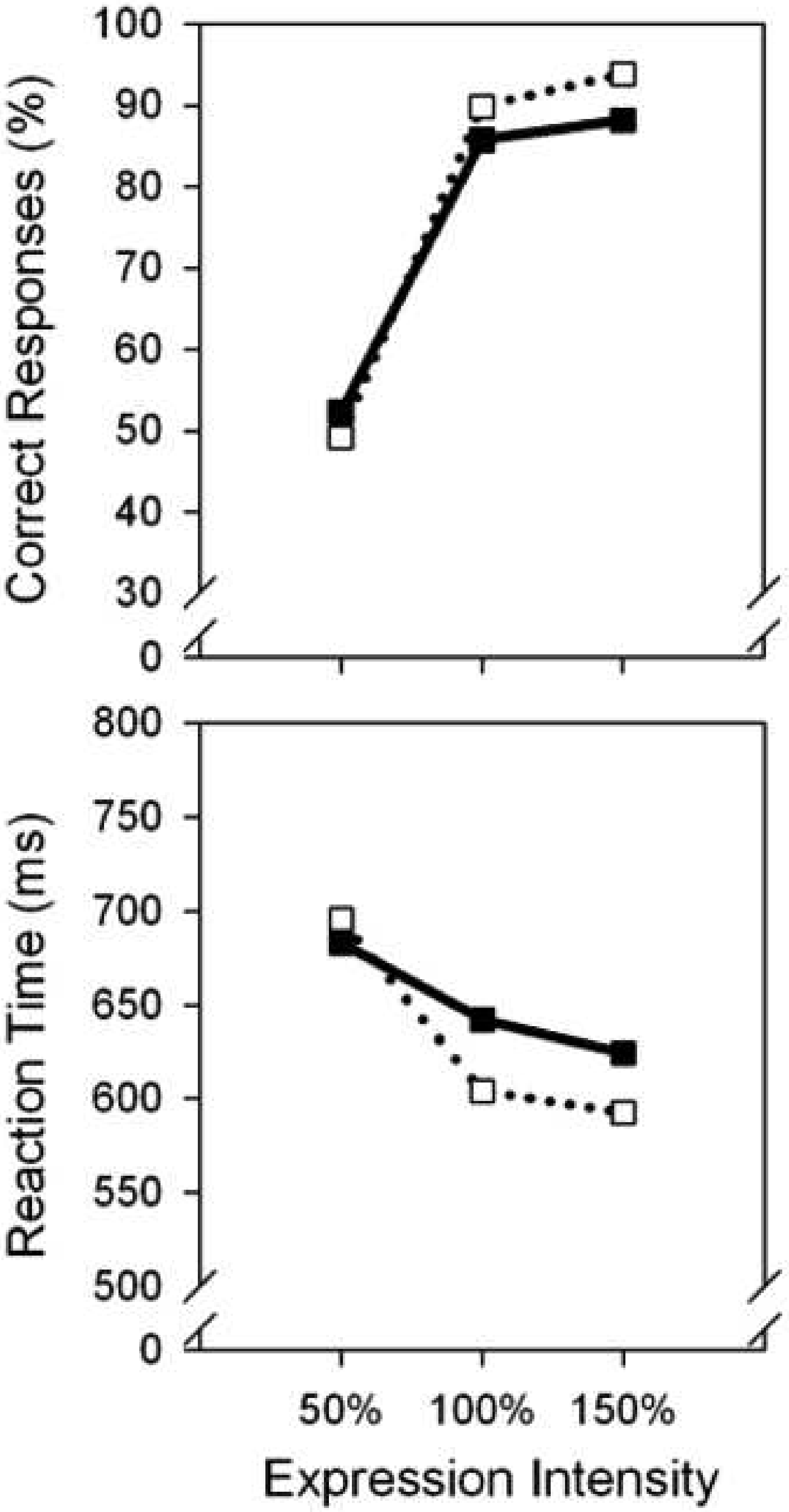
Figure 3. Average ERP waveforms for prototypical (solid line) and caricatured (dotted line) fearful and happy expressions at lateral temporal electrodes. The time windows used to measure early posterior negativity are indicated in grey.

Figure 4. Average ERPs to fearful (solid line) and happy (dotted line) expressions (averaged across intensity) at central (Cz) recording site. The time window used to measure late positive potential is indicated in grey.

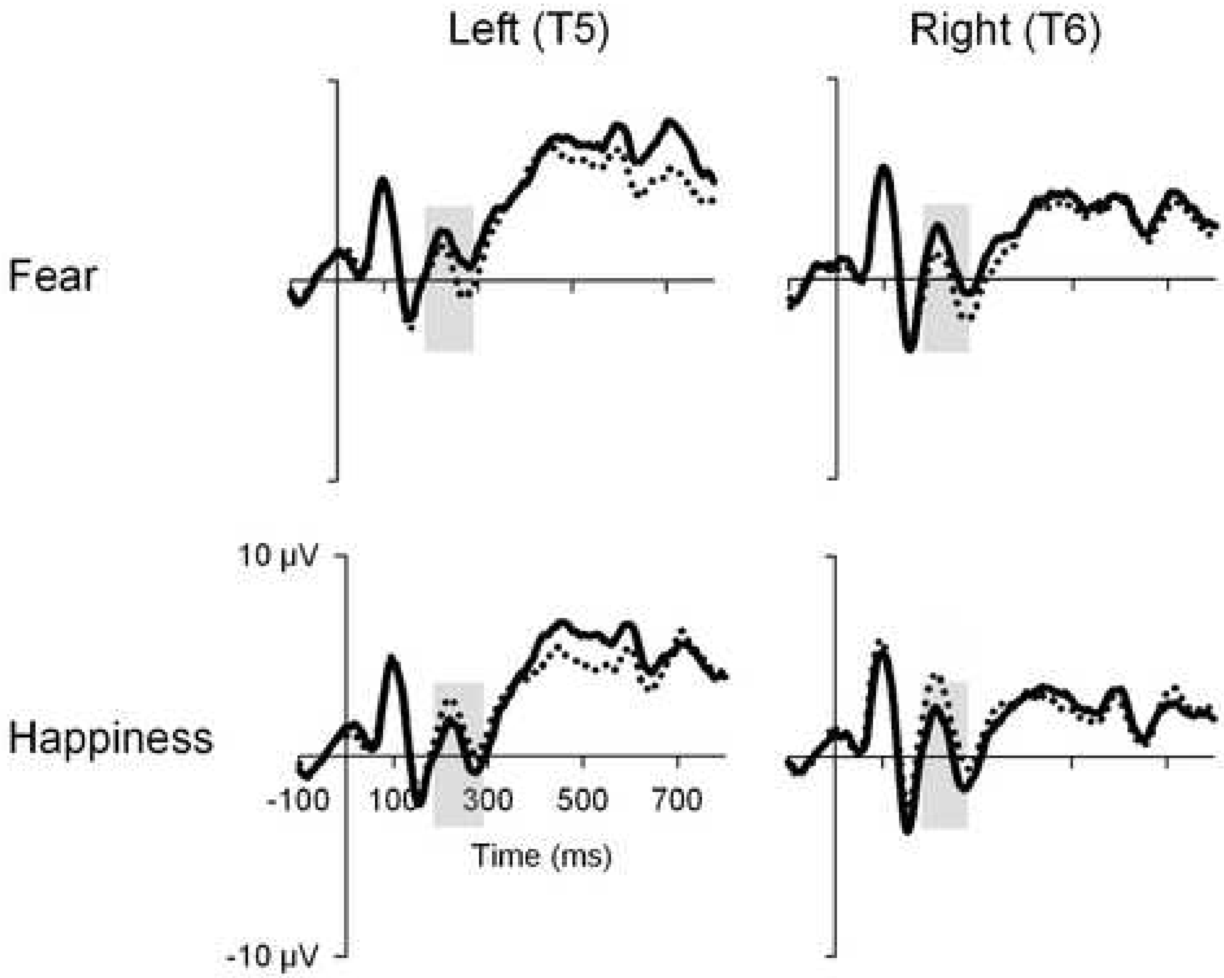
Leppänen et al. Figure 1.



Leppänen et al. Figure 2.



Leppänen et al. Figure 3.



Leppänen et al. Figure 4.