Human brain potentials related to the emotional expression, repetition, and gender of faces

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Event-related potentials were recorded from 20 healthy male subjects in response to a large number of color slides of unfamiliar faces with happy, sad, or no emotional expression. In an initial task, the subjects rated the emotional valence of the faces with a joystick. In comparison with neutral faces, both happy and sad faces evoked a larger lateral occipito-temporal negativity from 200 to 400 msec post-stimulus onset. Modulation of late positive complex (LPC: 450–600 msec) by emotional expressions was observed at the frontal sites only in this task, when attention to the emotional valence was required. In a second task, the subjects detected repeating faces among nonrepeating, novel faces. Emotionally expressive faces evoked more negative potential than neutral faces occipito-temporally between 270 and 540 msec latency. Although repetition had a large effect in decreasing the N4 and increasing the LPC, it did not interact with emotional expression, supporting previously proposed independence between processing of a face identity and emotional expression. These findings imply that emotional expression affects early perceptual stages as well as later cognitive stages of face processing. Nonrepeated male faces in both tasks evoked a larger late negativity than female faces.

A large body of literature concerning perceptive, expressive, physiological, emotional, social, and other aspects of facial communication has emphasized its exceptional importance in social interactions. Moreover, face-selective brain circuitry has apparently evolved as a natural adaptation to accommodate the need to interact quickly and reliably, predating the very recent development of human-specific verbal communication. Convergent evidence points at the basal temporo-occipital cortex (fusiform gyrus), which, as a part of the ventral processing stream, is important in face processing. Patients with lesions in this area are deficient in face recognition and are diagnosed with prosopagnosia (Damasio, Damasio, & Tranel, 1990; Meadows, 1974). Brain imaging techniques such as positron emission tomography and functional magnetic resonance imaging have verified the face-selective activation of this area (Clark et al., 1996; Halgren et al., (1999); Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Shinsuke, & Macdonald, 1992). Finally, studies measuring the electric and magnetic fields generated by the brain have offered a temporal aspect (around 170 msec poststimulus) to the face-specific processing of face stimuli (Allison et al., 1994; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Marinkovic, Raij, Halgren, & Hari, 1995).

Although we obtain a variety of information from the faces of people we encounter, face identity and emotional expression are probably the most salient and important aspects of nonverbal communication in social situations. Existing behavioral data on this issue have resulted in the formulation of a functional model of face processing (Bruce & Young, 1986), proposing that the identity and emotional expression of a face are processed in an independent and parallel manner. Using a pairwise matching task while recording event-related potentials (ERPs), Münte et al. (1998) reported that the processing of identity precedes the processing of emotional expressions by about 250 msec, supporting the hypothesis of independent processing. However, it has also been found with depth EEG that limbic and neocortical areas concerned with the processing of emotions and identity are simultaneously active in response to faces (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Chauvel, 1994). This suggests that contextual integration of different informational aspects of a stimulus such as semantic, mnestic, emotional, and so on, may all occur during the late processing negativity (N4).

The purpose of the present study was to obtain physiological indices of information processing during two conditions in which the emotional expressions of the presented

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faces were either essential to the emotional rating task or incidental to the recognition memory task, respectively. The effects of emotional expression and delayed repetition and their potential interaction on the cerebral stages of face processing in humans were explored with ERPs recorded on the scalp.

Only pictures of individuals previously unknown to the subjects were employed in this study, which prevented any image-laden associations related to familiar faces. Moreover, a large number of photos of different individuals (250 persons across both tasks) ensured that the subjects did not base their responses on a low-level visual pattern recognition. By using photos of different individuals with three different expressions, verbal mnemonic or labeling strategies were minimized and practice effects were controlled.

METHOD

Subjects

Subjects in this study were 20 healthy right-handed male nonsmokers without any medical or alcohol and drug abuse problems. They were between 21 and 28 years old (mean age = 23.5, SD = 2.5). Prospective subjects were recruited from an advertisement in the campus newspaper and from another study. Since some of the subjects subsequently also took part in a longitudinal study investigating effects of alcohol on the brain, females were not employed as subjects because their alcohol absorption and metabolism are altered by the menstrual cycle and oral contraceptives (Zeiner & Kegg, 1981). Signed statements of consent approved by the relevant institutional human subject review boards were obtained from all subjects. Participation was monetarily reimbursed. Physiological data from 18 subjects were available for analyses in each of the two tasks.

Apparatus and Procedure

Recording of ERPs. EEG was recorded with a lycra fitted electrode cap (Electro-Cap International, Inc.) using 13 scalp sites—Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, T5, T6, O1, O2—of the 10–20 international system. A circular neck electrode served as the reference and the right earlobe as ground. The electrooculogram (EOG) was recorded with bipolarly referred electrodes placed at the outer canthus of the right eye and just above the nasion, allowing off-line rejection of trials contaminated by eyeblinks and horizontal eye movements. The electrode impedance was kept below 5 kΩ.

The EEG and EOG were recorded with a Grass 16-channel polygraph with DC amplifiers set at .8-sec time constant and with a bandpass of 0.05–75 Hz (one-half amplitude). EEG and EOG data for each trial were digitized at a rate of 200 Hz (5 msec per point) with 12-bit accuracy and stored on an IBM-PC compatible computer for off-line analysis. A paper output for all channels, including the marker for stimulus onset and offset, was obtained for preliminary visual inspection of the data.

Stimulus presentation. The face stimuli were photographs of previously unfamiliar young adults of European descent without beards or mustaches. Glasses and jewelry were removed, and their hair was pulled back prior to photography. The background was black, and the clothing was obscured by a black drape. Volunteers posed in each photograph as happy, sad, or neutral, according to instructions and after practice. The stimulus set used in this study was selected from a much larger set based on a 95% consistency of emotional expression evaluations performed by 25 independent judges. The faces were presented as color slides on a back projection screen

tachistoscopically for 300 msec each. The images subtended a visual angle of 3.6º horizontal $\times$ 4.6º vertical. Kodak slide projector and Gerbrand shutter were controlled by an Apple IIe computer that also recorded behavioral responses obtained by means of a microswitch and a joystick.

Subjects reclined comfortably in an armchair in an electrically shielded room facing a back-projecting screen at a distance of 1.6 m. They were asked to avoid unnecessary body movements or eyeblinks.

Task description. During the emotional rating task, subjects were presented with 160 slides of unfamiliar faces and were asked to rate the valence and intensity of their emotional expressions with a joystick using their right hands. Emotional expression and gender of the faces in the photos were counterbalanced so that the 120 pictures of different people (half males) were composed of the faces with one third positive (smiling), one third neutral, and one third negative (sad) emotional expression. In addition, pictures of 10 people (to become targets in the second task, recognition memory) were repeated four times each. There was a brief rest midway through the presentation sequence. The slides were presented for 300 msec, with 4,250 msec onset-to-onset interstimulus interval (ISI). After completion of the task, the pictures of the 10 individuals (5 females) that were chosen to be targets were presented again for 1 sec each and the subjects were instructed to memorize them.

During the subsequent recognition memory task, the subjects were required to press a microswitch held in the right hand within 1,200 msec after presentation of a repeating face. One hundred twenty slides of the same 10 repeated target people were randomly interspersed with 120 new, unfamiliar faces (half males). Since the emotional expression was fully crossed with repetition, each of the three emotional expressions was repeated four times for each target face, whereas the new, nonrepeated faces were seen only once in the course of the whole experiment. At 1,200 msec poststimulus, a 55-msec sawtooth feedback tone was presented indicating whether the response (or lack thereof) had been correct (1000 Hz) or incorrect (200 Hz). Stimulus duration was 300 msec and the ISI was 3 sec. Subjects were allowed to take brief rests after 80 and 160 slides.

Repeats and nonrepeats were presented in semirandom order with the following restrictions: No individual could be presented on two successive trials, no more than three repeats or three nonrepeats could follow each other in a row, and each of the 10 targets occurred exactly once in each block of 20 slides. Consequently, the delay between successive presentations of a given face was filled with distractors and had a duration of 6 to 117 sec (average 61.5 sec). No more than five male or five female faces and no more than three faces with the same expression were presented in a row.

Data analysis. All ERP trials on which incorrect responses were made, or on which eyeblinks or other artifacts occurred, were eliminated from the analyses on the basis of an amplitude criterion. Separate average waveforms were obtained for each combination of levels of the repetition and emotional expression factors (e.g., nonrepeat–happy, repeat–happy, nonrepeat–sad, etc.) for all electrode sites for all subjects. The ERPs were quantified by an automatic algorithm measuring average voltages within latency windows encompassing amplitude maxima. All measures were expressed in microvolts (amplitudes) and milliseconds (latencies) with respect to a baseline period of 100 msec before stimulus onset. Prior to amplitude measurements, each subject's average waveforms were smoothed using a low-pass time-based digital filter with a Hamming window (12.1-Hz stop-band, 5.1-Hz transition width). Repeated measures analyses of variance (ANOVAs) were performed on all of the average voltage measures for 18 subjects for each task. In order to provide a conservative protection against the sphericity assumption violations in the repeated measures ANOVA, the probability values were adjusted with the Huynh–Feldt procedure (Huynh & Feldt, 1980). When simple main effects were investigated, the Tukey post

hoc procedure (Woodward, Bonett, & Brecht, 1990) was utilized as a protection against inflated probability values. The corrected p values are reported throughout.

RESULTS

Emotional Rating Task

Behavioral data. Analysis of the ratings of emotional expressions (available for 17 subjects) confirmed that the sad, neutral, and happy expressions were very easily discriminable, as revealed by the main effect of emotion $[F(2,32) = 121.3, p < .001]$. Subjects were faster at rating the repeated ($M = 1,434.2$ msec) than the nonrepeated ($M = 1,482.6$ msec) face stimuli $[F(1,16) = 8.1, p < .05]$. The main effect of emotion on the latency of judgment response $[F(2,32) = 20.02, p < .001]$ suggested that the happy emotional expression was the easiest to classify, since the latency to response was about 100 msec shorter than to sad $[F(1,16) = 25.1, p < .001]$ or neutral $[F(1,16) = 23.9, p < .001]$ expressions.

ERPs. ERP grand averages across all 18 subjects for the nonrepeated faces for the three emotions are presented in Figure 1. The earliest component, N1, peaked at about 110 msec after the picture onset and had the largest amplitude in fronto-central midline and dorsolateral sites. It was much smaller parietally and it seemed to invert in polarity in temporal sites. It was followed by a very prominent component peaking at about 170 msec (P170) that inverted occipito-temporally across the lateral parietal plane. This was followed by a deflection at about 240 msec that

was significantly lateralized at temporal sites with a larger positivity evoked on the right $[F(1,17) = 10.7, p < .05]$. Ensuing negativity spanned about 200 msec and encompassed a fronto-central deflection with a latency of about 430 msec (N4). A large centro-parietal late positive complex (LPC) peaked at about 530 msec. The ERP average amplitude values were analyzed for all 18 subjects with repeated measures ANOVA for the factors of emotion (neutral, happy, sad), gender of the face stimulus (female, male), and electrode sites.

Effects of emotional expression. Inspection of Figure 1 suggests that the earliest differences evoked by emotional face expressions were at the P170 peak at posterior sites. Indeed, a significant emotion $\times$ electrode sites interaction was observed $[F(24,408) = 2.6, p < .01]$ within 150- to 210-msec latency window. Simple comparison Tukey tests revealed a marginally significant difference between the neutral and positive expressions at temporal sites $[F(1,17) = 8.7, p < .1]$. The difference between the neutral and both emotional expressions was significant within the 200- to 400-msec latency frame at occipito-temporal sites $[F(1,17) = 12.6, p < .05]$. Investigation of the subsequent time window (450–600 msec) revealed a significant interaction between emotion and sites $[F(24,408) = 4.8, p < .0001]$. However, the topography of significant potential differences modulated by emotional expressions changed, shifting toward the frontal sites. Happy expressions evoked more positive potentials than the neutral expressions at fronto-central sites $[F(1,17) = 11.4, p < .05]$. In addition, the average potentials tended
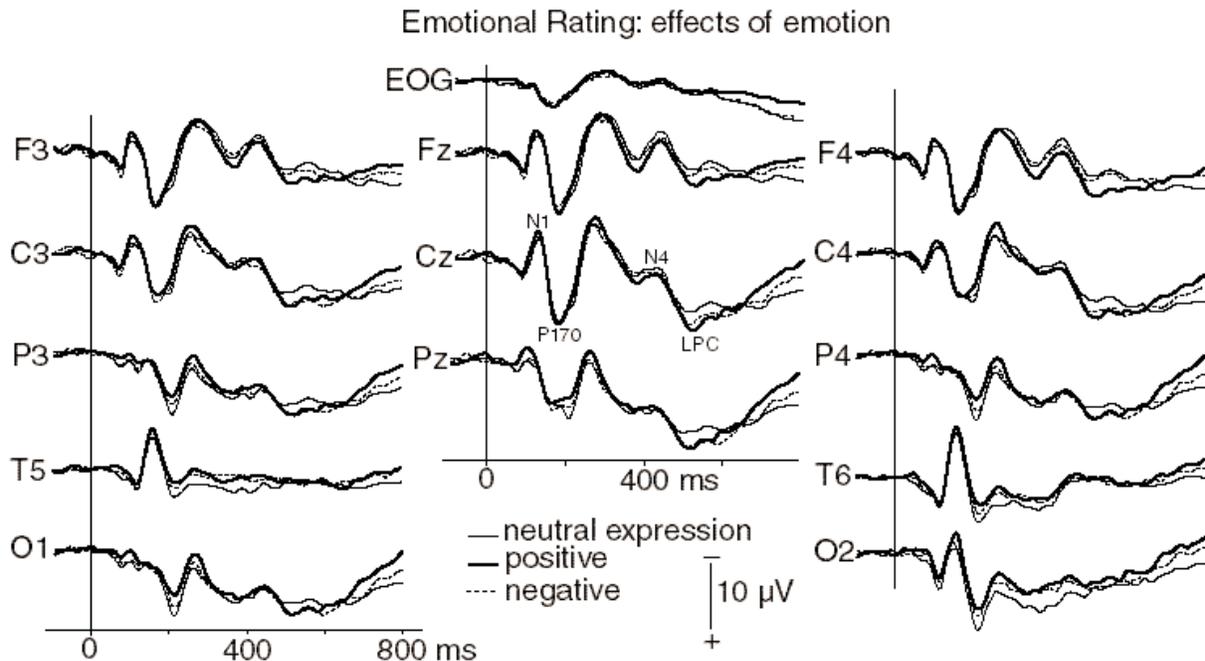

Figure 1. Grand average waveforms for all 13 electrode locations obtained during the emotional rating task. The waveforms were averaged for positive (happy), neutral, and negative (sad) emotional expressions for nonrepeated stimuli. Principal deflections (N1, P170, N4, and LPC) are indicated at Cz. Negative is up.

to be differentiated for positive versus negative facial emotions at frontal sites [$F(1,17) = 6.3, p < .1$]. This differentiation trend of the potentials evoked by the two emotional expressions was observed only within this time interval and in this task.

Effects of gender of the presented face stimuli. The earliest influence of the gender of the presented faces was seen for the P170 peak [gender $\times$ emotion interaction, $F(2,34) = 4.7, p < .05$], with a strong trend for the happy female faces to evoke a larger peak than the happy male faces [$F(1,17) = 9.4, p < .07$]. Within the 400- to 600-msec latency, a main effect of gender [$F(1,17) = 4.5, p < .05$] was obtained, with male faces evoking a more negative potential than female faces (Figure 2a).

Recognition Memory Task

Behavioral data. Average correct discrimination of repeated (target) from nonrepeated faces was well above 95% for all conditions. No reliable effects of emotions on reaction time ($M = 658$ msec) were observed.

ERPs. As indicated by Figure 3, the N1 and P170 peaks were followed by a series of negative peaks superimposed on a longer lasting negativity. They could be observed at most sites, especially frontally, between about 240 to 440 msec. This long-lasting negativity was elicited by new faces and started diverging in frontal sites from the more positive potentials elicited by repeated faces at about 240 msec after stimulus onset. The two waveforms continued in parallel for almost 200 msec and then diverged dramatically particularly in posterior sites. The LPC (530-msec latency) was especially large in response to repeated faces and was much smaller and peaked later in response to new faces. The ERP average amplitude values were analyzed for all 18 subjects with repeated measures ANOVA for the factors of repetition (new, repeated faces) emotion (neutral, happy, sad), and electrode site. Since no interaction between the factors of repetition and emotion was observed in any of the comparisons, their respective effects are presented *seriatim*.

Effects of stimulus repetition. It can be observed in Figure 3 that the earliest effect of repetition was obtained for the large P170 peak (measured within a 160- to 210-msec time window) as a significant interaction between the factors of repetition and sites [$F(12,204) = 4.3, p < .005$]. Although the Tukey post hoc procedure that investigated the repetition effects pooled over the central, parietal, and occipito-temporal areas, respectively, did not unveil any significant localized effects of repetition, a trend was observed over the frontal sites [$F(1,17) = 4.7, p < .1$]. A repetition effect was detected at frontal sites [Tukey $F(1,17) = 9.3, p < .07$] over the subsequent latency window (240–300 msec). The main effect of repetition was consistently obtained for subsequent latencies, but its dominance shifted toward posterior sites at longer latencies, particularly for the large late positivity (LPC) within the 440- to 540-msec latency window [Tukey $F(1,17) = 47.7, p < .001$]. The new–old waveform difference was latest to appear at temporal sites, at about 350 msec.

A deflection at 220 msec observed at temporal sites was more positive on the right than on the left [Tukey $F(1,17) = 10.7, p < .05$]. In addition, a laterality effect was obtained for the target stimuli within 270–540 msec. Since the responses were given with the right hand, this
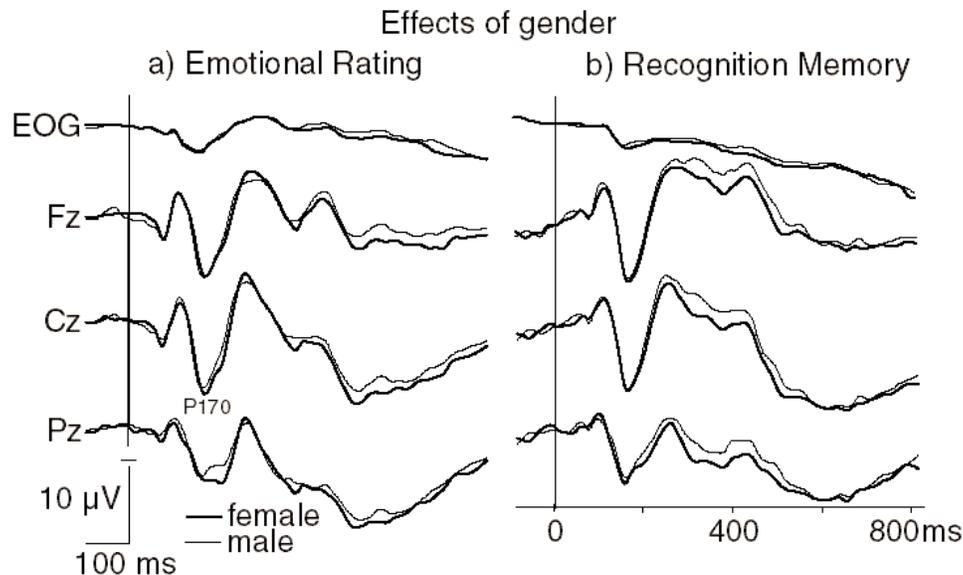
Effects of gender

Figure 2. Grand average waveforms obtained at Fz, Cz, and Pz during the emotional rating (a) and recognition memory tasks (b). The waveforms were averaged for female and male faces for nonrepeated stimuli. The P170 deflection is indicated at Cz. Negative is up.
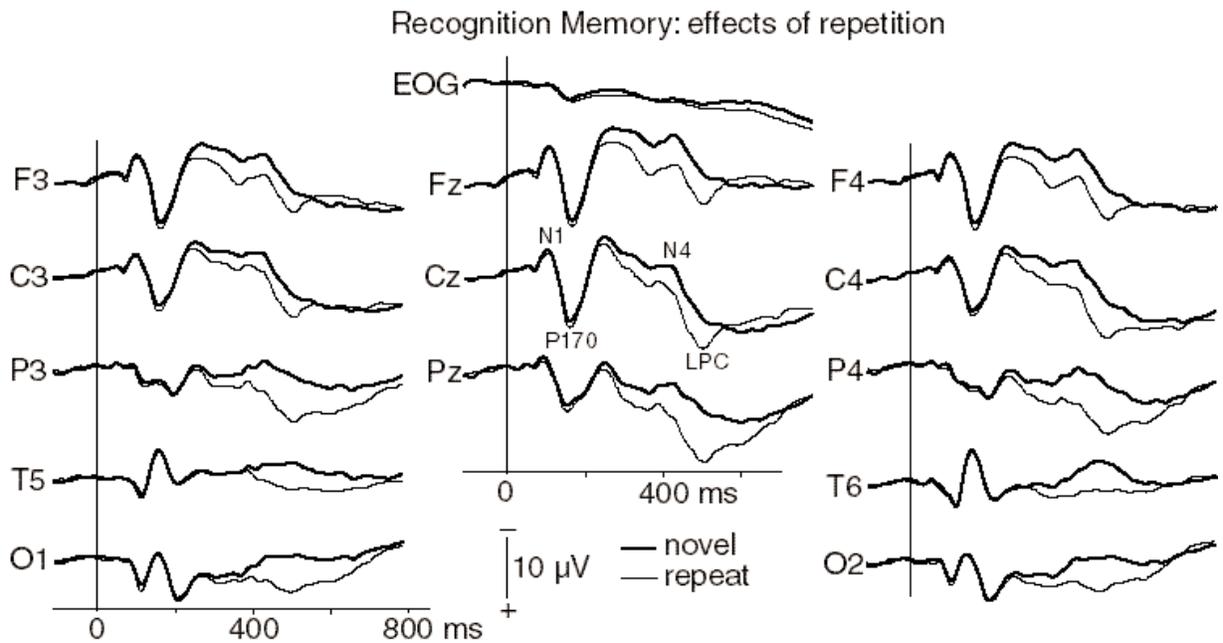
Recognition Memory: effects of repetition

Figure 3. Grand average waveforms for all 13 electrode locations obtained during the recognition memory task. The waveforms were averaged for repeated and novel stimuli, summing across all three emotional expressions. Principal deflections (N1, P170, N4, and LPC) are indicated at Cz. Negative is up.

laterality was most likely due to a larger negativity preceding the motor response (a lateralized readiness potential) that was evoked by the repeated faces over the left fronto-central scalp [Tukey $F = 34.2, p < .001$].

Effects of emotional expression. As can be seen in Figure 4, the main effect of emotion was observed for

the long negativity between 270- and 540-msec latency [$F(2,34) = 3.72, p < .05$]. Emotionally expressive faces tended to evoke more negative potential than neutral faces [$F(1,17) = 8.9, p < .1$], particularly at occipito-temporal sites. The same pattern was observed for the late positive deflection (580–660 msec), with the significant emotion $\times$
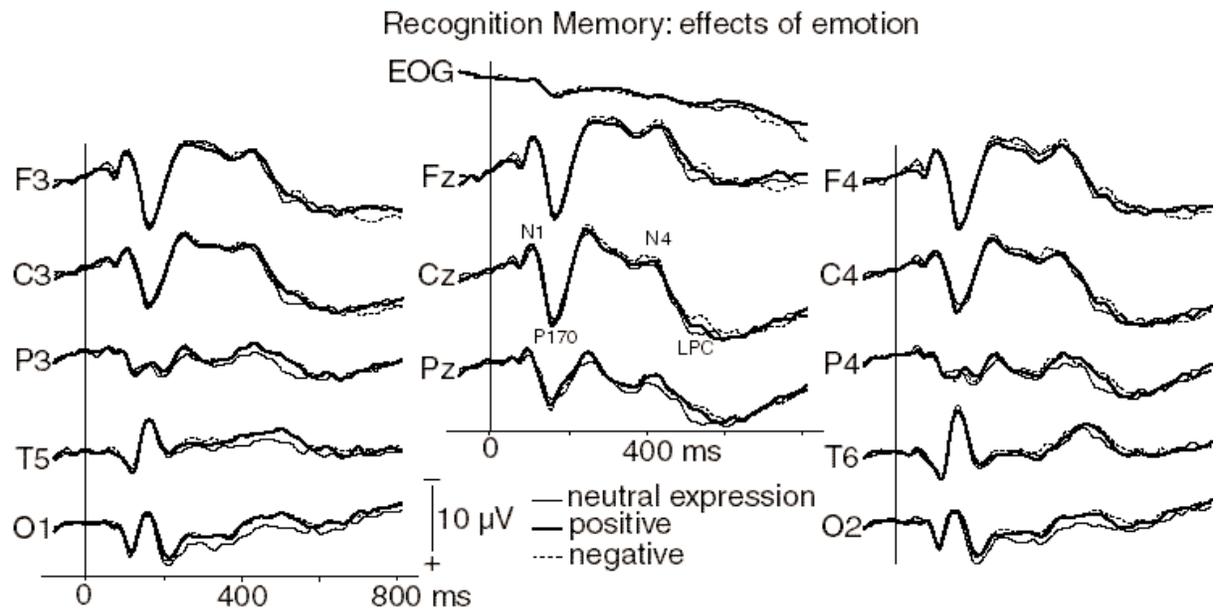
Recognition Memory: effects of emotion

Figure 4. Grand average waveforms for all 13 electrode locations obtained during the recognition memory task. The waveforms were averaged for positive (happy), neutral, and negative (sad) emotional expressions for nonrepeated stimuli. Principal deflections are indicated at Cz. Negative is up.

site interaction [$F(24,408) = 2.6, p < .05$] and with the trend of the emotional faces to evoke more negative potentials than the emotional faces [$F(1,17) = 5.0, p < .1$].

Effects of the gender of the face stimuli. Since half of the faces presented in this task were male and the other half female, it was possible to investigate the modulation of ERPs by gender of the presented faces. Unfortunately, the total number of the stimuli presented in both tasks was insufficient for testing the repetition × emotion × gender interactions. Instead, two-way interactions between the factors of repetition and gender and emotion and gender were tested separately.

As indicated by Figure 2b, a significant gender × repetition interaction [$F(1,17) = 5.0, p < .05$] within the 270- to 480-msec latency window indicated that the more negative potential evoked by male faces was significant for the new [$F(1,17) = 10.4, p < .05$] but not for the repeated faces. In addition, a gender × emotion interaction [$F(2,34) = 4.03, p < .05$] for the same latency frame suggested that the male sad faces evoked a more negative deflection than did the female sad faces [$F(1,17) = 9.4, p < .07$].

DISCUSSION

Faces evoked very similar ERP waveforms in both tasks, emotional rating and recognition memory. The earliest component, N1 (about 110-msec latency) was not reliably affected by any of the variables in this study. It was followed by a large and extrusive component (P170) that inverted occipito-temporally across the lateral parietal plane. This face-selective deflection was modulated by the emotional expressions, repetition, and gender of the presented faces. It was followed by a long-lasting negativity that, starting at about 240 msec, reflected a fronto-central difference between the novel and the repeated target faces. At about the same latency, a difference between the neutral and both emotional expressions was observed in posterior sites. The LPC (530 msec) tended to differentiate between the happy and sad expressions fronto-centrally only during the emotional rating task. During the recognition memory task, the LPC was much larger to the target faces over posterior sites.

Independence of Repetition and Emotion

In the present study, no interaction between the factors of face repetition (i.e., recognition memory) and emotional expression was obtained, suggesting independent physiological processing of face identity and emotional expression. This finding confirms previous evidence obtained from patients with brain lesions that selectively impaired face recognition versus perception of emotional expressions (Cicone, Wapner, & Gardner, 1980; Kolb, Milner, & Taylor, 1983). A double dissociation between the two functions has been demonstrated in prosopagnosic patients with preserved recognition of emotional expression (Bruyer et al., 1983; Tranel, Damasio, & Damasio, 1988) and those who are unable to recognize facial expres-

sion after regaining the ability to recognize faces (Kurucz & Feldmar, 1979). Similarly, behavioral studies of normal subjects suggest independence between identity and expression processing functions (Bruce, 1986; Etcoff, 1984), which has also led to a proposition of independent and parallel processing of face identity and emotion within a functional model encompassing various aspects of face perception (Bruce & Young, 1986). Results from the present study support such a proposal and suggest that the processing of face identity and emotion are independent processes and are possibly subserved by separate physiological mechanisms. Indeed, single-unit recordings in monkeys suggest that identity-responsive neurons are primarily located in the inferior temporal area, whereas expression-responsive neurons are found in superior temporal sulcus (Hasselmo, Rolls, & Baylis, 1989).

Effects of Emotion

Emotional expressions of the presented faces were task relevant during the emotional rating task, since the subjects were instructed to rate their emotional valence. Although all three expressions (happy, neutral, and sad) were easily and consistently recognized, the rating decisions were the fastest for the happy expressions, confirming other similar evidence (Hugdahl, Iversen, & Johnsen, 1993; Kirouac & Dore, 1983). Instructions to attend to the emotional expressions resulted in significantly different ERPs evoked by neutral and both emotional expressions at occipito-temporal sites 200–400 msec after stimulus onset. The LPC (450–600 msec), however, was more negative to neutral than to positive faces frontally, where it tended to show positive versus negative expression differentiation. These results are in overall agreement with the results obtained by Vanderploeg, Brown, and Marsh (1987) in their emotional expression rating task. In spite of large differences in the stimulus sets between the two studies (6 simple line drawings of faces in Vanderploeg et al. vs. 130 photos of the faces of different individuals in the present study), Vanderploeg et al. observed that both emotional stimuli evoked more negative amplitudes within 230–420 msec than did neutrally rated stimuli. This was specific for faces but not words. Moreover, within 500- to 624-msec latency, emotionally expressive face drawings evoked more positive potentials than those rated as neutral.

Emotional expressions of the presented faces were incidental to those in the face recognition task, since the subjects were asked to press a button to all repeated (target) faces. As in the preceding rating task, which explicitly required subjects to attend to the emotional expressions of the presented faces, both emotional expressions evoked more negative ERP potentials than did neutral faces within the 270- to 540-msec latency window occipito-temporally. This difference continued as a trend during the late positivity (580–660 msec).

Although comparable effects of emotion were obtained over posterior sites regardless of whether attention to face expression was essential or incidental to the task, the

emotion-related differences were more substantial during the emotional rating task. Emotional expressions modulated a P170 deflection, which has been shown to be sensitive to the "faceness" of a stimulus with scalp recordings (Bötzel & Grüsser, 1989; Jeffreys, 1989), with intracranial electrodes in humans (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994), and with magnetoencephalography (Marinkovic et al., 1995). These findings imply that emotional expression affects early perceptual stages as well as later cognitive stages of face processing. On the basis of results from their face identity and expression matching task, Münte et al. (1998) suggested that the processing of expressions occurs much later in time (at about 450 msec) than the identity matching (at about 200 msec). Although this may be true for a memory-dependent matching task, our data suggest that the emotional expressions are differentiated much earlier—starting at about 170 msec, during the processing of face-specific material that requires no involvement of primary memory. Since it has been suggested that the most salient aspects of face recognition such as identity or expression are processed in parallel (Bruce & Young, 1986), it is also plausible that they are processed not once, but multiple times, depending on the contextual task demands.

The responsivity of the posterior cortex to emotional valence observed in this study does not seem to be limited to face expressions. Johnston, Burleson, and Miller (1987) also observed a difference in LPC at Pz evoked by positively and negatively rated pictures as opposed to those evoked by neutral pictures. Using functional magnetic resonance imaging, Lang et al. (1998) recorded a greater activity to both pleasant and unpleasant pictures than to the pictures with neutral valence in posterior cortex. Similarly, posterior cortex was activated bilaterally by film-generated emotion in positron emission tomography studies (Reiman et al., 1997). Moreover, a bilateral parieto-occipital activation has been observed when subjects attended to spatial aspects and not emotional responses to pictures (Lane, Fink, Chau, & Dolan, 1997). This evidence corroborates the postulate of parallel and independent processing of face identity and face emotional expression (Bruce & Young, 1986), which could perhaps be extended to other types of emotional stimuli as well.

In contrast to the emotional rating task, no significant effects of emotional expression at frontal electrodes were observed during the recognition task. Only when expression was task relevant were distinct late frontal potentials (450–600 msec) evoked by neutral and positive expressions. Moreover, they tended to differentiate between the positive and negative emotional expressions. Brain imaging studies using positron emission tomography suggest that the frontal regions are active during tasks that require attention to emotional valence of the stimuli or the subjects' own emotional states. Lane, Fink, et al. (1997) observed an increase in activity in anterior cingulate gyrus when subjects attended to their own emotional states in response to emotionally laden pictures. Medial prefrontal cortex was activated during emotional states

evoked by both films, as well as by recall of emotional events (Reiman et al., 1997). Furthermore, substantiating the trend observed in the present study, happiness and sadness were differentiated by greater activation of mesial frontal cortex and anterior insula, respectively, in the emotional induction paradigm (Lane, Reiman, Ahern, Schwartz, & Davidson, 1997). This evidence suggests that involvement of prefrontal cortex in emotional perception or emotion generation may be independent of particular stimulus characteristics.

Most studies using the divided visual field technique found an overall right hemisphere advantage for both face identity and expression tasks as measured by reaction speed (Ley & Strauss, 1986; cf. Sergent, 1986). No indication of an emotion-modulated hemispheric asymmetry for either task was found in this study, confirming bilateral activation in response to emotional states observed in recent brain imaging studies (Reiman et al., 1997). However, an overall occipito-temporal right > left laterality observed in this study is in agreement with right hemisphere preponderance for the processing of face stimuli observed in lesion (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1996), MEG (Marinkovic et al., 1995; Sams, Hietanen, Hari, Ilmoniemi, & Lounasmaa, 1997), and PET and fMRI studies (Clark et al., 1996; Sergent et al., 1992).

Repetition Effects

Nonrepeated faces evoked more negative potentials starting at about 160 msec and continuing through the N4 and LPC time windows. The earliest reliable repetition effects were observed over the frontal regions starting at about 240 msec, followed by large repeat–nonrepeat differences shifting in distribution toward posterior sites at longer latencies. Similar distribution changes have been obtained in immediate repetition priming or identity matching paradigms (Barrett, Rugg, & Perrett, 1988; Münte et al., 1998), although Hertz, Porjesz, Begleiter, and Chorlian (1994) have reported an early priming effect with a right occipito-temporal maximum in an immediate matching task. At longer latency, large distributed negativity to nonrepeating faces (N4) seen in the present study has also been observed in other studies using faces (Barrett & Rugg, 1989; Smith & Halgren, 1987) or other types of meaningful, semantic material (Ganis, Kutas, & Sereno, 1996; Kutas & Van Petten, 1988). It has been suggested that the bilaterally distributed N4-like negativity elicited by the nonmatching or novel stimuli results from the difficulty of contextual integration (Halgren, 1990; Rugg, 1990) for both linguistic and nonverbal material alike, based on its decrease with repetition, semantic, or association priming. In contrast, the early priming effects have previously been observed only with immediate repetition of face stimuli, and thus could be associated with maintenance of the stimulus in active (primary, working, or iconic) memory (Barrett et al., 1988; Münte et al., 1998). In the present study, early priming effects were observed despite an average of about 60 sec and 20 stim-

uli intervening between repetitions of a given face. Furthermore, the number of faces to be remembered (10, each with three different expressions) reached the upper limit or exceeded the capacity of the working memory buffer, even if it could span the long delay and multiple similar distracting stimuli. Thus, the early repetition-related effects reported here do not appear to have resulted from active memory. It is possible that they reflect a facilitated access of the repeated face stimuli to contextual integration (Barrett & Rugg, 1989).

Effects of Gender

Observed effects of the gender of the presented face should be taken as preliminary findings since gender was incidental to both tasks. More importantly, a complete analysis of gender-related effects will be obtained only when both female and male subjects view faces of both genders. Overall, in comparison with female faces, male faces had a greater effect on the ERPs recorded from the male subjects in the present study. During the emotional rating task, happy male faces evoked a smaller P170 peak than did female faces. Within the 400–600 latency, nonrepeated male faces evoked more negative potentials than did female faces. Similarly, during the recognition task, nonrepeated male faces evoked a more negative deflection within 270–480 msec. Finally, pictures of males with sad expressions evoked a larger negativity than did the pictures of females. Although male faces evoked more negative potentials than female faces in both tasks, latency differences suggest that different deflections were affected in each of the two tasks. This may indicate that salient face attributes, including identity, expression, and gender, are processed at different times and exert their contributions at multiple points, depending on the instructional context. Although no ERP studies bearing on the gender issue have been reported, larger skin conductance responses to male stimulus faces have been previously observed (Donovan & Leavitt, 1980; Mazurski, Bond, Siddle, & Lovibond, 1996), with heart rate responses differing particularly for the male subjects that viewed pictures of male faces (Donovan & Leavitt, 1980).

In sum, emotional expressions affected the early (P170) face-selective deflection during the emotional rating task. They affected the posteriorly recorded ERPs in a comparable manner during the emotional rating and recognition memory tasks, with both emotional faces evoking a more negative potential than did faces with neutral expressions. These effects were more pronounced, however, and an expression-related modulation of late positivity was observed at frontal sites only during the first task, when attention to the emotional valence was explicitly required. These results suggest that emotional expression affects early perceptual stages as well as later cognitive stages of face processing. Following the early frontal effects of stimulus repetition were more negative potentials to nonrepeated faces (N4), comparable to those observed before with faces, as well as other semantic material. No interaction between the stimulus repetition and emotional expression was ever observed, confirming

functional models (Bruce & Young, 1986) proposing that processing of face identity and face expressions occurs independently and that they may be subserved by different neurophysiological substrates.

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