Categorical Perception of Happiness and Fear Facial Expressions: An ERP Study

S. Campanella, P. Quinet, R. Bruyer, M. Crommelinck, and J.-M. Guerit

Abstract

■ Behavioral studies have shown that two different morphed faces perceived as reflecting the same emotional expression are harder to discriminate than two faces considered as two different ones. This advantage of between-categorical differences compared with within-categorical ones is classically referred as the *categorical perception effect.*

The temporal course of this effect on fear and happiness facial expressions has been explored through event-related potentials (ERPs). Three kinds of pairs were presented in a delayed same–different matching task: (1) two different morphed faces perceived as the same emotional expression (within-categorical differences), (2) two other ones reflecting two different emotions (between-categorical differences), and (3) two identical morphed faces (same faces for methodological purpose).

Following the second face onset in the pair, the amplitude of the bilateral occipito-temporal negativities (N170) and of the vertex positive potential (P150 or VPP) was reduced for within and same pairs relative to between pairs. This suggests a repetition priming effect. We also observed a modulation of the P3b wave, as the amplitude of the responses for the between pairs was higher than for the within and same pairs. These results indicate that the categorical perception of human facial emotional expressions has a perceptual origin in the bilateral occipito-temporal regions, while typical prior studies found emotion-modulated ERP components considerably later. ■

INTRODUCTION

Categorical Perception of Facial Emotional Expressions

The environment provides a large amount of sensory inputs, which the human brain cannot exhaustively process. One strategy to simplify our perception of events is to categorize stimuli. This process reflects the ability to put into discrete categories different stimuli sharing some common properties (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). The perception of colors illustrates the categorization process along a natural physical continuum. A continuous range of light frequencies represents the color spectrum. Nevertheless, we perceive chunks of colors rather than a gradual continuum of color change. Categorization reflects a process by which linear physical changes of a stimulus have nonlinear perceptual effects. Moreover, it appears that two colors straddling a category boundary (green–yellow) are easier to discriminate than two colors stemming from the same category (green–green), even though physical differences in wavelength are identical within both pairs (Bornstein & Korda, 1984). This phenomenon, which consists in enhancing ''between-category'' differences while ''within-category'' differences are reduced, is known as the *categorical perception effect* (Harnad, 1987).

This effect was initially observed on unidimensional stimuli, such as speech sounds and color perception (Bornstein & Korda, 1984; Liberman, Harris, Hoffman, & Griffith, 1957). Even if humans are confronted with physical linear changes, they perceive both phonemes and hues categorically. Accordingly, a physical change in a stimulus is taken into account when it occurs at the boundary between two categories and neglected within a given category. Recently, developments in computer graphics have made it possible to explore categorical perception effects with multidimensional stimuli, such as faces.

Facial expressions constitute an excellent way to explore the categorical perception with multidimensional stimuli (Calder, Young, Perrett, Etcoff, & Rowland, 1996). First, people are very skilled at understanding other's facial expressions: Even babies precociously respond to different facial expressions (Field, Woodson, Greenberg, & Cohen, 1982). Second, it is nowadays largely accepted that some configurations of facial features, resulting from specific patterns of facial muscle movements, are perceived throughout the world as corresponding to particular basic emotions (Ekman, 1992, 1994). Moreover, people with Möbius syndrome, a congenital disorder producing facial paralysis, are able

Université Catholique de Louvain, Belgium

to recognize facial expressions. Thus, the ability to produce facial expressions is not a necessary prerequisite of their recognition (Calder, Keane, Cole, Campbell, & Young, 2000). Third, in vivo fundamental work including nonhuman primates has significantly improved the understanding of the neural substrates of facial emotion perception (see Rolls, 1994 for review). Neurons specifically responsive to facial expressions were found primarily in the cortex of the superior temporal sulcus (STS) of the macaque monkey (Hasselmo, Rolls, & Baylis, 1989), while neurons responsive to identity were found in the inferior temporal gyrus (Young & Yamane, 1992). Some of these neurons may be involved in social interactions, as outputs from the temporal cortical visual areas reach the amygdala and the orbitofrontal cortex, these areas being involved in social and emotional responses to faces (Rolls, 1992a, 1992b). Damage to this neural population may contribute to deficits in social behavior, which are part of the Kluver–Bucy syndrome provoked by temporal lobe damage in monkeys (Leonard, Rolls, Wilson, & Baylis, 1985). Fourth, studies of patients with lesions affecting face perception have demonstrated important correspondences with the findings on animals. Selective impairments in the recognition of facial expressions, sparing the ability to recognize identity, can occur after right temporoparietal lesions (Bowers, Bauer, Coslett, & Heilman, 1985). In keeping with this, experimental studies on normal subjects showed that, when they were asked to make quick judgments of emotional expressions, reaction times were equal for familiar and unfamiliar faces (Bruce, 1988). Experiments with positron emission tomography (PET) and with functional magnetic resonance imagery technique (fMRI) have also shown the activation of different brain areas during the perception of facial identity (Sergent, Otha, McDonald, & Zuck, 1994) and emotion (Philipps et al., 1998). These results strengthened the hypothesis that functionally independent processes mediate facial identity and facial emotion (Schweinberger, Burton, & Kelly, 1999; Bruce & Young, 1986). Moreover, selective impairments of specific emotions have been evidenced in Huntington's disease (Sprengelmeyer et al., 1997) and different cerebral networks are thought to be implied in the recognition of different expressions (Adolphs, Damasio, Tranel, & Damasio, 1996).

The investigation of categorical perception of facial expressions turns out to be of the greatest conceptual relevance, as we know little about the perceptual representation of facial affect, and the mechanisms used to decode it (Calder et al., 2000). One of the fundamental issues that is still discussed concerns whether facial expressions are perceived as varying continuously along underlying dimensions or as belonging to qualitatively discrete categories, as one might use existing theories to argue either way (Calder et al., 1996). Indeed, the idea of basic universally recognized emotions would suggest categorical perception, whereas dimensional accounts would not.

Etcoff and Magee (1992) carried out the first study on categorical perception of facial expressions. They converted photographs from the Ekman and Friesen (1976) series of pictures of facial affect into line drawings and used a computer program to generate drawings of equal interpolated steps between two different facial expressions posed by the same individual. These authors used a two-step procedure. First, subjects were confronted with an identification task, during which they had to categorize all the randomly interpolated faces falling along a particular expression continuum (e.g., from happiness to fear). Although the expression information was linearly manipulated, sharp boundaries appeared in the subjects' responses between regions of each continuum perceived as corresponding to one expression and a region corresponding to the other expression. Second, subjects were confronted with an ABX discrimination task, during which two drawings (A,B) were successively presented, followed by a third one (X). Subjects had to decide whether X was the same as A or B. Results showed that they discriminated more easily two pairs of drawings crossing a subjective category boundary (such as a drawing seen as happy in the identification task and one seen as fearful) as compared to pairs of drawings separated by an equal physical distance but laying within a category (e.g., two drawings identified as happy). This clearly demonstrated a categorical perception of facial expressions. By using photograph-quality morphed images of expression continua, Young et al. (1997) and Calder et al. (1996) replicated Etcoff and Magee's (1992) findings in that field.

These results lead to two main considerations. First, the categorical perception effect needs two stages to be assessed: (1) an identification task, showing nonlinear responses to linearly manipulated stimuli and allowing to define boundaries within each continuum, and (2) a discrimination task, defining the hallmark of categorical perception effect and which has to evidence an enhanced discriminability for between- (as compared to within-) categorical differences (Campanella et al., 2000; Campanella, Chrysochoos, & Bruyer, 2001). Second, findings of categorical perception of facial expressions were inconsistent concerning the emotion perception in terms of a two-dimensional model (such as pleasant–unpleasant and rejection–attention; e.g., Woodworth & Schlosberg, 1954) but provided strong evidence that facial expressions are perceived as belonging to discrete categories (Young et al., 1997).

The Current Study: Goals, Rationale, and Working Hypotheses

The above review shows behavioral evidence for a better discriminability for two morphed faces showing two different expressions than for two morphed faces show-

ing the same one (even if the physical distance inside each pair is identical). It is therefore a challenge for psychophysiologists to capture this phenomenon in order to find the temporal course and the neurophysiological correlates of the different steps implied in this categorical perception effect. Due to its better temporal resolution (as compared to PET or fMRI), event-related potentials (ERPs) were used in the current study to assess where and mainly when does the categorical perception of facial emotional expressions occur. Indeed, ERPs allow us to investigate the temporal course and the various stages of face processing. Moreover, when reviewing the psychological and electrophysiological literature on emotions, a discrepancy emerges. In fact, if behavioral studies have demonstrated that emotions are extracted preattentively and influence subsequent perception (Murphy & Zajonc, 1993; Kunst-Wilson & Zajonc, 1980), only one study (Pizzagalli, Regard, & Lehmann, 1999) has found neurophysiological correlates for these processes. Pizzagalli et al. (1999) showed that personal affective judgments of face images significantly modulated ERP responses at early stages, 80–116 msec after right hemisphere stimulation and 104–160 msec after left stimulation. However, prior studies found emotion-modulated ERP components considerably later, typically between 250 and 600 msec (Münte et al., 1998). Subjects of Potter and Parker (1989) had to decide whether the second face of a pair matched the first one in terms of expression. The ERPs showed a later difference in the 490–540-msec time range, only for a right parietal site. Accordingly, Hautecoeur et al. (1993) showed a modulation of a parietal P400 when subjects were asked to look for emotional expression of the face (smiling or nonsmiling) in comparison with a recognition task (known or unknown). More surprisingly, several studies limited a priori their analyses to the P300 component by investigating emotional processing using oddball paradigms (e.g., Oroczo & Ehlers, 1998). Finally, by using intracranial recordings, Halgren and Marinkovic (1995) showed that significant differentiation among waveforms evoked by different facial emotions appears frontocentrally in the 400–600-msec latency range.

In the present study, we created continua of morphed faces moving from one expression to the other (e.g., identity A ''happy'' to identity ''A'' fearful). Subjects were then confronted with three kinds of pairs of morphed faces: the between pairs (a face perceived as happy and the other one as fearful); the within pairs (two morphed faces perceived as happy or as fearful); and the same pairs (two identical faces) (Figure 1). Faces of within and between pairs are always separated by a physical distance of 30%. The participants had to decide as quickly and as accurately as possible whether the second face of the pair was exactly the same as the first one (delayed same–different matching task).

First, we hypothesize that this method will (behaviorally) replicate the categorical perception effect of facial expressions. Second, we assume that the categorical perception effect of happiness and fear facial expressions involves an early modulation of visual extrastriate areas. Indeed, Dehaene-Lambertz and Dehaene (1994) have demonstrated in 2-month-old infants that categorical perception of speech began at 220 msec following the stimulus onset. More recently, we showed (Campanella et al., 2000) the perceptual origin of the categorical perception effect of familiar facial identities, as suggested by the modulation of the N170, a negative occipito-temporal component maximally recorded in response to faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bentin & Deouell, 2000), probably generated from posterior temporal lobes (Taylor, McCarthy, Saliba, & Degiovanni, 1999) and functionally referred to the configurational analysis of faces (Jeffreys, 1996). Here, a similar observation would thus involve an early modulation of the N170 face-specific neural processing.

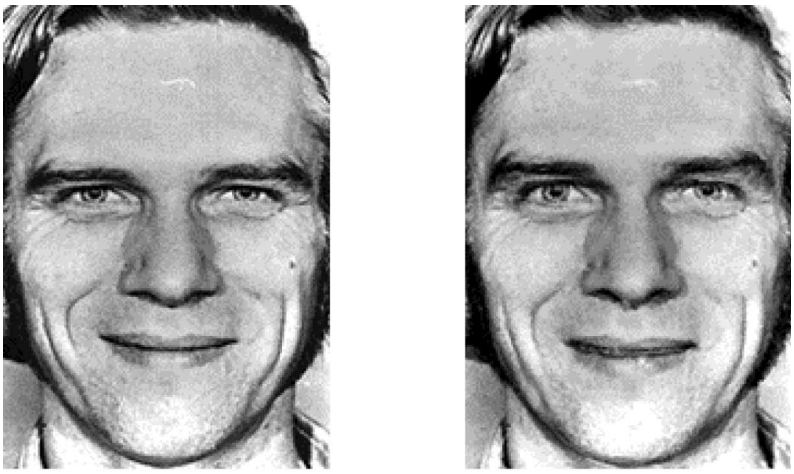
RESULTS

Behavioral Data

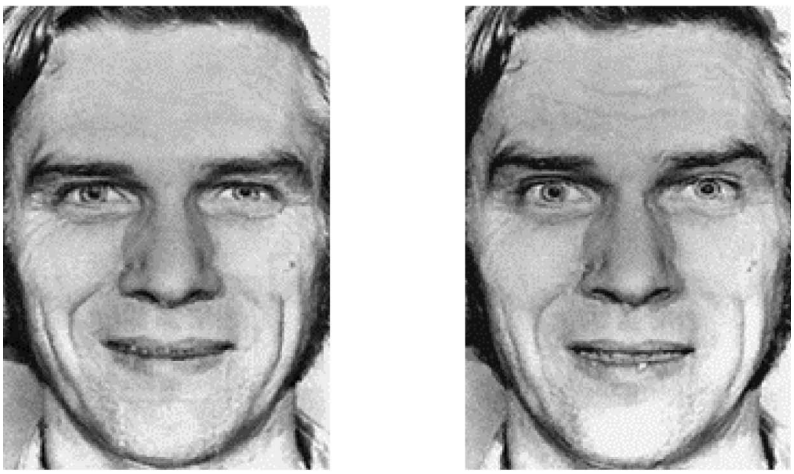
We wanted to replicate the categorical perception effect described in the literature, namely, a better performance for between as compared to within pairs (Young et al., 1997; Calder et al., 1996; Etcoff & Magee, 1992). This was statistically analyzed by a three-level analysis of variance (ANOVA) with condition (between, within, and same) as dependent variable, on the percentages of correct responses. The results revealed a clear condition effect [$F(2,18) = 16.072, p < .0001$]. Moreover, further paired Student's t tests showed a better performance for between as compared to within and same pairs [respectively, $t(9) = 4.769, p = .001$; $t(9) = 5.682, p < .0001$] while same pairs generated a better performance than within pairs [$t(9) = 2.622, p = .028$]. We carried out the same analyses on the correct response latencies. A clear condition effect emerged [$F(2,18) = 11.844, p = .001$]. Besides, further paired Student's t tests showed that correct response latencies are faster for between pairs as compared to within and same pairs [respectively, $t(9) = 3.893, p = .004$; $t(9) = 3.410, p = .008$] while within and same pairs did not show differences [$t(9) = 0.759$, ns]. These results suggest that subjects discriminate more easily two faces perceived as two different expressions (between pairs) than two faces perceived as showing the same expression (within pairs) or than two faces being completely identical (same pairs). Furthermore, it took a longer time to give a correct answer for within and same pairs relative to between pairs (Table 1).

Event-Related Potentials

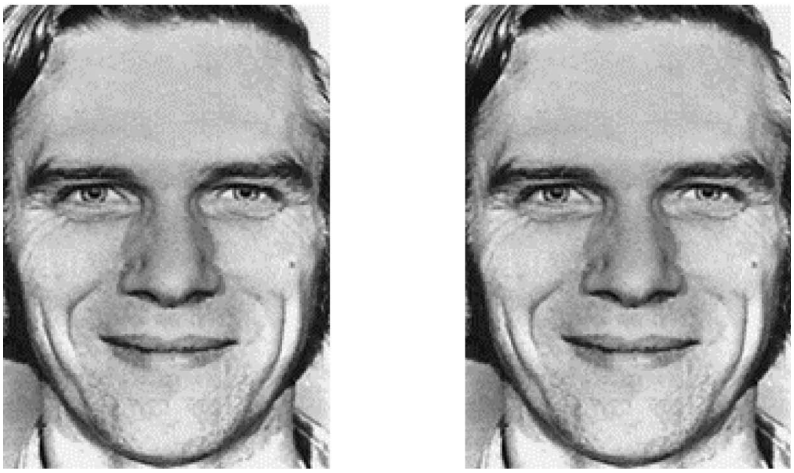
We considered ERPs elicited by between, within, and same pairs of morphed faces. In response to the second



WITHIN pair



BETWEEN pair



SAME pair

Figure 1. Pairs of morphed faces crossing (between) or not (within) the boundary were generated for each continuum. Pairs of identical stimuli (SAME) were also created for methodological purpose.

Table 1. Mean Correct Responses (*SD*) and Mean Correct Response Latencies (*SD*) for Same, Between, and Within Pairs

	Same	*Between*	*Within*
Performance (%)	86 (5)	94 (6)	76 (11)
Mean latencies (msec)	757 (116)	689 (119)	765 (112)

face of each pair, we observed three clear components for all subjects in all conditions (except for a few exceptions, see below) (Figure 2). These electrophysiological events were named according to their order of occurrence and polarity as an occipito-central bipolar P120/N120 complex, the N170 (Bentin et al., 1996; Bentin & Deouell, 2000) synchronized with the vertex positive potential (VPP; Jeffreys, 1996), and a posterior long-lasting positivity (LLP), identified as a P300. Note that the P300 was not observed in response to the first face of each pair.

The P120/N120 Complex

The first measurable electrophysiological event was a bipolar complex P120/N120, showing a large positivity over all posterior electrodes culminating (Oz) at 118 msec and a polarity reversal at central sites (Cz) (Figure 3A). Nine subjects out of 10 presented the P1 and all of them showed the N1 counterpart.

An ANOVA on peak voltage amplitudes with condition (between, within, and same) and lateralization (O1–O2)

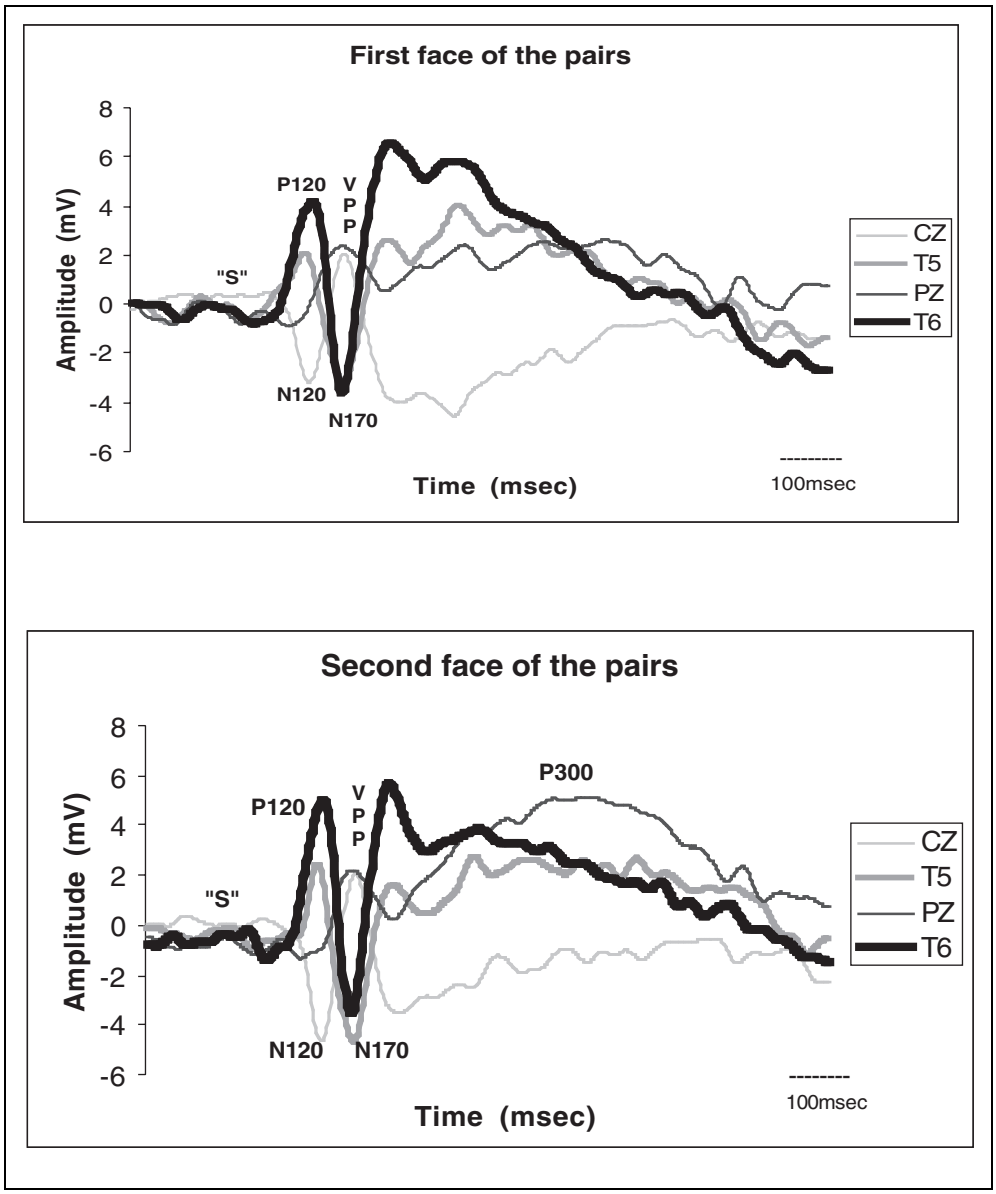


Figure 2. Illustration of the grand-average ERPs recorded from CZ, PZ, T5, and T6 in response to the first and the second face of within pairs. Note the appearance of the P300 only in response to the second face of the pairs.

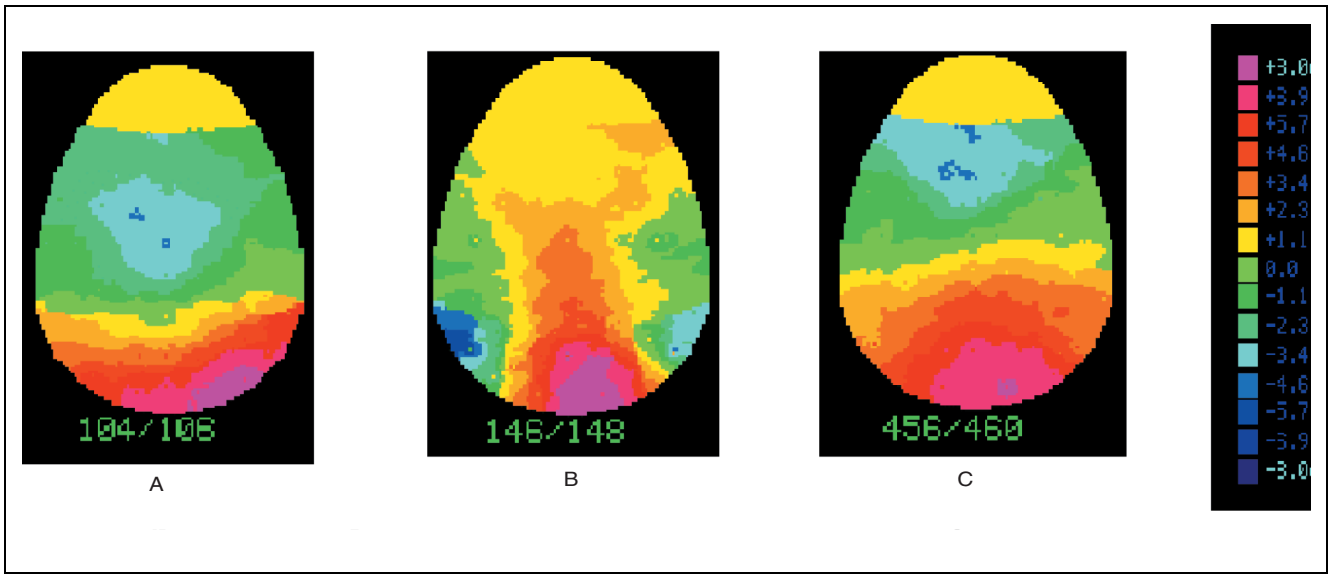


Figure 3. Grand-average brain topography of the complex P120/N120, N170/VPP, and P300 evoked in response to the second face of within pairs.

as factors did not reveal any significant effect neither for the responses to the first face of the pairs [condition: $F(2,16) = 0.577$, *ns*; lateralization: $F(1,8) = 1.420$, *ns*; interaction: $F(2,16) = 2.267$, *ns*] nor the second one [condition: $F(2,16) = 1.883$, *ns*; lateralization: $F(1,8) = 2.555$, *ns*; interaction: $F(2,16) = 3.203$, *ns*].[1]

An identical analysis was performed on the negative counterpart of the P1 at central electrodes at the same latency. The same pattern of results was found for the responses to the first image of the pairs [condition: $F(2,18) = 2.127$, *ns*; lateralization (C1–C2): $F(1,9) = 2.434$, *ns*; interaction: $F(2,18) = 0.928$, *ns*] as well as for the second one [condition: $F(2,18) = 1.666$, *ns*; lateralization: $F(1,9) = 3.688$, *ns*; interaction: $F(2,18) = 1.580$, *ns*].

The N170/VPP Complex

The next major electrophysiological event was the N170, observable bilaterally in all subjects. It culminated at T5/T6 electrodes at 150 msec and was synchronized with a VPP maximally recorded at Cz at 152 msec (Figure 3B).

The N170 appeared to be similar in latency and amplitude for the different conditions when the first face of the pairs was taken into account. However, its amplitude was bilaterally lower when the second face was identical (same) or belonged to the same facial expression than the first one (within), than for a face that shows a different expression than the first one (between).

Statistical analyses confirmed these observations. First, an ANOVA with condition (between, within, and same) and lateralization (left T5 and right T6) as factors failed to find any significant difference in the responses to the first face of the pairs [condition: $F(2,18) = 0.335$, *ns*; lateralization: $F(1,9) = 0.169$, *ns*; interaction: $F(2,18) = 0.093$, *ns*]. However, the same ANOVA found a clear main condition effect [$F(2,18) = 7.587$, $p = .004$], but neither significant interaction [$F(2,18) = 0.721$, *ns*] nor main lateralization effect [$F(1,9) = 0.278$, *ns*] when responses to the second image of the pairs were considered. Post hoc Student's t tests showed a significant difference between within and between pairs when mean amplitudes (mean of T5 and T6) are considered [$t(9) = 2.455$, $p = .036$] and between same and between pairs [$t(9) = 3.761$, $p = .004$], while no difference was found between same and within pairs [$t(9) = 0.938$, *ns*] (Figure 4A). In the same way, an ANOVA 2 × 3 with position (first or second face in the pair) and condition (between, within, and same) showed no significant main position effect [$F(1,9) = 0.101$, *ns*] and condition effect [$F(2,18) = 1.958$, *ns*], but a significant interaction [$F(2,18) = 6.711$, $p = .007$]. This suggests that while the second face of within and same pairs evoked N170 of smaller amplitudes than the first one, the opposite pattern was true for between pairs (as suggested by Figure 4B).

Similar analyses were performed on the VPP, suggesting the same pattern of results. Indeed, the VPP was identical in latency and amplitude for all the conditions when the first stimulus of the pair is taken into consideration. However, its amplitude was reduced when the second face was identical (same) or was perceived as showing the same emotion (within) as compared to the amplitude of the VPP following a morphed face perceived as showing a different emotion. An ANOVA with condition (between, within, and same) and lateralization (left C1 and right C2) as factors

Figure 4. (A) Illustration of the difference observed (for the second faces of the pairs) on the N170 and on the VPP between the within = same and between pairs at T6 and Cz, respectively (single subject). (B) Illustration of the difference on the N170 between the first and the second faces of between and within pairs at T6 (grand average).

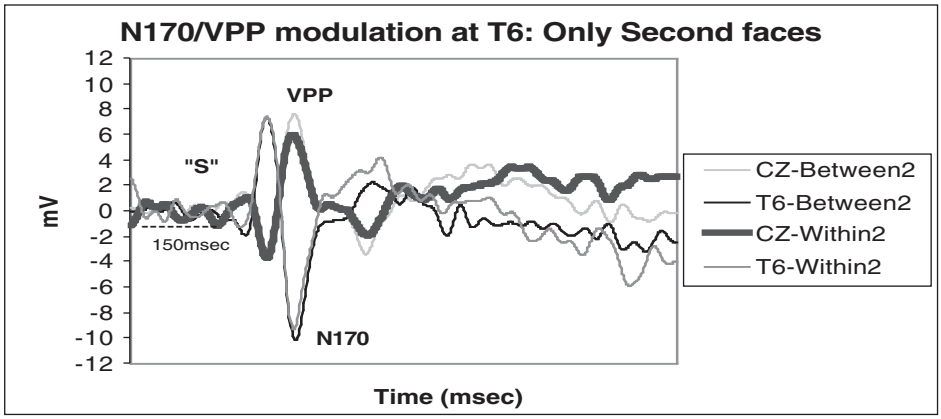
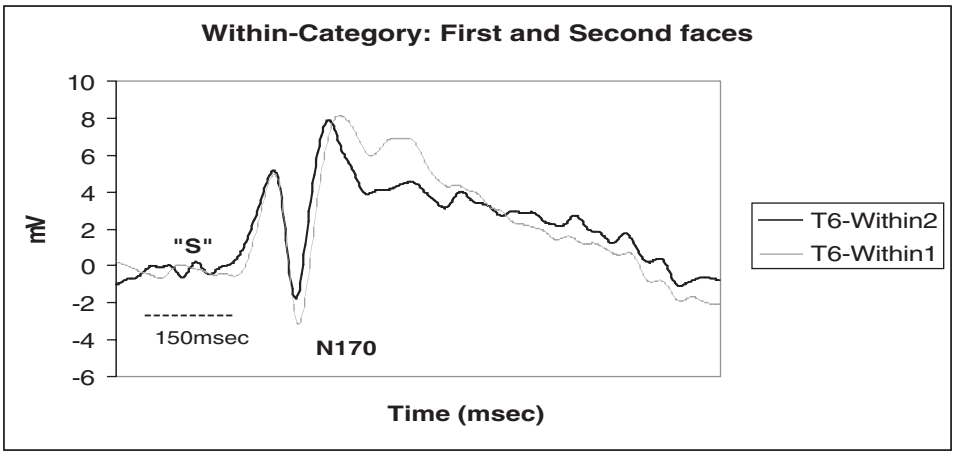


Figure 4A



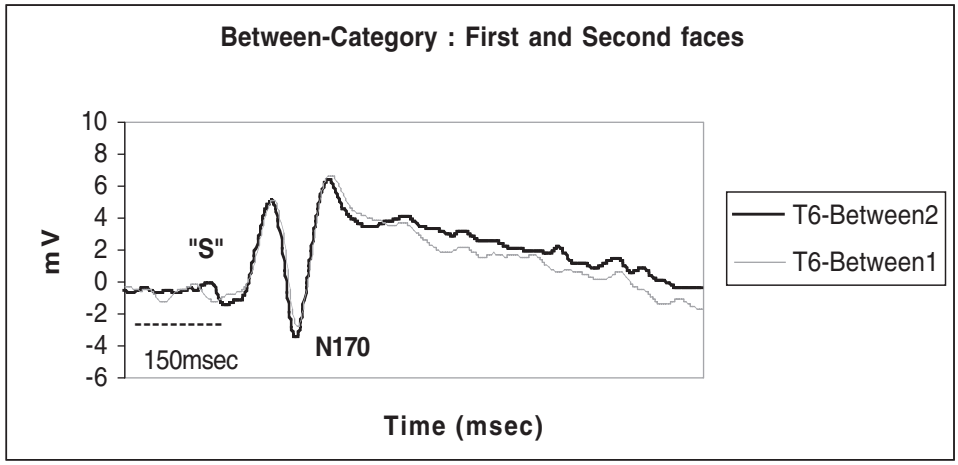


Figure 4B

failed to find any significant difference for the responses to the first face of the pairs [condition: $F(2,18) = 1.638$, *ns*; lateralization: $F(1,9) = 2.911$, *ns*; interaction: $F(2,18) = 1.251$, *ns*]. However, the same ANOVA found a clear main condition effect when responses to the second face were considered [$F(2,18) = 5.484$, $p = .014$], while lateralization and the Condition × Lateralization interaction did not show

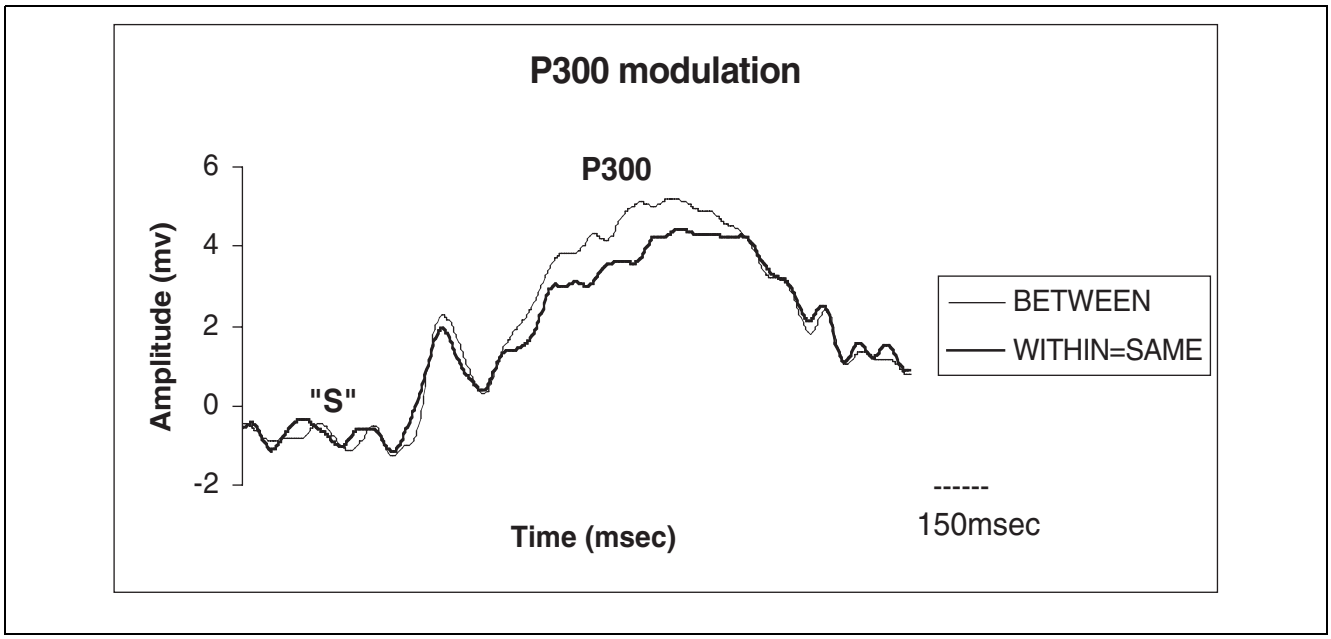


Figure 5. Illustration of the difference observed on the P300 between the within = same and between pairs.

significant effect [respectively, $F(1,9) = 0.037$, *ns*; $F(2,18) = 0.641$, *ns*]. Further paired Student's t tests showed differences in voltage amplitude of the VPP at Cz between within and between pairs [$t(9) = 2.912$, $p = .017$] and between same and between pairs [$t(9) = 2.984$, $p = .015$], while no difference emerged between same and within pairs [$t(9) = 0.030$, *ns*] (Figure 4A).

To sum up, the voltage amplitude differences found on the VPP and the N170 in response to the second face of the pairs are consistent. We observed an amplitude reduction of the N170 (bilaterally) and of the VPP when subjects are confronted with a second identical face (same) or perceived as showing the same emotion (within) than the first face of the pair, relative to the N170/VPP amplitude generated by the second face of a between pair (happy and fear).

The P300

A P300, maximally recorded at Pz and beginning around 250 msec, followed the N170/VPP complex. This P300 was observed for all subjects only in response to the presentation of the second face of the pairs (Figure 3C). This is in agreement with the functional role assigned to the P300 component, which is seen as reflecting a decision-making process (Rohrbaugh, Donchin, & Ericksen, 1974).

On the average waveforms, the P300 appeared to be larger in the between condition than in the within and same conditions. The mean amplitude of this P300 was obtained for each subject by averaging the amplitude points in the window 250–550 msec. An ANOVA was performed on these mean values with condition (between, within, and same) as a three-level factor. Results showed a main condition effect [$F(2,18) = 5.258$, $p = .016$]. Post hoc Student's paired t tests showed that between pairs have significant P300 differences as compared to within pairs [$t(9) = 2.961$, $p = .016$] and same pairs [$t(9) = 2.342$, $p = .044$], while no difference existed between same and within pairs [$t(9) = 0.319$, *ns*] (Figure 5).

Summary of Results

Above all, it is interesting to note that (1) the behavioral data indexing a categorical perception effect, namely, a better discriminability for between- (as compared with within-) differences, was replicated; (2) no significant ERP differences were observed in response to the first face of the pairs; (3) no significant differences were observed for the P120/N120 complex evoked by the second face of the pairs; and (4) the N170 and the VPP evoked by the second face of the pairs showed a consistent pattern of responses (between ≠ same = within) that is identical than that found on the P300 and that is correlated be the behavioral mean correct latencies (Table 2).

Dipole Modeling

Dipole localization was carried out on the N170/VPP complex identified in this study. The chosen time window was 140–160 msec. We found two main results. Firstly, if we constrain the system to work with only one pair of dipoles, the best solution (overall goodness of fit = .94) was defined by two mirrored dipoles, whose position was compatible with the fusiform gyri (coordinates: $x = -48, y = -37, z = -24; x = -48, y = 37, z =$

Table 2. Synthesis of the Significant Differences Found by Comparing Between and Within Pairs, Within and Same Pairs, and Same and Between Pairs for the Behavioral Data and the Evoked Brain Response to the Second Faces of the Pairs

	Behavioral Performance (%)	*Behavioral Latencies (msec)*	*P120/ N120*	*N170/VPP*	*P300*
Between Versus Within	≠	≠	•	≠	≠
Within Versus Same	≠	•	•	•	•
Same Versus Between	≠	≠	•	≠	≠

−24). Note that the negative values correspond to voxels to the left (y) or below (z) the intercommisural line, or behind the intersection of the intercommisural and vertical anterior commissural lines (x). Secondly, if the system is working with one additional pair of dipoles, compatible in position with the STS region (coordinates: $x = -48$, $y = -66$, $z = -1$; $x = -48$, $y = 66$, $z = -1$), (1) we do not significantly increase the goodness of fit (overall goodness of fit = .90); and (2) the N170/VPP activity could be totally explained by the activity of the two dipoles of the fusiform region, the other two showing a very weak intensity (almost invisible). The rationale of the present dipole analysis was discussed in the further section.

DISCUSSION

Behavioral Data

Even if subjects were confronted with pairs of different stimuli separated by a same percentage of physical difference (30% on the continua), they discriminated more easily between pairs than within ones. The categorical perception effect described by Young et al. (1997), Calder et al. (1996), and Etcoff and Magee (1992) was thus replicated: This facilitation effect means that subjects discriminated more easily two faces perceived as two different emotional expressions (fear and happiness) than two faces perceived as the same one. Moreover, there was also a significant difference (in percentages of correct responses and correct response latencies) between the same and between pairs: This suggests that subjects responded more easily to between pairs than to same pairs. We are thus confronted with a facilitation effect due to the passage from one category to the other one. Finally, even if the general performance for the same pairs is better than for the within ones, the complexity of the task for within and for same pairs seems to be very closed, as suggested by the equal mean correct response latencies.

Event-Related Potentials and Dipole Localization

Three complexes—the P120/N120, the N170 synchronized with a VPP, and the P300—were clearly obtained in response to the second face of the pairs for all the conditions (between, within, and same) in almost all subjects. The N170/VPP is the only one usually considered as face-specific (Campanella et al., 2000; Eimer & McCarthy, 1999; Rossion et al., 1999; Schendan, Ganis, & Kutas, 1998; Bentin et al., 1996; Bentin, Deouell, & Soroker, 1999; Bentin & Deouell, 2000; Jeffreys, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996).

The P120/N120 Complex

The first positive peak observed at Oz corresponds to the P120. The centro-frontal (Cz) negativity occurring with a similar latency (118 msec) is considered as its dipolar negative counterpart (Bötzel, Schulze, & Stodieck, 1995). A striate and extrastriate origin is proposed for the P120/N120 component, typically described in visual ERP studies to reflect early visual processing (see the complex P1/N1, Gomez, Clark, Luck, Fan, & Hillyard, 1994; Heinze et al., 1994). As suggested by statistical analyses, there was no significant difference between conditions (same, within, between pairs) in response to the first image of each presented pair. At first glance, this is not surprising as all stimuli were of identical luminance, spatial frequency, contrast, and complexity. Nevertheless, we had to test this effect, to check (1) that the signal-to-noise ratio, and thus the quality of the ERP recording, was comparable between the different conditions; and (2) that, regardless of the condition, subjects processed in the same way the first image of each pair. Moreover, the absence of significant difference in response to the second face of the pairs suggests that the P120/N120 complex defines a primary visual process, which is too ''early'' to be modulated by the category of emotion shown by faces.

The N170/VPP Complex

Several studies have described an N170 component to faces with characteristics (latency, amplitude, and topography) comparable to those described in this study (Campanella et al., 2000; Bentin et al., 1996; George et al., 1996). According to other studies, the N170 recorded at temporal sites (T5 and T6) reverses polarity at the level of Cz in order to give rise to an activity better known as the VPP (Rossion et al., 1999; Bötzel &

Grüsser, 1989; Bötzel et al., 1995; Jeffreys, 1989; Jeffreys & Tukmachi, 1992). First, we will discuss the consistent effects observed on the N170 and on the VPP. Second, we will comment some differences between the present data and those obtained with a similar paradigm for the categorical perception of familiar identities (Campanella et al., 2000).

Modulation of the N170/VPP

The results showed that the N170 and the VPP were identical for all the conditions for the first stimulus of the pair. The N170/VPP is considered as the process indexing the structural analysis of facial information in order to obtain a configurational face representation (Jeffreys, 1996). The absence of N170/VPP differences in response to the first face of between, within, and same pairs suggests an identical configurational analysis of these faces.

However, considering N170/VPP responses to the second face of these pairs, the results showed (1) that the N170 is reduced for within and same pairs as compared to between pairs, (2) that the same effect was observed for the VPP, and (3) that this effect is bilateral. The higher amplitude of the N170/VPP for the second face of between pairs as compared to within and same pairs can be understood when that subjects are confronted with two faces (in between pairs) perceived as different expressions (happiness and fear) by the perceptual system. Two different configurational facial analyses have thus to be performed successively in the between condition, whereas in the within and same conditions, the second facial expression belongs to the same expression as the first one. Several ERP studies have shown that successive repetitions of words, objects, and faces lead to a reduction in ERPs amplitudes (Paller & Gross, 1998; Schweinberger, 1996). Concerning face processing in particular, repetition priming effects on ERPs, indexed by a lower amplitude to the second face presentation, have already been observed (Henson, Shallice, & Dolan, 2000; Ji, Porjesz, & Begleiter, 1998; Begleiter, Porjesz, & Wang, 1995).

Considering these evidences, we propose that the striking reduction in the N170/VPP amplitude to the second face of the same and within pairs reflects a repetition priming effect. In fact, between pairs are constituted by two faces showing two different emotional expressions, while same and within pairs refer to the same one. In keeping with this, the second face of within and same pairs showed N170 of smaller amplitudes as compared with the first face of these pairs, whereas the second face of between pairs shows N170 of almost the same amplitude than the first one (see Figure 4). According to this, the priming effect indicates that the perceptual system considered the two physical different faces of the within (and, obviously, same) pairs as referring to an identical facial expression.

Comparison with Categorical Perception of Familiar Identities

In the present study, we show a bilateral repetition priming effect of the N170/VPP complex. However, these results underline two principal differences as compared to a previous study of ours. Indeed, we investigated the categorical perception effect for familiar facial identities with a similar paradigm (Campanella et al., 2000). If an identical and consistent N170 priming effect was observed, we have to note that, contrary to the present study, (1) this effect was strictly right-lateralized and (2) this effect does not appear when we consider the VPP amplitude.

On one hand, several studies suggest a right hemisphere advantage in face processing, as shown by neuropsychological observations (e.g., Rapcsak, Polster, Glisky, & Comer, 1996; Landis, Cummings, Christen, Bogen, & Himhof, 1986), divided visual field stimulations (e.g., Hillger & Koenig, 1991), intracranial ERP recordings (Allison, Puce, Spencer, & McCarthy, 1999), and neuroimaging studies (e.g., Swithenby et al., 1998; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). On the other hand, several studies show that the human amygdala is processing the emotional salience of faces, with a specificity of the left amygdala response to fear faces (Morris et al., 1996; Breiter et al., 1996), even if they were not perceived consciously (Whalen et al., 1998). But more interestingly, bilateral activations in the occipito-temporal cortex during unpleasant emotions have also been observed (e.g., Lane et al., 1997). It is suggested that the amygdala may be playing some role in tuning the visual system to become more sensitive to threat cues (Davidson & Irwin, 1999) by means of efferent projections to primary sensory areas (Ledoux, 1995; Amaral, Price, Pitkanen, & Carmichael, 1992). We suggest that, due to the fact that we used happiness and fear as facial expressions, the bilateral priming effect on the N170 could result from the conjunction of all the facts mentioned above, and we think that (1) this strengthens the fact that at least different anatomical processes are involved in facial recognition of identity and emotion (e.g., Sergent et al., 1994), and that (2) this could explain why, contrary to the present study, the priming effect was not observable for the VPP in a paradigm of categorical perception of familiar faces.[2] Indeed, the N170 priming effect for the categorical perception of familiar identities was strictly right lateralized. Hence, it seems highly plausible that the closer the current sources are to the electrodes, the larger the differences between two experimental conditions will be observed (Campanella et al., 2000). The N170 topography suggests a potential distribution by tangen-

tially oriented dipole generators directly beneath the site of the polarity reversal, that is, from posterior temporal lobes (Taylor et al., 1999; Jeffreys, 1989). Thus, since the VPP is supposed to be far from the sources (contrary to the N170 recorded at T5–T6) and since the effects observed on the N170 are limited to the right hemisphere, it appears that some effects generated by right posterior temporal regions could only be detected by closer electrodes (in the case of categorical perception of familiar identities, T6). Conversely, the effects observed here are bilateral and then enough ''strong'' to be also detectable at central electrodes on the VPP.[3] The current explanation seems to support the thesis of an N170 and a VPP representing identical processes. An interesting way to explore this question could be furnished by the use of dipole source analysis. Indeed, an anatomical dissociation between the generators of the N170 and the VPP (with, e.g., the VPP conceivably due to facial expression STS region and the N170 to the fusiform facial identification region) would be an important finding, resulting in the observed dissociation between face identification and expression effects. Keeping this in mind, a dipole analysis was performed on the present data. Two main results were found. Firstly, if we constrain the system to work with only one pair of dipoles, the best solution (overall goodness of fit = .94) was defined by two mirrored dipoles, whose position was compatible with the fusiform gyri. Secondly, if the system is working with one additional pair of dipoles, compatible in position with the STS region, (1) we do not significantly increase the goodness of fit (overall goodness of fit = .90); and (2) as illustrated by Figure 6, the N170/VPP activity could be totally explained by the activity of the two dipoles of the fusiform region, the other two showing a very weak intensity (almost invisible). Even if these results could not be considered as a sufficient proof (due to the poor spatial resolution of source analysis as compared with PET or fMRI), it strengthens the idea of an N170/VPP complex generated by the same anatomical region (the fusiform gyrus; Taylor et al., 1999) and indexing functional similar processes.

The P300

The long-lasting positivity responding to the second face of between, within, and same pairs has the same latency, amplitude, and topography than the P3b activity described in others studies and referring to a decision-making process (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Halgren et al., 1994). Indeed, several studies have emphasized the distinction between a fronto-central (''P3a'') and a parietal (''P3b'') component of the P300. In the present study, the centro-parietal distribution identified it as a P3b (see Figure 2). This confirms the fact that no P3b was observed in response to the first face of each pair, as no decision was required at this point.

The P3b showed a greater activity for between pairs in comparison with same and within pairs. It is of particular interest that these P3b modulations are correlated with behavioral correct response latencies: The time required for correctly evaluating within and same pairs was significantly higher than for between pairs. Hence, it is well known that the P3b amplitude is modulated by task demands (Comerchero & Polich, 1999; Ravden & Polich, 1998). Then, for between pairs, subjects had, at the end of the structural analysis of faces, two configurational representations of the same identity but with a different facial expression: They can then easily answer ''different'' in the delayed same–different matching task. The situation is different for within pairs: At the end of the structural analysis of the two presented faces, the same configurational face representation is activated as the two images represented the same identity with an identical facial expression. However, the two images are physically different. Then, to give a correct answer in the same–different matching task (i.e., ''different''), subjects have to rely on the observed physical differences between the two images while inhibiting their ''configurational equivalence.'' This explains why it is more difficult when they are confronted with within pairs as compared to between pairs. Moreover, it appears that judging two faces as completely identical took as much time as to discriminate within-categorical differences. This could be explained by the fact that subjects look for nonexistent differences.

In accordance with Bentin, Mouchetant-Rostaing, et al. (1999), two neurophysiological mechanisms can be put forward to account for P3b modulations. First, it could be that the amplitude of the P300 in different tasks is proportionate to their complexity. Indeed, a recent study shows, by using an oddball paradigm, that when target/standard discrimination is difficult, the target amplitude (P3b) is parietally larger and occurs later as compared to nontarget components, for both visual and auditory stimuli (Comerchero & Polich, 1999). Moreover, in our study of the categorical perception of familiar faces (Campanella et al., 2000), we showed a P3b of greater amplitude for within pairs than for same and between pairs. Hence, behavioral results indexed a lower performance and a higher response correct latency for within pairs than for same = between pairs.

However, the situation here is quite different. Indeed, the present data showed a lesser amplitude of the P3b for the behaviorally complex tasks (within and same pairs) as compared to the easiest one (between pairs). A similar pattern of results was obtained in others studies (e.g., Bentin, Mouchetant-Rostaing, et al., 1999). As a consequence, a second explanation should be found for the present data. It is plausible to think that the more complex is the task, the more different is the time required to perform it. This will be indexed by a differ-

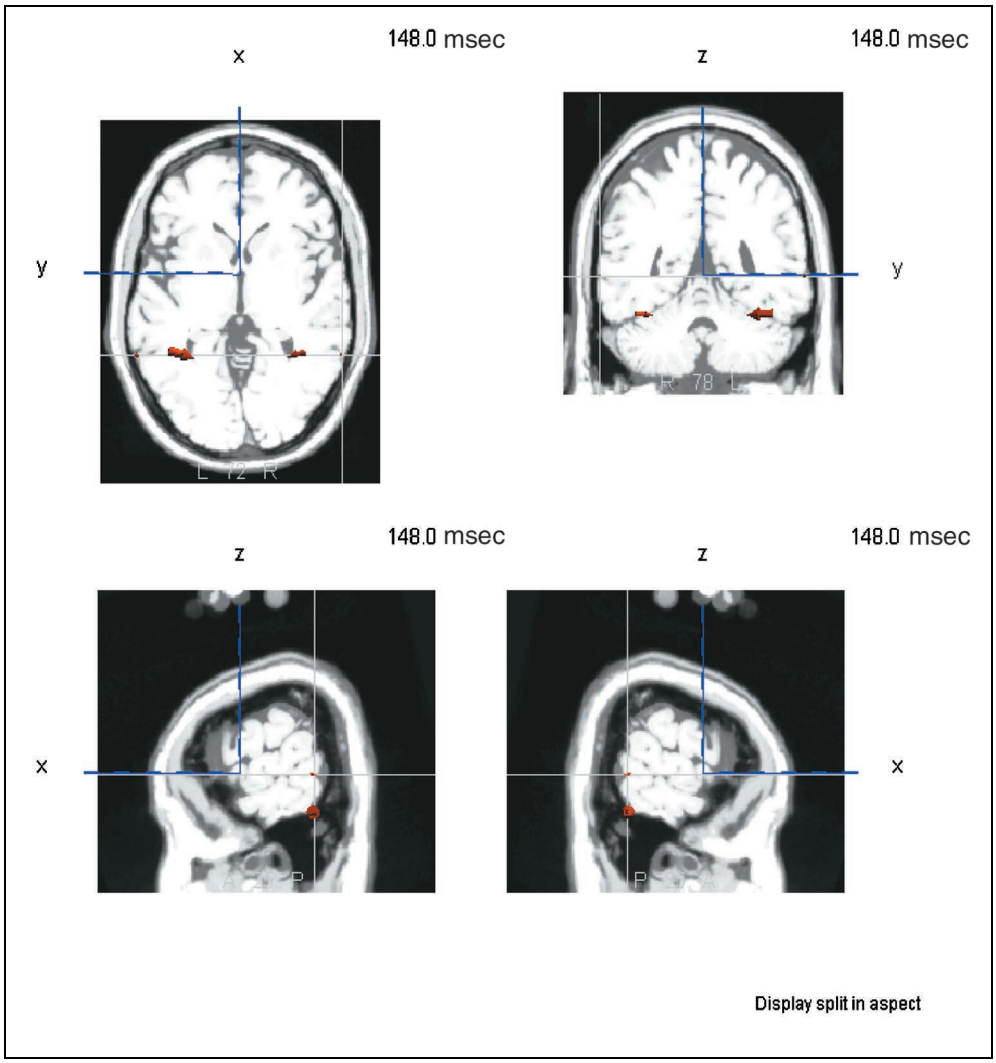


Figure 6. Localization and intensity of the solution using two pairs of dipoles for generating the N170/VPP complex.

ential ''jitter'' in the latency of single trials and the average decision-related ERP should have lower amplitude (and a larger duration) in the complex tasks.

Another explanation could be that the strongest characteristic of the P300 is that it is larger to rarer events (Ducan-Johnson & Donchin, 1982). Here, the behavioral results show that within and same trials are often perceived as perceptually identical (given the 75% accuracy rate of the within trials). Then, the between trials could represent subjectively a rarer event and therefore have a larger P300 response.

To conclude, it is important to outline that opposite pattern of results are obtained in different studies manipulating task complexity, and that this highlights the necessity to define more clearly the conditions and the mechanisms responsible for P3b modulations.

Conclusions

The hallmark of categorical perception effect is a better discrimination for between-categorical differences than for within-categorical ones (Young et al., 1997). We determined the temporal course of the perceptual categorization of happiness and fear facial expressions: It takes place early in the perceptual face processing system, at around 150 msec following stimulus onset, in the bilateral occipito-temporal regions. Discrimination of within-categorical differences is more complex because the two images of these pairs are physically different but give rise to an identical configurational face representation. A bilateral priming effect described on the N170 (around 150 msec at T5 and T6) and on the VPP (at the same time, at Cz) for within pairs as compared to between pairs demonstrated it. Consequently, because our system has to overcome the identity–emotion similarity of the two images in order to rely on their physical differences, the process leading subjects to give a correct answer (''different'') to within pairs is more complex than the one implied in between pairs, as behaviorally suggested by the lower rate of correct responses and by the longer correct response latencies. Furthermore, the priming effect on the N170 and the VPP was also

observable for same pairs. The two faces of same pairs were identical and thus gave rise to a same configurational face representation that led subjects to give a correct answer (''same''), as indexed by the good rate of performance (mean of 87%). However, perhaps due to instructions (''Are faces A and B totally identical?''), subjects could be induced in same pairs to look for differences that did not exist: This could explain why correct response latencies of same pairs took longer time than those of between pairs and were as long as those of within pairs. This pattern of correct response latencies (between $\neq$ same = within) was consistent with ERP data, which show a P3b, generally referred to the decision-making process (Halgren et al., 1994), of equal (or lower) amplitude for within and same pairs. Then, we suggest that the effect described on the N170/VPP referred to face encoding processes, whereas the effect shown on the P3b could be closely tied to the subjective rarity of between pairs (the within and same pairs being more often perceived as showing an identical emotion).

Besides, it is interesting to note that a previous study on categorical perception of familiar faces (Campanella et al., 2000) also shows a priming effect on the N170 for within and same pairs as compared to between pairs. However, contrary to the present study, this priming effect was right lateralized and not observable on the VPP. Hence, as suggested above, a large variety of data (animal cells recordings, neuropsychological data, experimental psychology data, neuroimaging studies by means of PET, fMRI, or ERP) showed that facial identity and facial emotion are mediated by different cerebral mechanisms. Due to its optimal temporal resolution, the present ERP study allows to show that the segregation of the neural mechanisms implied in facial identity and that facial emotion discrimination began at early stages, around 150 msec, in the occipito-temporal regions. However, whether the results so far suggest that both face familiarity (Campanella et al., 2000) and face expression affect structural encoding if the task requires face matching, we have to note that some studies showed that face familiarity has no effect neither on intracranial N200 (Puce, Allison, & McCarthy, 1999) nor on the scalp-recorded N170, regardless of whether the task was a simple oddball or a speeded face recognition (Bentin & Deouell, 2000). Moreover, regarding the N200, Puce et al. (1999) reported no semantic or perceptual repetition priming effects. Then, we put forward the hypothesis that, unlike identification, face matching is a shallow perceptual task that is probably based on shallow (structural encoding) processes.

METHODS

Stimuli

Three male faces (A, B, and C) with happy and fear expressions were taken from Ekman and Friesen series (1976) (Figure 7). Three continua of pairs were therefore possible (''A happy'' to ''A fear,'' ''B happy'' to ''B fear,'' and ''C happy'' to ''C fear'').

Five morphed images were created for each continuum. They were prepared by blending two faces in proportion of 90:10 (i.e., 90% ''A happy'' and 10% ''A fear''), 70:30, 50:50, 30:70, and 10:90. We will refer to these as 90%, 70%, 50%, 30%, and 10% morphs along the appropriate continuum.

The preparation of each continuum involved four steps. First, the ''A happy,'' ''A fear,'' ''B happy,'' ''B fear,'' ''C happy,'' and ''C fear'' photographs (Ekman & Friesen, 1976) were downloaded into a Macintosh computer and were edited by Adobe Photoshop 4.0.1. to remove backgrounds, everything beyond the chin, hair, and ears. Gray-scale images were created and scaled to 150 × 191 pixels. Second, morphed stimuli were generated using the Morph 2.5. program. One hundred fifty points were located manually onto the sources. The location of these points was specified in terms of facial features such as corners of the mouth, tip and bridge of the nose, or outlines of the eyes. We applied the same method to the other sources so that there was a correspondence of the 150 points for all of them. Third, a vector equation for each of the 150 points was computed on the sources in order to determine which position a point on ''A happy''s face will have on the morphed image after moving to 10%, 30%, 50%, 70%, or 90% to the position of the corresponding point on ''A fear''s face. Fourth, the Morph program used a warping procedure to move from one source to the other by allowing the shift of the 150 control points from their initial position (in one source) to their final position (in the other) along linear changes. For example, in the 90% ''A happy''/10% ''A fear'' morphed face, the pixel intensities have deformed the ''A happy''s face by 10% toward the ''A fear''s face and the ''A fear''s face by 90% toward the ''A happy''s face. In total, 15 images were drawn (five from each of the three continua). These faces were converted to a PCX format in order to be displayed on a monitor using a commercial visual stimulator (STIM, Neuroscan SCAN).

Behavioral Preexperiments

The aim of this behavioral experiment was to identify the categorical boundary of the three face continua in order to prepare pairs of faces for the ERP experiment.

An identification task allowed the determination of the categorical boundary of the three continua. Eighteen subjects were confronted with the 15 morphed faces that randomly presented and repeated four times each. Their task consisted in deciding to which expression (happy or fear) the presented morphed face was more similar. As shown previously (Young et al., 1997; Calder et al., 1996; Etcoff & Magge, 1992), this task allows us to

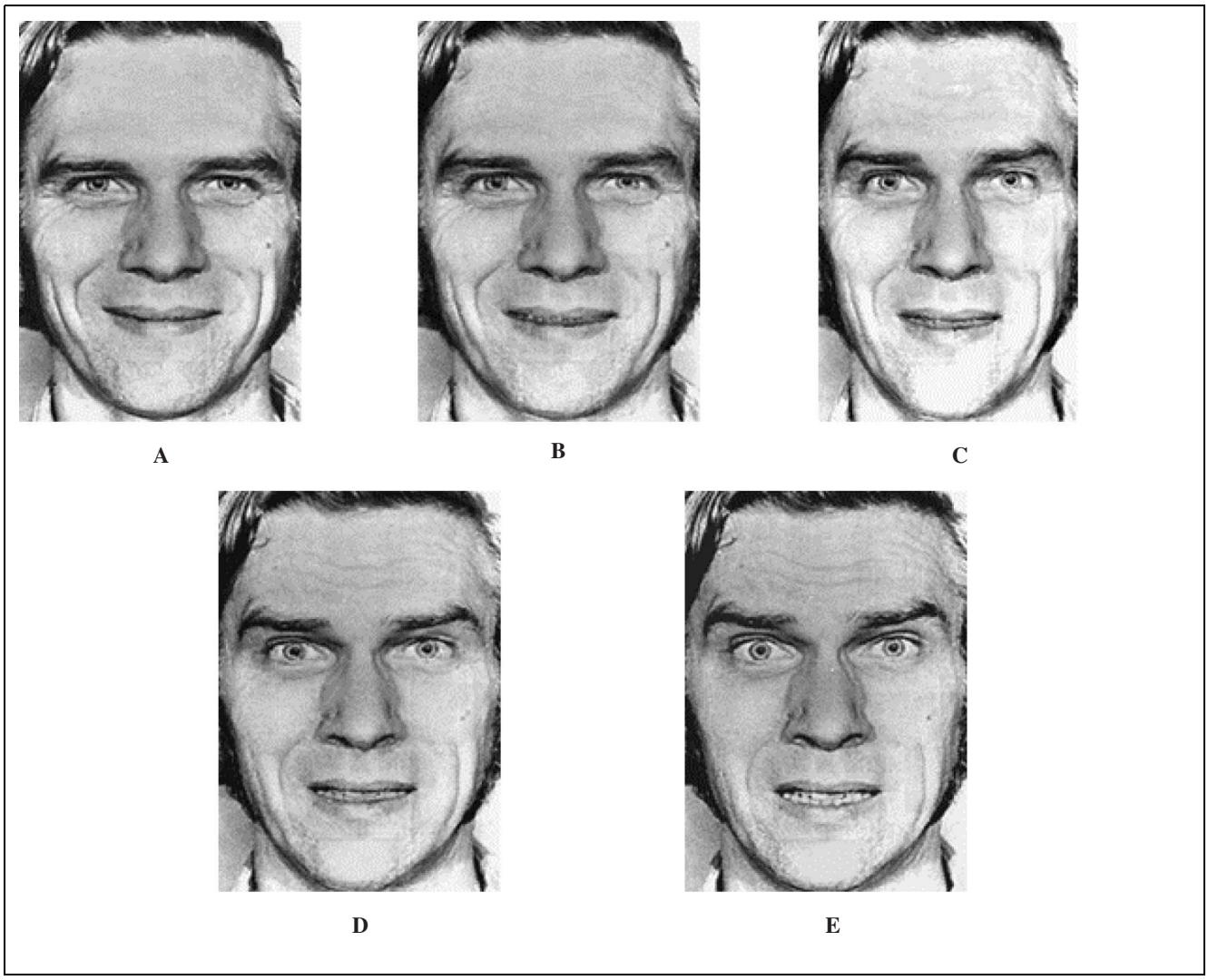


Figure 7. Illustration of the morphed faces for the continuum ''A happy'' to ''A fear.''

define for each of the three continua the categorical boundary, which is necessary to create between and within pairs (i.e., pairs that, respectively, passed through or not the categorical boundary) that will be used in the delayed same–different matching task during the ERP recording. The generation of these pairs is necessary to assess, in a discrimination task, an enhanced discriminability for between-categorical differences as compared to within ones.

Procedure

Data of the behavioral preexperiments were used to define boundaries between categories. For example, Figure 8 shows the percentages of ''happy'' and ''fear'' responses for each stimuli (10%, 30%, 50%, 70%, and 90%) of one continuum (''A happy'' to ''A fear''). The intersection of the two curves indicates the point where half of the subjects would respond ''happy'' and the other half ''fear'' (56% in this example). This point was taken as the subjective categorical boundary of the continuum ''A happy to A fear.''

The same procedure was applied to each of the three continua in order to obtain their own categorical boundary. For the three continua, categorical boundaries were 56% for ''A happy to A fear,'' 42% for ''B happy to B fear,'' and 41% for ''C happy to C fear.'' Each continuum gave rise to three kinds of pairs of morphed faces. First, four between pairs (e.g., a pair in which the first image was a morph identified as happy and the second one as fear) were pulled out of the continuum ''A happy to A fear,'' i.e., pairs ''36–66%,'' ''38–68%,'' ''40–70%,'' and ''42–72%'' while between pairs pulled out of the continua ''B happy to B fear'' and ''C happy to C fear'' are ''30–60%,'' ''32–62%,'' ''34–64%,'' and ''36–66%, in order to respect the categorical boundary for all the three continua. Second, four within pairs (two different morphed images both identified as fear, for instance) were created. These pairs were for continua A, B, and C: ''1–31%,'' ''8–38%,'' ''64–94%,'' and ''69–99%.''

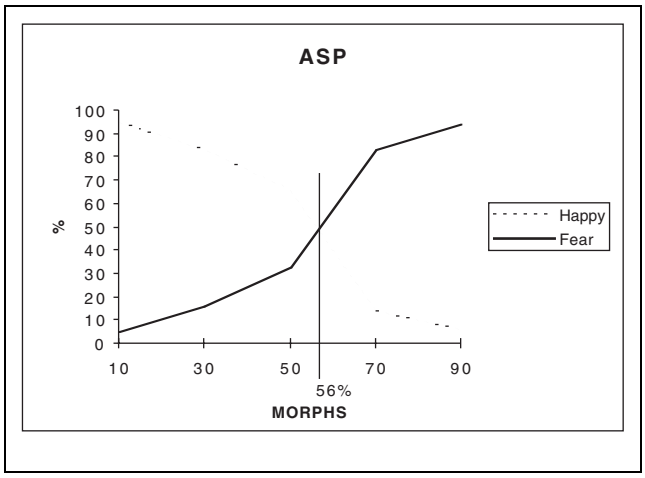


Figure 8. For the continuum ''A happy to A fear,'' mean frequencies of responses were calculated. The intersection point of the two curves gives a point corresponding to the morphed face 56%. This point indicates the categorical boundary of this continuum, i.e., the subjective point where 50% of the subjects responded ''happy'' and the other half responded ''fear.'' The same procedure was applied to the other two continua.

Third, eight same pairs were generated for methodological purpose (the same image presented twice). Indeed, we made same pairs in order to have an equivalent number of same and different pairs to present to subjects. These same pairs are for continua A, B, and C: ''10–10%,'' ''20–20%,'' ''30–30%,'' ''40–40%,'' ''60–60%,'' ''70–70%,'' ''80–80%,'' and ''90–90%.'' Note that the physical difference between the stimuli of between and within pairs was fixed (30%) (see Figure 1).

Forty-eight pairs were available (24 same pairs and 24 different pairs with 12 between and 12 within pairs). In order to increase the signal-to-noise ratio, these pairs were repeated six times, so that 288 trials (144 same, 72 between, and 72 within) were recorded. All stimuli were used equally often in each of the three conditions.

During the EEG recording, subjects sat on a chair in a dark room with their head restrained by a chin rest. Their heads were placed 1 m from the screen, and stimuli were 6 cm horizontal and 8 cm vertical; stimuli thus subtended a visual angle of $3^\circ \times 4^\circ$. Subjects were presented with 12 blocks of 24 pairs of stimuli, the between, within, and same pairs being randomly intermixed within each block of trials. The order of the 12 blocks was also counterbalanced across subjects. A small white cross lasting 300 msec on the center of the screen followed then by a black screen for 400 msec signaled the beginning of each trial. Then, the first image was presented for 400 msec. A black screen was displayed for 1300 msec before the onset of the second image for 400 msec. The intertrial interval lasted 1500 msec (black screen), but subjects had 1200 msec after the second stimulus onset to answer. The participants had to decide as quickly and as accurately as possible whether the second image of the pair was exactly the same as the first one (delayed same–different matching task). This task shares the same goal with the ABX discrimination task used in the categorical perception literature, that is, to show an enhanced discriminability for between-categorical differences as compared to within-categorical differences; with the advantage that memory load component is reduced (Campanella et al., 2000). Subjects had to press the right or left key on a mouse with the right finger. The labeling (same/different) of the buttons was counterbalanced across subjects.

Subjects

Twelve new participants (right-handed males, 21–26 years, without neurological disease and with normal/corrected vision) volunteered for cash in the ERP experiment.

EEG Recordings

Fifty-eight electrodes mounted in an electrode cap recorded EEG. Electrode positions included the standard 10–20 system locations and additional intermediate positions. Recordings were made with the left ear as the physical reference. The EEG was amplified by battery-operated SYNAMPS amplifiers with a gain of 30,000 and a band pass of 0.01–100 Hz. The impedance of all electrodes was kept below 5 kΩ. EEG was continuously recorded (sampling rate 500 Hz, Neuroscan) and stored on disk for further analyses. EOG artifacts were eliminated and epochs beginning 150 msec prior to stimulus onset and continuing for 850 msec were created. A recalculation was made in order to obtain common average reference recordings (Bertrand, Perrin, & Perrier, 1985). Codes synchronized with stimulus delivery were used to average selectively epochs associated with different stimulus types. Three parameters were coded for every stimulus: (1) the position in the pair (first or second image), (2) the type of the pair (between, within, and same), and (3) the response type (same and different). This coding allowed us to compute different averages of ERP target stimuli. These averages were made for each subject individually. A sample grand average was obtained by averaging across the subjects the averages for each experimental conditions, that is, the first and the second face of a between pair (BET1 and BET2), of a within pair (WIT1 and WIT2), and of a same pair (SAM1 and SAM2). Only correct trials were included in averages of BET2, WIT2, and SAM2. Finally, the data were filtered from 1 to 30 Hz.

Statistical Analyses

Correct latencies and percentages of correct responses were computed and analyzed with Systat 5.1. Two subjects did not reach the threshold of 70% of correct

responses for the same pairs. As a consequence, their data were not taken into account. All further analyses were then computed on 10 subjects. At selected electrodes, individual peak amplitudes of different components were obtained for the different conditions and for each subject individually. These values were tested using paired *t* tests and repeated measures ANOVAs. Finally, the analysis of the intracranial dipoles of the N170/VPP complex was performed with the ASA software, which determines the position and orientations of intracranial dipoles and their time-varying strength by using a 100-mm diameter spherical head model.

Acknowledgments

This study was supported by Grant No. 95/00-189. The Belgian Fund of Scientific Research (FNRS) supports S.C.

Reprint requests should be sent to Salvatore Campanella, Faculté de Psychologie—Unité NECO, Université Catholique de Louvain, Place du Cardinal Mercier, 10, B-1348 Louvain-la-Neuve, Belgium, or via e-mail: salvatore.campanella@psp.ucl.ac.be.

Notes

1. Due to the high proximity of O1–O2 electrodes, which can occlude a potential lateralization effect, the same analysis was performed for the P1 amplitude on T5 and T6 electrodes. No significant effect was found for the responses to either the first face of the pairs [condition: $F(2,16) = 0.290$, *ns*; lateralization: $F(1,8) = 3.077$, *ns*; interaction: $F(2,16) = 2.930$, *ns*] or the second one [condition: $F(2,16) = 1.984$, *ns*; lateralization: $F(1,8) = 3.6$, *ns*; interaction: $F(2,16) = 0.272$, *ns*].
2. For this purpose, it would be useful to carry out an ERP study in which the responses evoked specifically by positive between-differences (for instance, happiness and surprise) and negative ones (for instance, fear and sadness) are compared, in order to contrast these effects with the bilateral ones found in the present study.
3. Even if the N170 and the VPP are considered as face-specific components, whether the VPP is the positive counterpart of the N170 or not is still matter of debate (Rossion et al., 1999; George et al., 1996). The similarity of the effects found on the N170 and the VPP here suggests that they indexed similar processes. However, it does not mean that N170 and VPP reflect totally similar dipole activities.

REFERENCES

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A. R. (1996). Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience, 16,* 7678–7687.

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9,* 415–430.

Amaral, D. G., Price, J. L., Pitkanen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In J. Aggleton (Ed.), *The amygdala—Neurobiological aspects of emotion, memory and mental dysfunction* (pp. 1–66). New York: Wiley.

Begleiter, H., Porjesz, B., & Wang, W. Y. (1995). Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalography and Clinical Neurophysiology, 94,* 41–49.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8,* 551–565.

Bentin, S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology, 17,* 35–54.

Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *NeuroReport, 10,* 823–827.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11,* 235–260.

Bertrand, O., Perrin, F., & Perrier, J. (1985). A theoretical justification of the average reference in topographic evoked potentials studies. *Clinical Neurophysiology, 62,* 462–464.

Bornstein, M. H., & Korda, N. O. (1984). Discrimination and matching within and between hues measured by reaction times: Some implications for categorical perception and levels of information processing. *Psychological Research, 46,* 207–222.

Bötzel, K., & Grüsser, O. J. (1989). Electric brain potentials evoked by pictures of faces and non-faces: A search for ''face specific'' EEG potentials. *Experimental Brain Research, 77,* 349–360.

Bötzel, K., Schulze, S., & Stodieck, R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research, 104,* 135–143.

Bowers, D., Bauer, R. M., Coslett, H. B., & Heilman, K. M. (1985). Processing of faces by patients with unilateral lesions: 1. Dissociation between judgments of facial affect and facial identity. *Brain and Cognition, 4,* 258–272.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., & Rosen, B. R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17,* 875–887.

Bruce, V. (1988). *Recognising faces.* Hove, UK: Erlbaum.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77,* 305–327.

Calder, A. J., Keane, J., Cole, J., Campbell, R., & Young, A. W. (2000). Facial expression recognition by people with Möbius syndrome. *Cognitive Neuropsychology, 17,* 73–87.

Calder, A. J., Young, A. W., Perrett, D. I., Etcoff, N. L., & Rowland, D. (1996). Categorical perception of morphed facial expressions. *Visual Cognition, 3,* 81–117.

Campanella, S., Chrysochoos, A., & Bruyer, R. (2001). Categorical perception of facial gender information: Behavioral evidence and the face–space metaphor. *Visual Cognition, 8,* 237–262.

Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., & Guerit, J. M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology, 37,* 796–806.

Comechero, M. D., & Polich, J. (1999). P3a and P3b from typical auditory and visual stimuli. *Clinical Neurophysiology, 110,* 24–30.

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences, 3,* 11–21.

Dehaene-Lambertz, G., & Dehaene, S. (1994). Speed and cerebral correlates of syllable discrimination in infants. *Nature, 370,* 292–295.

Duncan-Johnson, C. C., & Donchin, E. (1982). The P300 component of the event-related brain potentials as an index of information processing. *Biological Psychology, 14,* 1–52.
Eimer, M., & McCarthy, R. A. (1999). Prosopagnosia and structural encoding of faces: Evidence from event-related potentials. *NeuroReport, 10,* 255–259.
Ekman, P. (1992). Facial expressions of emotion: An old controversy and new findings. *Philosophical Transactions of the Royal Society of London, Series B: Biological Science, B335,* 63–69.
Ekman, P. (1994). Strong evidence for universals in facial expressions: A reply to Russell's mistaken critique. *Psychological Bulletin, 115,* 268–287.
Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect.* Palo Alto, CA: Consulting Psychologists Press.
Etcoff, N. L., & Magee, J. J. (1992). Categorical perception of facial expressions. *Cognition, 44,* 227–240.
Field, T. M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expressions by neonates. *Science, 218,* 179–181.
George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research, 4,* 65–76.
Gomez, C. M., Clark, V. P., Luck, S. J., Fan, S., & Hillyard, S. A. (1994). Sources of attention-sensitive visual event-related potentials. *Brain Topography, 7,* 41–51.
Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., & Chauvel, P. (1994). Spatio-temporal stages in face and word processing: 2. Depth-recorded potentials in the human frontal and Rolandic cortices. *Journal of Physiology, 88,* 51–80.
Halgren, E., & Marinkovic, K. (1995). Neurophysiological networks integrating human emotions. In M. S. Gazzaniga (Ed.), *The cognitive neuroscience* (pp. 1137–1151). Cambridge: MIT Press.
Harnad, S. (Ed.) (1987). *Categorical perception: The groundwork of cognition*. Cambridge: Cambridge University Press.
Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioral and Brain Research, 32,* 203–218.
Hautecoeur, P., Debruyne, P., Forzy, G., Gallois, P., Hache, J.-C., Dereux, J.-F. (1993). Potentiels évoqués visuels et reconnaissance des visages. Influence de la célébrite´et de l'expression émotionnelle. *Revue Neurologique (Paris), 149,* 207–212.
Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholtz, M., Münte, T. F., Gös, A., Scherg, M., Johannes, S., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during selective attention in humans. *Nature, 372,* 543–546.
Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science, 287,* 1269–1272.
Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience, 3,* 42–57.
Jeffreys, D. A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research, 78,* 193–202.
Jeffreys, D. A. (1996). Evoked potentials studies of face and object processing. *Visual Cognition, 3,* 1–38.
Jeffreys, D. A., & Tukmachi, E. S. A. (1992). The vertex-positive scalp potential evoked by faces. *Experimental Brain Research, 91,* 340–350.
Ji, J., Porjesz, B., & Begleiter, H. (1998). ERP components in category matching tasks. *Evoked Potentials—Electroencephalography and Clinical Neurophysiology, 108,* 380–389.
Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17,* 4302–4311.
Kunst-Wilson, W. R., & Zajonc, R. B. (1980). Affective discrimination of stimuli that cannot be recognized. *Science, 207,* 557–558.
Landis, T., Cummings, J. L., Christen, L., Bogen, J. E., & Imhof, H.-G. (1986). Are unilateral right posterior cerebral lesions sufficient to cause prosopagnosia? *Cortex, 22,* 243–252.
Lane, R. D., Reiman, E. M., Bradley, M. M., Lang, P. J., Ahern, G. L., Davidson, R. J., & Schwartz, G. E. (1997). Neuroanatomical correlates of pleasant and unpleasant emotion. *Neuropsychologia, 35,* 1437–1444.
Ledoux, J. E. (1995). In search of an emotional system in the brain: Leaping from fear to emotion and consciousness. In M. S. Gazzaniga (Ed.), *The cognitive neuroscience* (pp. 1049–1061). Cambridge: MIT Press.
Leonard, C. M., Rolls, E. T., Wilson, F. A. W., & Baylis, G. C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioral and Brain Research, 15,* 159–176.
Liberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology, 53,* 368–385.
McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 9,* 605–610.
Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature, 383,* 812–815.
Münte, T. F., Brack, M., Grootheer, O., Wieringa, B. M., Matzke, M., & Johannes, S. (1998). Brain potentials reveal the timing of face identity and expression judgments. *Neuroscience Research, 30,* 25–34.
Murphy, S. T., & Zajonc, R. B. (1993). Affect, cognition, and awareness: Affective priming with optimal and suboptimal stimulus exposure. *Journal of Personality and Social Psychology, 64,* 723–739.
Orozco, S., & Ehlers, C. L. (1998). Gender differences in electrophysiological responses to facial stimuli. *Biological Psychiatry, 44,* 281–289.
Paller, K. A., & Gross, M. (1998). Brain potentials associated with perceptual priming vs. explicit remembering during the repetition of visual word-form. *Neuropsychologia, 36,* 559–571.
Philipps, M. L., Bullmore, E. T., Howard, R., Woodruff, P. W. R., Wright, I. C., Williams, S. C. R., Simmons, A., Andrew, C., Brammer, M., & David, A. S. (1998). Investigation of facial recognition memory and happy and sad facial expression perception: An fMRI study. *Psychiatry Research: Neuroimaging Section, 83,* 127–138.
Pizzagalli, D., Regard, M., & Lehmann, D. (1999). Rapid emotional face processing in the human right and left brain hemispheres: An ERP study. *NeuroReport, 10,* 2691–2698.
Potter, D. D., & Parker, D. M. (1989). Electrophysiological correlates of facial identity and expression processing. In J. R. Crawford & D. M. Parker (Eds.), *Developments in clinical and experimental neuropsychology* (pp. 143–155). New York: Plenum.
Puce, A., Allison, T., & McCarthy, G. (1999). Electrophysiological studies of human face perception: Effects of top-down processing on face-specific potentials. *Cerebral Cortex, 9,* 445–458.
Rapcsak, S. Z., Polster, M. R., Glisky, M. L., & Comer, J. F. (1996). False recognition of unfamiliar faces following right

hemisphere damage: Neuropsychological and anatomical observations. *Cortex, 32,* 593–611.
Ravden, D., & Polich, J. (1998). Habituation of P300 from visual stimuli. *International Journal of Psychophysiology, 30,* 359–365.
Rohrbaugh, J. W., Donchin, E., & Eriksen, C. W. (1974). Decision making and the P300 component of the cortical evoked response. *Perception and Psychophysics, 15,* 368–374.
Rolls, E. T. (1992a). Neurophysiology and functions of the primate amygdala. In J. P. Aggleton (Ed.), *The amygdala* (chap. 5, pp. 143–165). New York: Wiley-Liss.
Rolls, E. T. (1992b). Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas. *Philosophical Transactions of the Royal Society, London, 335,* 11–21.
Rolls, E. T. (1994). Brain mechanisms for invariant visual recognition and learning. *Behavioral Processes, 33,* 113–138.
Rosch, E., Mervis, C. B., Gray, W., Johnson, D., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology, 7,* 573–605.
Rossion, B., Campanella, S., Guerit, J. M., Debatisse, D., Liard, L., Gomez, C., Dubois, S., Delinte, A., Bruyer, R., & Crommelinck, M. (1999). Task modulation of brain activity related to familiar and unfamiliar face processing: An ERP study. *Clinical Neurophysiology, 110,* 449–462.
Schendan, H. E., Ganis, G., & Kutas, M. (1998). Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. *Psychophysiology, 35,* 240–251.
Schweinberger, S. R. (1996). How Gorbachev primed Yeltsin: Analyses of associative priming in person recognition by means of reaction times and event-related potentials. *Journal of Experimental Psychology, Learning, Memory and Cognition, 22,* 1383–1407.
Schweinberger, S. R., Burton, A. M., & Kelly, S. W. (1999). Asymmetric dependencies in perceiving identity and emotion: Experiments with morphed faces. *Perception and Psychophysics, 61,* 1102–1115.
Sergent, J., Otha, S., McDonald, B., & Zuck, E. (1994). Segregated processing of facial identity and emotion in the human brain: A PET study. *Visual Cognition, 1,* 349–369.
Sprengelmeyer, R., Young, A. W., Sprengelmeyer, A., Calder, A. J., Rowland, D., Perrett, D., Homberg, V., & Lange, H. (1997). Recognition of facial expressions: Selective impairment of specific emotions in Huntington's disease. *Cognitive Neuropsychology, 14,* 839–879.
Swithenby, S. J., Bailey, A. J., Bräutigam, S., Josephs, O. E., Jousmäki, V., & Tesche, C. D. (1998). Neural processing of human faces: A magnetoencephalographic study. *Experimental Brain Research, 118,* 501–510.
Taylor, M. J., McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology, 110,* 910–915.
Whalen, P. J., Rauch, S. L., Etcoff, N., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18,* 411–418.
Woodworth, R. S., & Schlosberg, H. (1954). *Experimental psychology* (Rev. ed). New York: Henry Holt.
Young, A. W., Rowland, D., Calder, A. J., Etcoff, N. L., Seth, A., & Perrett, D. I. (1997). Facial expression megamix: Tests of dimensional and category accounts of emotion recognition. *Cognition, 63,* 271–313.
Young, M. P., & Yamane, S. (1992). Sparse population encoding of faces in the inferotemporal cortex. *Science, 256,* 1327–1331.