ELSEVIER

Clinical Neurophysiology 110 (1999) 449–462

Task modulation of brain activity related to familiar and unfamiliar face processing: an ERP study

B. Rossion[a, b,*], S. Campanella[a], C.M. Gomez[d], A. Delinte[b], D. Debatisse[b], L. Liard[a], S. Dubois[a], R. Bruyer[a], M. Crommelinck[b], J.-M. Guerit[c]

[a]*Unité de Neuropsychologie Cognitive (NECO), UCL, Louvain-la-Neuve, Belgium*
[b]*Laboratoire de Neurophysiologie, UCL, Brussels, Belgium*
[c]*Unité d'Explorations Electrophysiologique du Système Nerveux, Cliniques Universitaires St. Luc, St. Luc, Belgium*
[d]*Laboratorio de Psicobiologia, Dpto. de Psicologià Experimental, Universidad de Sevilla, Seville, Spain*

Accepted 14 September 1998

Abstract

In order to investigate stimulus-related and task-related electrophysiological activity relevant for face processing, event-related potentials (ERPs) from 58 electrodes at standard EEG sites were recorded while subjects performed a simple visual discrimination (control) task, in addition to various face processing tasks: recognition of previously learned faces and gender decision on familiar and unfamiliar faces. Three electrophysiological components or dipolar complex were recorded in all subjects: an occipital early component (P1, around 110 ms); a vertex positive potential (VPP; around 158 ms) which appeared to be specific to faces; and a negative central component, N2 (around 230 ms). Parametric analysis and source localization were applied to these components by means of a single-subject analysis methodology. No effect of familiarity was observed on any of these early component. While the VPP appears to be independent of the kind of processing performed, face task modulations of the early P1 and the N2 were observed, with a higher amplitude for the recognition than for the gender discrimination task. An attentional modulation of early visual areas is proposed for the first effect (P1 modulation), while the N2 seems to be related to general visual memory processing. This study strongly suggests that the VPP reflects an early visual stage of face processing in the fusiform gyrus that is strictly stimulus-related and independent of familiarity. It also shows that source localization algorithms may give reliable solutions on single subject averages for early visual components despite high inter-subject variability of the surface characteristics of ERPs.

Keywords: Face processing; Event-related potentials; Source location; Vertex positivity; Single subject analysis

1. Introduction

The ability to recognize faces plays an important role in the adaptation of individuals to social contexts.

The multi-stage cognitive model of Bruce and Young (1986) describes the different operations involved in face processing. This model is largely based on neuropsychological data (Warrington and James, 1967; Malone et al., 1982; Etcoff, 1984; Campbell et al., 1986), but is also based on analyses of the failures of face processing in everyday life (Young et al., 1985) or in mental chronometry studies (Bruce, 1986; Bruce et al., 1987).

According to this model, the first stage specific to face processing is a structural encoding component aimed at providing an invariant (i.e. independent of distance, orientation and expression) face representation to several higher-level functional components. Then, two parallel pathways are conceived as underlying face processing. A known face representation will activate a face recognition unit (FRU), which is a kind of template or long-term store of known face representations, each recognition unit corresponding to a single known face. These units are the key component for face recognition. Semantic information and (eventually) the name of the person can then be accessed through the FRU. Thus, structural encoding of faces, activation of face recognition units, retrieval of biographical information and name recall, unfold in a sequential way (Bruce and Young, 1986; Bruyer, 1990; Brédart and Bruyer, 1994). On the contrary, operations leading to gender discrimination or emotional categoriza-

* Corresponding author. Université Catholique de Louvain, Faculté de psychologie et des sciences de l'éducation PSP/EXPE/NECO, Place du Cardinal Mercier, 10 1348 Louvain-la-Neuve, Belgium. Tel.: + 32-10-473-831; fax: + 32-10-473-774.

E-mail address: rossion@neco.ucl.ac.be (B. Rossion)

1388-2457/99/$ - see front matter CLINPH 97813
PII: S1388-2457(98)00037-6

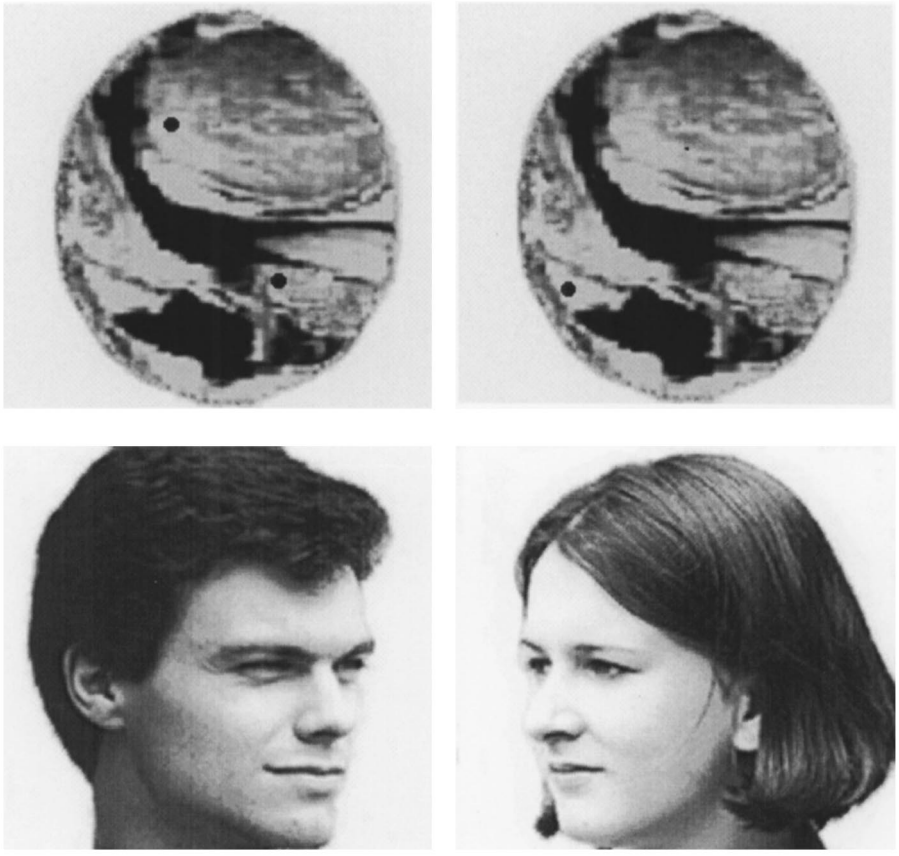


Fig. 1. Examples of stimuli used in the experiment. Above: stimuli used in the control (dot discrimination) task. The visual patterns had to be classified according to the number of black dots (left: two; right: one) superimposed on the original images (taken from Haxby et al., 1994). Below: examples of photographs of male (left) and female (right) faces used in the face processing tasks (gender discrimination and individual recognition).

tion can occur on every face (known or unknown) from the invariant or non-invariant description and would proceed in parallel (Bruce et al., 1987) with the recognition process.

Many studies have used ERPs to analyze these temporal aspects related to face processing (for reviews see Jeffreys, 1996; George, 1997).

Face presentation produces a sequence of characteristic ERPs (Jeffreys, 1989; Bötzel et al., 1995). The most characteristic ERP component is a vertex positive potential (VPP), which has a larger amplitude and shorter latency than the equivalent potentials evoked by other visual stimuli (Bötzel and Grüsser, 1989; Jeffreys, 1989). The peak latency of this VPP is in the 150–200 ms range with relatively high inter-subject variability ($\pm$ 40 ms). Although the VPP is largest over mid-line parieto-central areas, its coronal scalp distribution (Jeffreys, 1989) and dipole source localization (Bötzel et al., 1995) are consistent with bilateral sites originating from areas of the temporal cortex. Its functional correspondence has been related by Jeffreys (1996) to a low-level stage of face processing which may form part of the 'structural encoding' component of Bruce and Young's model (1986), while others (Bötzel et al., 1995) have argued that the VPP may be involved in face memory processes.

The VPP has also been considered by Jeffreys (1996) as reflecting on the scalp surface the activity of face-responsive cells found in the temporal cortex of monkeys (Perrett et al., 1985; Desimone, 1991) and sheep (Kendrick and Baldwin, 1987).

Using intracranial electrophysiological recordings in humans, Allison et al. (1994) also found a face negative potential (latency 200 ms) in regions of the fusiform gyrus, which they proposed as being the negative counterpart of the VPP.

The other electrical activities which seem to be related to face processing have been barely described by more than one study. While some authors (Jeffreys, 1989; George et al., 1996) consider the face negative potential recorded by the temporal electrodes during the same epoch as the VPP as its negative counterpart, Bötzel et al. (1995) considered these two peaks as reflecting the activities of two different generators. Allison et al. (1994) have also described an intracranial positive potential (peak latency between 250 and 350 ms) and a late negative potential (300–500 ms). These potentials were specifically related to face perception but the passive stimulation paradigm used prevented any interpretation of these potentials in terms of functional correlates.

Generally, these studies use passive[1] presentation of unknown stimuli (faces or other visual objects) and rely on the hypothesis that response specificities of visual cortical neurons are basically stimulus-related (Jeffreys, 1996). However, several positron emission tomography (PET) studies showed task-related (and stimulus independent) activations in human normal visual cortex (Corbetta et al., 1991; Dupont et al., 1993; Haxby et al., 1994; Vandenberghe et al., 1996). For instance, Haxby et al. (1994) found no difference of activation for a visuo-spatial localization task whether it was performed on faces or meaningless patterns.

We considered the following objectives in the present ERP study:

1. A definition of ERPs devoted to face processing by means of active tasks. These ERPs for faces were compared with those elicited by a control task made on a visual pattern of the same complexity as faces.
2. An investigation of whether the characteristics of the face ERPs, especially the VPP, can be modulated by the face task performed (i.e. whether they are not only stimulus-related but also task-related).
3. To explore the influence of visual familiarity on face processing. Other ERP studies used familiar and unfamiliar faces (Barrett et al., 1988; Grüsser et al., 1991). However, these studies have mainly investigated priming effects, by means of delayed tasks. They also used famous faces and semantic tasks. In our study, we wanted to avoid any 'semantic contamination' of ERPs, by using totally unknown faces which were learned during training sessions.
   We hypothesized that if the VPP reflects memory processes (Bötzel et al., 1995), then its latency or amplitude should vary when known or unknown faces are presented, and/or between a visual categorization task and a recognition task. On the contrary, no influence of these factors would reinforce the proposal of a strictly stimulus-related visual stage (Jeffreys, 1989, 1996) associated with this component.
4. Finally, we investigated the intracranial sources of the recorded potentials by means of a dipole source localization program (EMSE, BESA algorithm; Scherg, 1990).

2. Materials and methods

2.1. Subjects

Thirteen right-handed male adults (Edinbrugh scale; Oldfield, 1971), aged between 19 and 26 years old, participated. One was rejected for experimenter errors and 3 for a very poor signal-to-noise ratio. All subjects were in good health, had normal or corrected vision, and reported no history of neurological impairment. All analyses were thus computed on the data of 9 subjects.

2.2. Stimuli

Two kinds of stimuli were used. Complex visual patterns (Fig. 1) taken from Haxby et al. (1994)[2], on which one or two black dots were added for special purposes of this experiment. Thirty patterns, which differed only by dot positions and number, were made. Three-quarter profile photographs of faces taken from medical students (Fig. 1). The faces were all Caucasian males or females, without glasses. All male faces were well-shaved and the few cues (including clothing) that were still visible for some faces were masked using the Corel Draw graphic package. These photographs were scanned so that they could be displayed on the monitor using the commercial visual stimulator (STIM, Neuroscan).

2.3. Procedure

The experiment consisted of a training phase followed by an experimental phase, described in chronological order.

2.3.1. Training phase

This phase consisted first in introducing the subject to the experiment, obtaining his formal consent and testing his handedness and vision. The training phase lasted for the 3 consecutive days preceding the EEG experiment. Subjects were first shown a short (14 min) video film sequence of young persons in action (pretending to write a letter). The recordings focalized on the face. Twenty faces were presented (40 s each), one after the other, to each subject. Immediately after the presentation, a testing procedure took place: subjects were given 40 photographs of faces (3/4 profiles), half of them corresponding to people presented in the videotape recordings (the other half were new). Subjects were required to categorize the photographs into two samples: the faces that appeared in the videotape sequence and the distracters. Whatever the subject's performance[3], the videotape was presented once again. The next day, subjects were first tested with the 40 photographs. Either they obtained a maximum score (20/20) and the training phase was completed, or another videotape presentation was made and a last test took place the third day. As it turned out that two subjects did not reach the criteria of 20/20 at the end of the training

[1] The term 'passive' refers here to the fact that subjects did not have to make a discrimination based on the displayed stimulus.

[2] With permission of the first author.

[3] His score (number of faces recognized, out of 20) was given to the subject but no information concerning what kind of errors were made, in order to prevent any learning from the test.

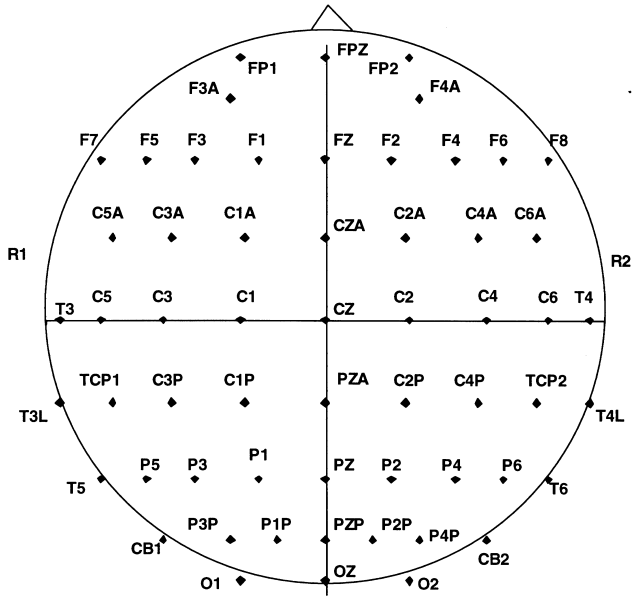


Fig. 2. Electrode locations on the scalp.

phase[4], they were shown the faces they did not recognize, together with the corresponding images on the videos[5].

2.3.2. Experimental phase

The experimental phase took place the day following the training phase and consisted of measuring EEG and behavioral responses in 4 conditions.

These 4 conditions were:

1. A visual discrimination control task (CONT), which consisted of a visual detection of dots on the visual pattern (Fig. 1). The subject's task was to press the left mouse button if there was only one dot on the pattern (half of the stimuli) and the other button if two dots were detected[6].
2. A gender discrimination task on unknown faces (GUF). The subjects had to categorize unknown (not shown during the learning phase) faces as male or female by pressing one of the two buttons (male = left). The whole set of stimuli was equally divided in the two categories.
3. A gender discrimination task on known faces (GKF). The instruction, the task and the proportion of stimuli were exactly the same as for condition 2, but the stimuli were photographs of familiar (previously learned on video) people.
4. A face recognition task (REC). The task consisted of categorizing the faces as previously seen on the videotapes or new and responded by pressing one of the two buttons (left = learnt faces). Two-thirds of the stimuli were known (familiar) faces[7]. The new faces were different from the ones used in condition GUF. As for all other face conditions, half of the faces were three-quarter left profiles and the other half three-quarter right profiles.

The stimuli were displayed on a high resolution monitor, in darkness. All images were presented for 1 s with an interstimulus interval of 2 s. In the 4 conditions, the subjects responded by pressing, with the right index finger and medius, one of two buttons of the computer mouse. Subjects sat in front of the monitor, at a viewing distance of 134 cm. The subject's head was restrained by a chin-rest. The stimuli were black-and-white square images, appearing in the center of the screen (Fig. 1). Their size (4° of visual angle) and luminance (about 7 cd/m^2) were constant across conditions.

Before starting the EEG recording, the different tasks were briefly explained to the subjects, using stimuli not employed in the experiment.

Three blocks of the 4 conditions were presented to the subjects and the order of conditions was randomized for each block. The order of blocks was constant during all the experiment. As there were 60 images for each condition in a block, a total of 720 images (12 trials) were presented to the subjects. A rest of about 1 min was allowed between blocks.

The whole experiment lasted about 2 h, including installation of the electrode cap and debriefing of the subject.

2.4. Recording and analyses

Correct latencies (interval between the onset of the stimulus and the subject's key press) and the percentage of errors were computed and analyzed (Systat 5, Macintosh). Latencies which were two standard deviations above or below the mean of each subject in each condition were discarded.

Scalp electrical activity (EEG) was recorded by 58 electrodes mounted in an electrode cap. Electrode positions included the standard 10–20 system locations and additional intermediate positions (Fig. 2). Recordings were made with a left earlobe reference. The EEG was amplified by battery-operated SYNAMPS amplifiers with a gain of 30 000 through a bandpass of 0.01–100 Hz. Electrode impedances were kept below 5 kΩ. EEG was continuously recorded (rate 1000 Hz, Neuroscan) and stored on a disk for off-line analysis. Then, epochs beginning 100 ms prior to stimulus onset and continuing for 924 ms were established, and a recalculation was made to obtain common average reference recordings. During the averaging procedure, epochs contaminated with EOG artifacts were eliminated. Codes synchronized to stimulus delivery were used to average selectively epochs associated with different stimulus types. Each stimulus was coded according to 6 parameters: (1) task

[4] No subjects reached the criteria after the second presentation of the videos. Two subjects only (including one whose EEG data were eventually not taken into account due to a very low signal-to-noise ratio) did not reach the criteria on the third day (after 3 presentations). One subject missed two faces (18/20) and the other missed one (19/20).

[5] The most important thing is for the subjects to be able to perform the task properly during the EEG recording.

[6] Distance between dots was always between 1 and 2 degrees of visual angle.

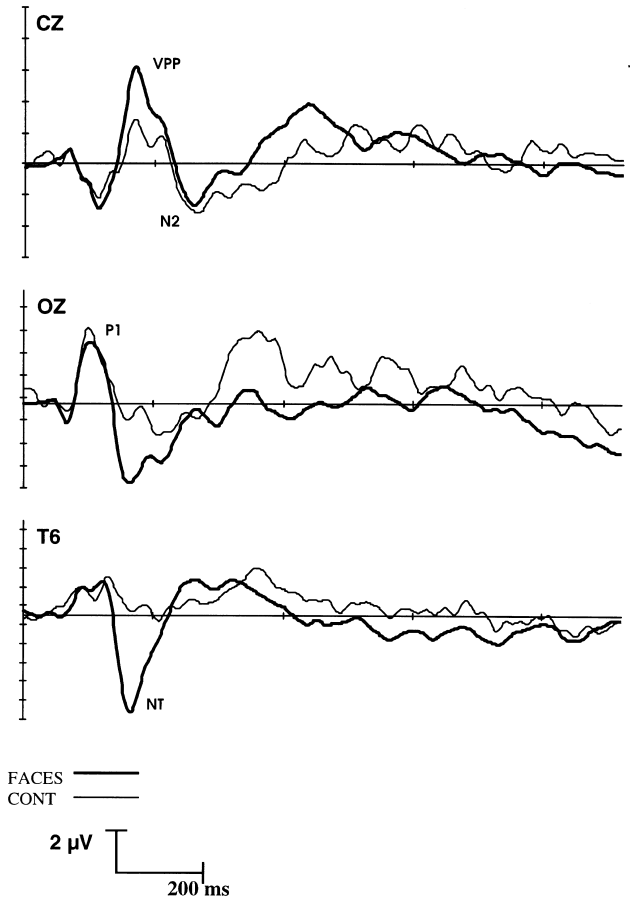


Fig. 3. ERPs obtained from one subject at central (Cz), occipital (Oz) and right temporal (T6) sites for both FACES and CONT averages. The curves illustrate the polarity oppositions for components P1 and VPP at central (Cz) and occipital (Oz) sites. The highest polarity opposition for the VPP is found at temporal sites (T6). The curves also illustrate the marked amplitude difference between CONT and FACE averages for the VPP, which was observed in all subjects.

(face recognition-gender discrimination); (2) familiarity (known or unknown face); (3) order of occurrence of the stimulus (1–2–3 or more); (4) response (left or right key); (5) face profile (left or right); (6) face gender (male or female). This coding enabled us to make several averages and to take into account the number of repetitions of each stimulus, which differed in amount between known and unknown faces[7]. Six averages were computed for each subject individually: FACES (all face stimuli which appeared 4 times in each condition; mean number of sweeps: 197; range: 170–243); CONT (all control stimuli appearing 4 times for the whole experiment; mean: 84, range: 62–118); GUF (all face stimuli appearing 3 times in the GUF condition; mean: 86; range: 66–109); GKF (all face stimuli appearing 3 times in the GKF condition; mean: 73; range: 57–98); RECU (all unknown faces appearing 3 times in the REC condition; mean: 61; range: 52–66); RECK (all known faces appearing 3 times in the REC condition; mean: 73; range: 64–80). Only correct trials were averaged. Trials associated with latencies of two SDs above or below the mean for each subject (each condition) were not taken into consideration. Finally, the data were filtered with a low-pass filter (cut-off = 45 Hz) and displayed off-line in the forms of raw data and topographical maps (Fig. 3 and Fig. 4).

The peak amplitudes (mean over a 20 ms window around the peak) and latencies of particular components at selected electrodes were obtained for the different conditions for each subject individually. This procedure was used for peaks under 250 ms, which were easily discriminated for all subjects in each condition. With the exception of a large P3 component which could be observed in some subjects and in the grand averages (Campanella et al., 1999), it turned out to be impossible to identify reliably later components in all or most of the subjects.

For each component identified, significant differences between measures in the different conditions were tested using paired *t* tests (CONT vs. FACES) and repeated-measures analysis of variance (ANOVAs). Post-hoc comparisons were evaluated using Tukey's test.

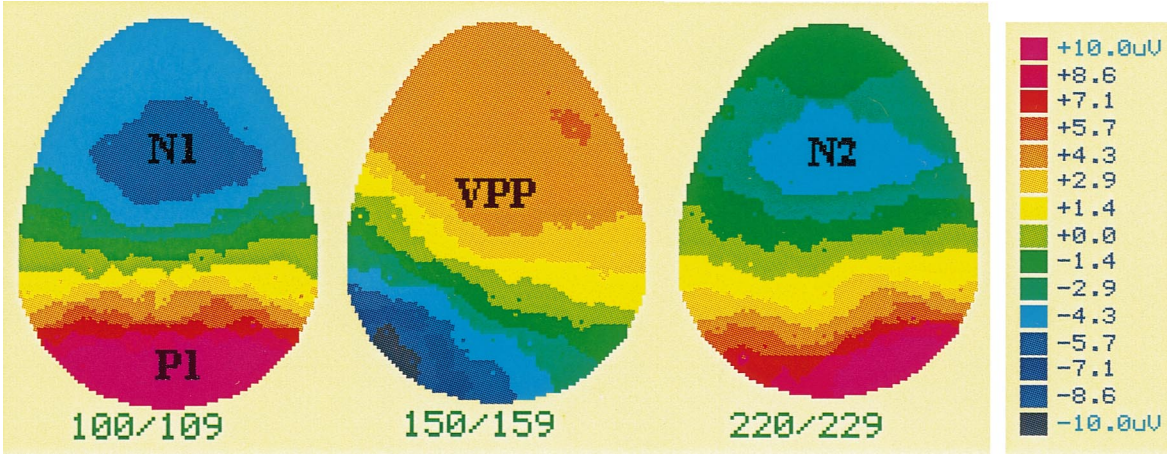


Fig. 4. Scalp topographies of the 3 components described in this study (single-subject). Note that the 3 components appear clearly as bipolar (positive and negative parts) complex.

Table 1
Correct response latencies in milliseconds and percentage of hits in the different conditions of the experiment[a]

	CONT	FACES	GUF	GKF	RECU	RECK
Hits (%)	71.6	97.57	97.59	98.09	96.54	97.46
Latencies (ms)	883	658	649	636	762	659

[a] CONT, control task; FACES, average on all face conditions; GUF, gender task, unknown faces; GKF, gender task, known faces; RECU, recognition task; unknown faces; RECK, recognition task; known faces).

The analysis of intracranial dipoles was performed with the EMSE software (BESA algorithm, Neuroscan), which determines the position and orientations of intracranial dipoles and their time-varying strength. This program calculates dipoles in a 100 mm diameter spherical head model and takes into account the different conductances of the cerebrospinal fluid, skull and scalp (Scherg, 1990). The *X* axis of the coordinate system is a line joining electrodes Fpz and Oz, the *Y* axis passes through T3 and T4, and the vertical *Z* axis passes through the center of the head and electrode Cz. The most important requirement for a dipole analysis using BESA is that the number of parameters to be determined (6; 3 for location and 3 for dipole moment) does not exceed the number of constraints (number of electrodes, 58 in this study).

For each component described in this study, we introduced dipole pairs (10 ms around the peak) symmetrically located along the sagittal plane in each subject for FACES averages. When the numerical solution (percentage of variance in the voltage surface observed) or the physiological validity criteria was unsatisfactory, another pair of dipoles was introduced in the system.

3. Results

3.1. Behavioral data

Correct latencies and error rates are presented in Table 1. Latencies were computed on the trials for which the corresponding ERPs had been averaged. For error rates, we considered the trials which fitted the criteria of repetition (3 or 4, depending on the averages).

First, the latencies for FACES and CONT averages were compared using the paired *t* test which was statistically significant ($t_8 = 5.07$; $P = 0.001$): latencies were shorter when faces were presented compared to control stimuli. Longer reaction times were also observed in the CONT task when only one dot was present on the pattern (917 ms; 847 ms for two dots; paired *t* test: $P = 0.05$). Then, the 4 face averages were subjected to a two-way repeated measure ANOVA. The two factors were familiarity (known, unknown) and task (gender, recognition). There was a main effect of task ($F(1,8) = 11.81$; $P < 0.009$), the gender discrimination task being performed faster than the recognition task; and a main effect of familiarity ($F(1,8) = 22.27$; $P < 0.002$, slower responses for unknown than for known stimuli). Interestingly, the interaction was also highly significant ($F(1,8) = 21.12$; $P = 0.002$), mainly due to an increase of latencies in the recognition task on unknown stimuli (RECU). This last result was confirmed by a post hoc *t* test ($P < 0.001$). There was also a significant difference between the two recognition tasks ($P < 0.001$). All other contrasts were not significant.

A similar analysis on error rates was carried out. The only difference which was statistically significant was between FACES and CONT averages (paired *t* test; $t_8 = 8.76$; $P = 0.001$). The 2×2 ANOVA on face conditions showed no effect of any of these two factors (task: $F(1,8) = 1.15$; $P = 0.305$; familiarity: $F(3,8) = 1.11$; $P = 0.313$), and no interaction ($F(3,8) = 0.964$; $P = 0.346$).

3.2. Event-related potentials

3.2.1. Description of components and statistical evaluation

Following the stimulation, 3 clear components were observed for all subjects in all conditions (except for a few exceptions, see below). These electrophysiological events were named according to their order of occurrence and polarity (Figs. 3 and 4; Table 2) as P1 (occipital), VPP (central) and N2 (central).

3.2.1.1. P1 The first measurable electrophysiological event was the P1 which culminated (Oz) at 108 ms (CONT) or 110 ms (FACES) with a higher inter-subject variability for the CONT (SD 15 ms) condition than for the FACES average (SD 8 ms) (Table 2). Topographically, the P1 was characterized in all (but one) subjects by a large positivity over all the posterior (occipital) electrodes with polarity reversal at central and frontal sites (Figs. 3 and 4). There was not any significant

Table 2
Mean latencies (ms, SD) for the 3 electrophysiological events recorded in this study[a]

	CONT	FACES	GUF	GKF	RECU	RECK
P1 (Oz)	108 (15)	110 8)	110 (9)	109 (10)	111 (9)	110 (7)
VPP (Cz)	152 (12)	158 (8)	157 (8)	160 (9)	158 (8)	158 (6)
N2 (Cz)	228 (19)	230 (17)	229 (21)	232 (17)	227 (18)	226 (16)

[a] CONT, control task; FACES, average on all face conditions; GUF, gender task, unknown faces; GKF, gender task, known faces; RECU, recognition task; unknown faces; RECK, recognition task; known faces.

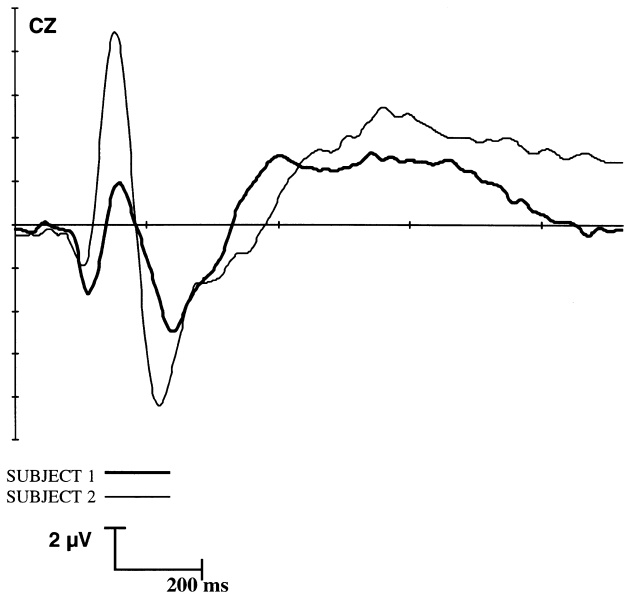


Fig. 5. Variability of the VPP. The ERPs recorded at Cz for two different subjects show the very high inter-subject variability that may be observed for face related ERPs (FACES average).

difference between FACES and CONT for voltage amplitude of the P1 at Oz (FACES vs. CONT: $t = 0.499$; $P = 0.647$), although the mean amplitude was slightly larger for CONT average (Table 3).

An ANOVA on peak amplitudes with task (FACES-CONT) and lateralization (O1-O2) as factors did not reveal any significant effect (task: $F(1,7) = 5.11$, $P = 0.058$; lateralization: $F(1,7) = 1.98$, $P = 0.251$; interaction: $F(1,7) = 0.51$, $P = 0.496$), even if there was clearly a trend towards an amplitude superiority of the P1 peak for the CONT task.

Among face averages, the mean amplitudes of the P1 appeared higher for 7 subjects (out of 8) during the recognition tasks than the gender discrimination tasks (Fig. 4). An ANOVA with 3 factors, (1) task (gender or recognition), (2) familiarity (known or unknown) and (3) lateralization (O1-O2) confirmed a strong task effect ($F(1,7) = 17.487$; $P = 0.004$) while all other effects were not significant (familiarity: $F(1,7) = 1.319$; $P = 0.289$; lateralization: $F(1,7) = 1.413$, $P = 0.273$). The interactions did not reach significant levels (task × familiarity: $F(1,7) = 0.039$, $P = 0.850$; lateralization × familiarity: $F(1,7) = 4.747$, $P = 0.066$; task × lateralization: $F(1,7) = 0.322$, $P = 0.399$; triple interaction: $F(1,7) = 1.446$, $P = 0.268$).

An identical analysis was performed on the negative counterpart of the P1 at Cz at the same latencies. However, its amplitude did not differ between tasks, familiar or unfamiliar faces, or left or right (C1-C2) electrodes (task $F(1,7) = 0.819$; $P = 0.392$; familiarity: $F(1,7) = 0.431$; $P = 0.530$; lateralization: $F(1,7) = 2.453$, $P = 0.156$; task × familiarity: $F(1,7) = 0.020$, $P = 0.892$; lateralization × familiarity: $F(1,7) = 1.141$, $P = 0.264$; task × lateralization: $F(1,7) = 0.195$, $P = 0.671$; triple interaction: $F(1,7) = 1.629$, $P = 0.238$).

3.2.1.2. VPP The next major electrophysiological event corresponded to the so-called vertex positivity (VPP), which was easily discriminable in all subjects for FACES (mean latency ± SD, 158 ± 8 ms, Cz) and all other face averages (Table 2; Fig. 3 and Fig. 5). A relatively high inter-subject variability could be observed either on the time course or amplitude of the peak, which reverses polarity at occipital and temporal sites. This vertex positivity was also present for the CONT averaging in 7 subjects (152 ± 12 ms). However, the amplitude of this peak was clearly reduced in these subjects in CONT (0.86 mV) versus FACES averages (3.88 mV; $t_6 = 6.3$; $P = 0.001$; see Fig. 3, Table 3).

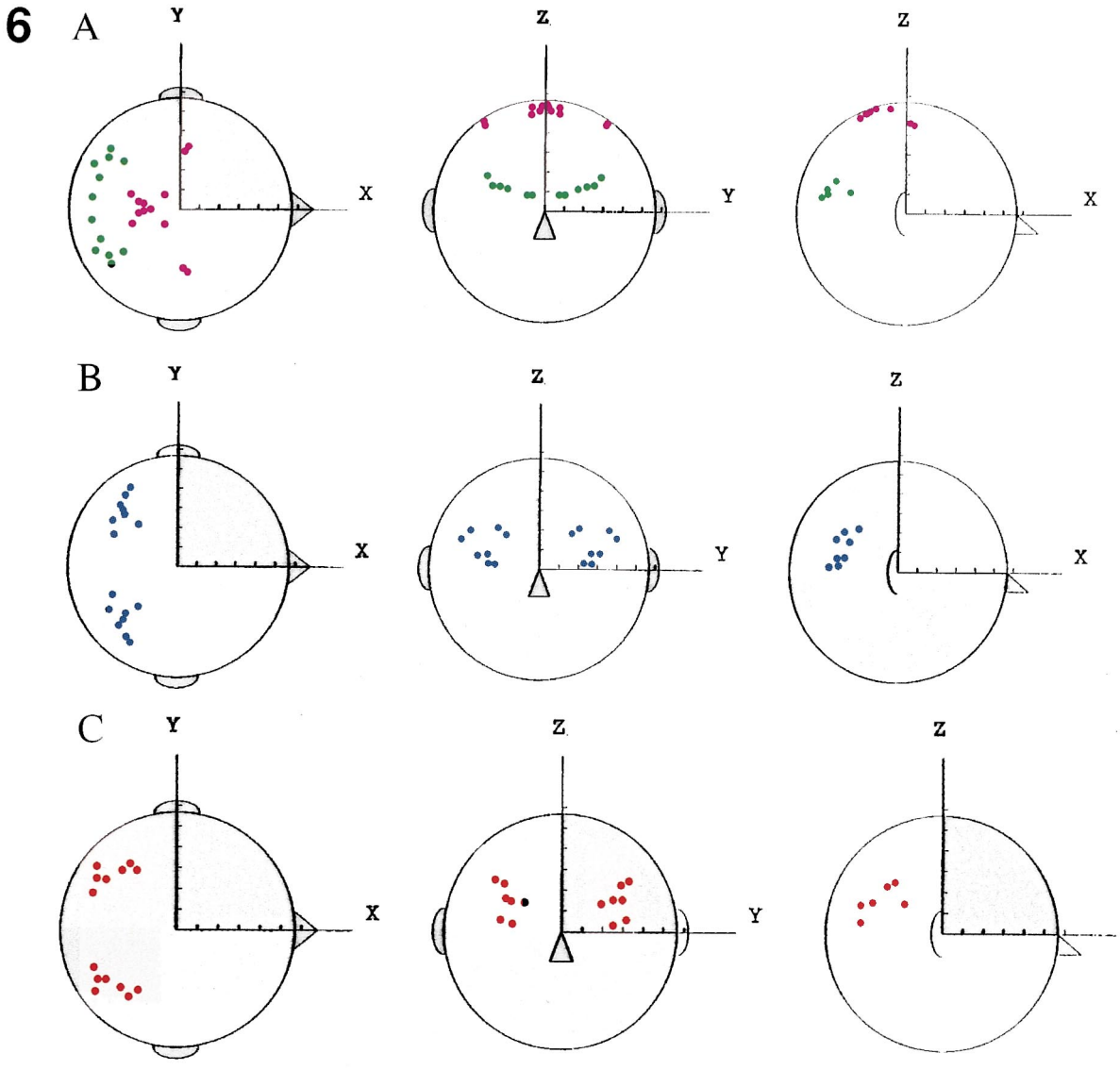
We then performed several analyses, in order to assess any influence of the face task or the familiarity of the face to this VPP activity. An ANOVA with task (gender, recognition) and familiarity as factors (known, unknown faces) failed to find any significant difference between face conditions: task: $F(1,8) = 0.218$, $P = 0.653$; familiarity: $F(1,8) = 0.516$, $P = 0.493$; interaction: $F(1,8) = 0.208$, $P = 0.660$). An ANOVA with lateralization (C1, C2), task and familiarity as factors was also computed. None of these factors had a significant effect on peak amplitudes of the VPP (lateralization: $F(1,8) = 2.264$; $P = 0.171$; task: $F(1,8) = 0.022$, $P = 0.887$; familiarity: $F(1,8) = 0.210$, $P = 0.659$; lateralization × task: $F(1,8) = 0.064$; $P = 0.807$; lateralization × familiarity: $F(1,8) = 0.349$;

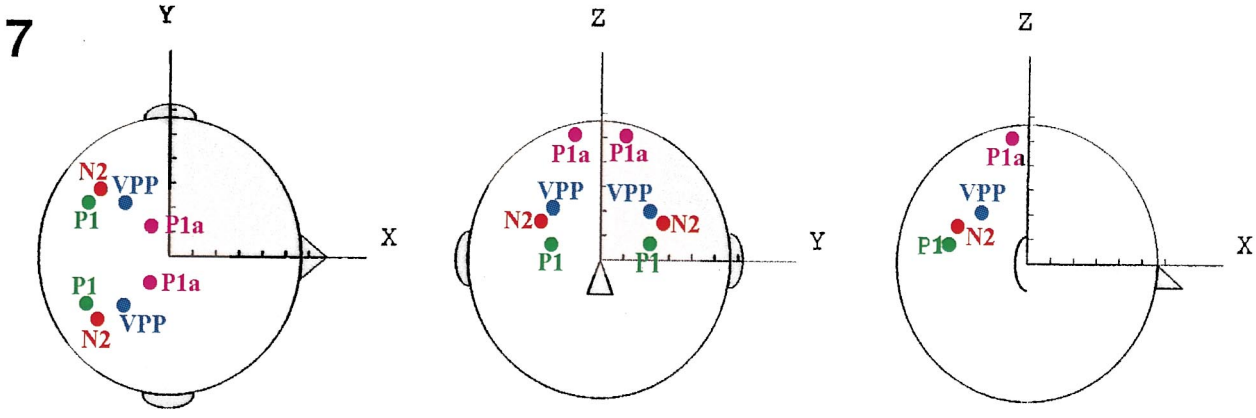
Table 3
Mean amplitudes (μV, SD) for the 3 electrophysiological events recorded in this study[a]

	CONT	FACES	GUF	GKF	RECU	RECK
P1 (Oz)	6.94 (3.15)	6.78 (3.21)	6.55 (3.75)	6.63 (2.92)	7.17 (3.53)	6.93 (2.78)
P1 (O1)	7.39 (2.73)	6.64 (3.06)	6.34 (3.53)	6.35 (2.72)	7.04 (3.11)	7.26 (2.8)
P1 (O2)	8.70 (4.34)	7.69 (4.98)	7.20 (5.16)	7.80 (4.48)	8.56 (5.12)	7.43 (4.41)
VPP (Cz)	0.86 (2.65)	3.88 (2.50)	4.00 (2.5)	3.99 (2.41)	4.16 (3.72)	3.39 (1.74)
N2 (Cz)	− 5.74 (2.96)	− 4.73 (2.53)	− 4.47 (2.37)	− 4.97 (2.96)	− 4.95 (3.43)	− 5.63 (2.48)

[a] Note the larger amplitudes for the P1 component during the recognition (compared with the gender discrimination tasks), particularly on the left side (O1 electrode). CONT, control task; FACES, average on all face conditions; GUF, gender task, unknown faces; GKF, gender task, known faces; RECU, recognition task; unknown faces; RECK, recognition task; known faces.

$P = 0.571$; task × familiarity: $F(1,8) = 0.202$; $P = 0.665$; triple interaction: $F(1,8) = 5.117$; $P = 0.054$). Finally, this analysis was also extended to more lateral electrodes (C3 and C4) This latter analysis had electrodes, task, familiarity and lateralization as factors. There was a significant effect of electrodes ($F(1,8) = 8.825$, $P = 0.018$), due to the larger amplitudes for central (C1-C2, closer to CZ, where the maximum voltage amplitude is recorded) electrodes and a





significant interaction between lateralization and electrodes ($F(1,8) = 7.844$, $P = 0.023$), due to a decrease in amplitude for more lateralized electrodes that was larger on the left side (C3) than on the right side (C4). To support this right superiority, there was a general trend for a larger amplitude on the right side, although it was not statistically significant ($F(1,8) = 4.487$, $P = 0.059$).

At about the same latency as the VPP, there were also corresponding temporal negativities recorded maximally at T5 and T6 (Fig. 2) for both FACES (T5: 157 ± 9 ms; T6: 158 ± 9 ms) and CONT (T5: 150 ± 13 ms; T6: 154 ± 13 ms) averages. These merely appeared as relative negativities (decrease in positive amplitude) for 5 subjects in the CONT average. Identical statistical tests as those for the VPP were applied to these negativities which appeared clearly larger for FACES than CONT (ANOVA 2×2, task: $F(1,8) = 45.811$, $P < 0.0001$; lateralization: $F(1,8) = 1.106$, $P = 0.324$; interaction: $F(1,8) = 0,930$, $P = 0,363$). However, as for the VPP, there were no differences among face conditions, nor lateralization effects, as confirmed by an ANOVA (task: $F(1,8) = 2.908$, $P = 0.127$; familiarity: $F(1,8) = 1.677$, $P = 0.231$; lateralization: $F(1,8) = 0.380$, $P = 0.555$; task × familiarity: $F(1,8) = 0.657$, $P = 0.441$; lateralization × familiarity: $F(1,8) = 0.457$, $P = 0.518$; task × lateralization: $F(1,8) = 0.238$, $P = 0.639$; triple interaction: $F(1,8) = 2.466$, $P = 0.155$). Two close occipito-temporal electrodes (CB1 and CB2; Fig. 2) were also added to analyze the NT components and a similar ANOVA (4 factors: electrodes, task, familiarity and lateralization) was performed. There was not any significant effect or trend for this analysis.

3.2.1.3. N200 Following the VPP, there was a CZ negativity (Oz positivity) occurring around 230 ms (Cz, SD = 17 ms) for FACES and 229 ms for CONT (SD = 19 ms) averages (Fig. 3). There was no amplitude difference between the two averages ($t_8 = 2.464$; $P = 0.269$). The N200 component was also tested at CZ (ANOVA 2, repeated measures, task and familiarity as factors). There was a trend for the factor task to be significant ($F(1,8) = 4.699$, $P = 0.062$). This task modulation was found to be significant with C1 and C2 in the analysis as well as with additional electrodes (C3 and C4, see below). For the analysis made on CZ, other effects were not significant although there was a slight trend for a familiarity effect ($F(1,8) = 4.259$, $P = 0.073$) which was not supported by further analyses made on this component.

An ANOVA with task, familiarity and lateralization (C1-C2) as factors was computed on the face averages and showed a significant effect of task ($F(1,8) = 5.833$, $P = 0,042$), reflecting an amplitude superiority for the recognition tasks. The triple interaction was also significant ($F(1,8) = 10.011$, $P = 0,013$) due to the fact that, while all mean amplitudes were superior when familiar faces and recognition tasks were used, the recognition task on known faces (RECK) gave smaller amplitudes for N2 only at the right (C2) electrode than for the same task on unknown faces. All other effects did not reach statistical significance (familiarity: $F(1,8) = 0.199$; $P = 0.667$; lateralization: $F(1,8) = 4.615$, $P = 0.064$; task × familiarity: $F(1,8) = 0.167$, $P = 0.694$; lateralization × familiarity: $F(1,8) = 0.837$, $P = 0.387$; task × lateralization: $F(1,8) = 0.598$, $P = 0.461$). The analysis performed with C3 and C4 electrodes and 4 factors (electrodes, task, familiarity and lateralization) confirmed the task effect on N2 ($F(1,8) = 5.859$, $P = 0.042$) and there was also a trend for the electrode factor ($F(1,8) = 4.765$, $P = 0.061$) due to a decrease in amplitude for more lateralized electrodes (C3 and C4) as compared with C1 and C2.

3.3. Dipole localization

Dipole localization was carried out for each subject individually on the 3 components (Fig. 4) identified in this study. As these results must be accepted with some caution for the above-mentioned reasons and the obvious difference between the spherical head model used and the real brains of subjects, no relationships between the dipole configurations which were found, and the anatomical structures probably involved in the recorded ERPs will be made in this section and will be reserved for Section 4.

3.3.1. P1

A clear P1 was observed in 8 subjects out of 9. The dipole localization procedure was achieved successfully in 6 subjects (out of 8). The percentage of variance explained was acceptable for a seventh subject (95.5) and very good for the last one (98.6), but both gave neurophysiologically unplausible solutions which may be due to a weaker signal-to-noise ratio observed in the time window of the P1/N1 complex. A first modelization with a single pair of dipoles did not give a satisfactory solution; the dipoles being localized in anterior regions of the brain, a result strongly contradictory to the probable sources of the P1 in occipito-lateral regions (Clark et al., 1996; Gomez et al.,

Fig. 6. Source locations (dipole models) on the spherical model for the 3 components described in this study for all subjects (FACES average). Upper row (A). Source locations for the P1/N1 component (6 subjects, FACES average). Two dipole pairs were introduced simultaneously to get an acceptable numerical (variance between 97.5 and 99.1%) and neurophysiological solution. Middle row (B). Dipoles models explaining possible sources of the VPP component (8 subjects; FACES average; variance between 94.6 and 99%). Lower row (C). Dipole models explaining possible sources of the N2 component (8 subjects; FACES average; variance between 95.6 and 98.5%).

Fig. 7. Mean source locations for the 3 components described in this study. Note the close position in the spherical model of dipoles accounting for VPP and N2 and the two dipole solution found for the P1 component.

1994). A plausible solution, which gave very high signal-to-noise ratios (between 97.5 and 99.1%), was found when two pairs of dipoles were introduced simultaneously. One pair was located 67 mm posterior, 36 mm lateral and 13 mm (mean values across subjects) above the center of the spherical head model (Figs. 6 and 7). Dipole strengths, which were not constrained, did not differ between left and right sides of the brain (paired t test, $P = 0.57$). The other pair was located more anteriorly (14 mm posterior) and less laterally (23 mm) and occupied the roof of the head model (87 mm above the center of the sphere), with no momentum differences between the left and right sides (paired t test, $P = 0.28$).

3.3.2. VPP (VPP)

A plausible solution, both in terms of numerical validity (variance between 94.6 and 99%) and physiological plausibility, was found when a single dipole pair was introduced in the time epoch of 10 ms around the VPP peak for 8 subjects[8]. When two pairs of dipoles were introduced, the percentage of variance increased significantly (between 94.2 and 99.3%; paired t test: 0.014). However, contrary to what was found for the P1, the two dipole pairs were located remarkably at virtually the same place in the spherical head model (mean distance = 1 mm antero-posterior; 6 mm laterally and 1 mm vertically). These small differences are absolutely meaningless when one considers the spatial resolution of the ERP generator localization in neurophysiology (Swick et al., 1994), and so the single, economical, dipole pair solution was kept. These dipoles were found 49 mm posterior, 48 mm lateral and 21 mm above the center of the spherical head model (Figs. 6 and 7).

3.3.3. N200

For the N2 component, we found a satisfactory solution with one pair of dipoles (variance between 95.6 and 98.5%) for 7 subjects. This component presented a very low signal-to-noise ratio for two other subjects. As for the VPP, variance increased significantly (between 95.1 and 99%; paired t test; $P = 0.019$) when another pair of dipoles was introduced in the system, but the two pairs also tended to locate at the same place (distance: $X = 12$ mm; $Y = 2$ mm; $Z = 0$ mm). The dipoles associated with the N2 component were found slightly more posteriorly (54 mm), less laterally (47 mm) and above (25 mm) the solution found for the VPP component (Fig. 6). In fact, the differences between the solutions found for both components, VPP and N2, were very small (5 mm in the X coordinate; 2 mm in the Y coordinate and 4 mm in the Z coordinate; Figs. 6 and 7).

[8] For one subject, it turned out to be impossible to find an acceptable numerical solution which could be explained by the weak (1,84 mV) amplitude of the peak and signal-to-noise ratio, as well as the lack of a reversing polarity at posterior sites which was clear in all other subjects (Fig. 4).

4. Discussion

4.1. Behavioral data

First, the control task turned out to be more complex than originally anticipated: it required a longer processing time and generated more errors than the other tasks. Among face conditions, the recognition task took longer than the gender categorization task, which is common in the literature (Sergent et al., 1994a). Processing of unknown stimuli also took more time than known stimuli, particularly for the recognition task (Sergent et al., 1994a). The absence of significant differences in processing times between known (636 ms) and unknown (649 ms) stimuli for the gender categorization task is consistent with a previous study (Bruce, 1986) aimed at demonstrating the absence of any role of familiarity on this task.

4.2. Event-related potentials

Three clear potentials were described in nearly all subjects both for face and visual pattern processing. All these components appeared as dipolar complexes and only one of them, namely the vertex positivity (occipito-temporal negativity) or VPP, occurring after more or less 160 ms following stimulus onset, appeared to be face-specific. Components occurring after 250 ms could not be easily and reliably observed in all or even a small subset of individual subjects, even if grand-average data (Campanella et al., 1999) show a large P3 component over centro-parietal sites. Several arguments could account for the lack of reliable and easily identifiable components after 250 ms. First, averages were made for each subject separately and on relatively few sweeps by condition. Signal-to-noise ratio is thus not as strong as usually observed in classical ERPs studies. Secondly, we used a rather conservative procedure as we did not account for the analyses ERPs that could be observed on grand average data, but not in less than 7 subjects out of 9. Finally, as noted by Dehaene (1996), when ERPs are averaged time-locked to stimulus onset, as in this study, the factors related to early processing stages will not be affected much by the variance of earlier processes. However, later stages can be highly affected by differences in the duration of the preceding stages, due either to experimental factors or to trial-to-trial variability or, as in this study, by inter-subject variability.

4.2.1. P1 and visual selective attention

The first positive peak observed corresponds to the P1. The centro-frontal negativity (Figs. 3 and 4) occurring with a similar latency can be considered as the negative counterpart of this dipole. A striate and extrastriate origin has been proposed for this P1 component (Gomez et al., 1994; Heinze et al., 1994). The voltage maps and the dipole localization obtained in the present study are partially coherent with this view. Indeed, the posterior lateral locations of the first pair

of dipoles is compatible with an extrastriate location of the P1 generators, as found in previous studies (Clark et al., 1995; Gomez et al., 1994). However, a second pair of dipoles which located somewhat in posterior parietal regions had to be introduced to obtain this posterior localization of the first pair. This observation suggests a parallel activation of the dorsal stream of the brain, which is known to be involved in spatial processing of the stimulus. Even if faces activate mainly structures of the ventral stream, it is clear that an accurate perceptual representation cannot be formed if the stimulus information is not extracted by the two pathways and later re-integrated (Robertson et al., 1997).

A task modulation of the P1 activity was observed in the present study, its amplitude being larger during face recognition tasks than during gender discrimination tasks. At first glance, one may find it surprising to observe a modulation of a relatively early visual potential to stimuli of identical luminosity, contrast and complexity. However, as illustrated by the behavioral data recorded, task complexity is not kept equivalent among (face) tasks: the recognition of pre-learnt individual photographs took more time and probably required more attentional resources than the gender categorization task, which is a less subtle and easier discrimination. Modulation of P1 amplitude, as found in this study, may thus reflect an attentional modulatory effect on occipital visual areas. Such attentional modulations of the P1 component have been described in several previous ERP studies (Clark and Hillyard, 1996; Eason et al., 1969; Rugg et al., 1987). In agreement with these electrophysiological findings, several PET studies of human visual information processing have shown modulations (increases) of blood flow in medial visual regions during active discriminations on a visual stimulus in contrast to passive viewing (Corbetta et al., 1990, 1991, 1995; Petersen et al., 1990; Raichle et al., 1994). Both these ERP and PET studies suggest that selective and non-selective[9] attentional, top-down, mechanisms may act to amplify the neural activity in early visual areas (Clark and Hillyard, 1996; Shulman et al., 1997). A strong argument in favor of a selective attentional mechanism in the present study comes from the fact that a non-selective increase of general arousal should normally have the same effect on all electrophysiological components observed. Accordingly, a task modulation of amplitude should be observed for the VPP (taking place 50 ms or so after the P1 component), which is clearly not the case in our study (see below). Clark and Hillyard (1996) recently observed a strong increase of visual P1 amplitude due to spatial selective attention mechanisms. Combining ERP and PET, Heinze et al. (1994) also demonstrated that visual inputs from attended locations enhanced processing in the extrastriate cortex (posterior fusiform gyrus) during the time course of the P1 component (80–130 ms after stimulus onset). The present study suggests that non-spatial attention, such that attending to particular attributes of the face stimulus, may influence activity in the human occipito-temporal or ventral stream, in order to allow inputs from attended regions to gain preferential access to higher stages of feature analysis, pattern identification and object recognition[10].

4.2.2. The VPP as a face specific potential

Many studies have described a VPP component with characteristics (latencies, amplitudes and topographies) comparable to the ones described in this study (Bötzel and Grüsser, 1989; Jeffreys and Tukmachi, 1992; Bötzel et al., 1995; George et al., 1996). This VPP is largely specific to face stimuli in the present study and thus confirms the results obtained in the aforementioned studies.

4.2.2.1. Relation between the vertex positivity and the temporal negativities Also in keeping with previous studies (George et al., 1996; Jeffreys, 1989), the VPP observed in our study reverses polarity at the level of temporal electrodes (T5 and T6; Figs. 2 and 3). Here, the amplitude of the temporal negativities is equal, indeed often larger than that of the vertex positivity itself (Fig. 3). This latter result proceeds from the choice in this study of a common average reference. Bötzel et al. (1995) have indeed demonstrated that the amplitude of the temporal negativities was equal to that of the VPP when a common average reference was used, but that these temporal negativities were minimized or masked when a mastoïd or earlobe reference was used, as in most previous studies (Jeffreys and Tukmachi, 1992; Jeffreys et al., 1992; Seeck and Grüsser, 1992), due to the close proximity of the earlobe to temporal sites. In this latter study, however, the authors argued that the negative potentials at the temporal electrodes peaked some 20 ms earlier than the vertex positive potential and that the two had probably different intracranial sources. However, a careful look at their data shows that the latency difference they refer to is the one obtained with the earlobe reference, and that a much smaller difference in latency (4 or 5 ms earlier for the temporal negativities than the VPP) is actually found in their study with a common average reference. In our study, the VPP and temporal negativities show remarkable temporal coincidence for each subject, as seen in the mean latencies for both components[11]. Using a nose reference, George et al. (1996) also observed a very small latency

[9] According to Shulman et al. (1997), top-down modulations can be separated into two general cases, selective and non-selective. In the selective case, performance of a task modulates a set of neurons concerned with a task, object or modality. In the non-selective case, performance of a task modulates all sensory responses irrespective of their task relevance. Non-selective modulations are often thought to reflect the effects of tonic or phasic arousal.

[10] Note that it would have been interesting to further test this task influence on the two dipole pairs found in the modelization. However, the small number of sweeps recorded in a task and the choice of a single subject method in this study did not provide a good enough signal-to-noise ratio to find plausible dipole solutions on either the gender discrimination task or the recognition task alone.

difference between the VPP and its negative counterpart. Moreover, careful observation of topographies (Fig. 4) reveals that the VPP is always associated, not only with temporal negativities but also with large negativities encompassing all posterior electrodes (Fig. 4). This observation argues for a single dipolar complex rather than two different generators. Another argument in favor of a dipolar complex rather than two distinct sources comes from the localization procedure used in this study. A satisfactory solution was found for 8 subjects with a single pair of dipoles and when a second pair was introduced, it located exactly at the same place as the first one in the sphere.

4.2.2.2. The VPP as a visual face process The present study shows that neither long-term familiarity for faces nor recognition tasks influence the characteristics of the VPP, a result for which a memory interpretation (Bötzel et al., 1995) of this component could hardly account. Rather, our results support the idea of the VPP being an early, essentially stimulus-related visual stage of face processing, as claimed by Jeffreys (1996). Previous differences between long-term familiar and unfamiliar faces have been described in the ERP literature (Barrett et al., 1988; Uhl et al., 1990; Münte et al., 1998), but they all concerned late potentials[12]. Although it might be critical to discuss non-significant effects, the absence of any long-term familiarity influence before 250 ms following stimulus onset supports Bruce and Young's cognitive model Bruce and Young (1986) of face processing for which any face – whether known or unknown – proceeds through identical initial stages of processing.

According to Jeffreys (1996), the VPP generators form part of the ''structural encoding'' component in Bruce and Young (1986) functional model of face processing, a component which provides an invariant face representation for several higher-level functional components. The absence of any (face) task modulation of the VPP component is all the more noticeable as both the preceding (P1) and following (N200) components were significantly influenced by the nature of the task on hand. If the VPP (and the occipito-temporal negativities) reflects a visual stage of face processing rather than memory operations, regions of the fusiform gyrus are certainly better candidates for being neural sources than the hippocampus, as it was previously suggested (Bötzel et al., 1995). Indeed, regions of the fusiform gyrus have been activated by nearly all face processing PET (Haxby et al., 1994; Sergent et al., 1994a,b) and fMRI studies (Clark et al., 1995; Sabbah et al., 1995; Puce et al., 1996; Kanwisher et al., 1997), whatever the task realized. Besides, intracerebral recordings of face-related activity (VPP or negative counterpart) have been described in the fusiform gyrus (Allison et al., 1994; Halgren et al., 1994). Moreover, preliminary results of a PET study carried out in our laboratory (Dubois et al., 1996, 1999), using the same tasks as in this ERP study, show that the only regions activated by all face tasks (compared with the dot discrimination task) were located in anterior (BA37) and posterior (BA19) parts of the fusiform gyrus. These activations were bilateral though a small quantitative (height and size of activity peaks, reflecting changes in rCBF) superiority was found in the right hemisphere (Dubois et al., 1996).

All these arguments support the idea of a stage of face (or object) processing taking place after 150–200 ms in regions of the fusiform gyrus of both hemispheres and giving rise to a dipolar complex at the surface of the scalp. Further work, combining good spatial and temporal resolution techniques, is needed to clarify the relationships between the neurophysiological and neuropsychological data.

4.2.3. N2: visual memory processing

This component may be certainly related to the visual scalp potential described by Begleiter et al. (1993), as well as by Hertz et al. (1994). These authors described a relative positive potential over posterior electrodes taking place at around 240 ms (C240), which corresponds to a negativity at Cz (reference in their study). The authors located the component, which was referred to as a visual memory potential (VMP), in the occipito-temporal region. Importantly, this component seemed to be involved in all visual processing, since it was observed for line diagrams without any apparent semantic representation in the first study (Begleiter et al., 1993), as well as for highly meaningful stimuli such as faces in the second study (Hertz et al., 1994). These observations are in line with our own findings of no amplitude difference between visual meaningless pattern stimuli and faces. Moreover, Hertz et al. (1994) observed a modulation of C240 amplitude for repeated faces especially when the task required explicit recognition, which might correspond to an amplitude diminution at posterior sites (the interpretation of the authors) or a larger negative potential recorded at the reference site (Cz) used in their study. Although the designs and objectives were clearly different in their study and in this experiment, our results (larger amplitude of the N2 for recognition tasks) support this second interpretation. The source localization algorithms used in this study have shown that the generators of the VPP and of the following N2 were very close to each other and the low spatial resolution of neurophysiological techniques (Swick et al., 1994) could not rule out the possibility of spatially overlapping generators. Functional properties and characteristics of the two components are,

[11] Mean latencies for the dipolar complex being (FACES): Cz: 158 ms; T5157; T6: 158 and (CONT): Cz: 152; T5: 150; T6: 154. Moreover, the correlation between T6 and Cz latencies for FACES average was 0.90 (T5 and Cz: 0,89).

[12] Although Seeck et al. (1993) observed differences between familiar and unfamiliar faces as early as 150 ms. However, these potentials were recorded intracranially in the amygdala of a single patient. In addition to the already mentioned difficulty of relating intracranial and external electrophysiological recordings, the amygdala is a subcortical structure from which it is difficult to record scalp potentials, due to its anatomical organization.

however, clearly different: while the VPP appears as a perceptual face-specific process, the N2 seems to be related to visual memory processing of any kind of stimuli. Further work is needed to determine the temporal characteristics of specific mechanisms and structures related to memory processes of human faces.

To summarize, this study has first shown that early visual components can be modulated by the kind of task performed. However, the very first face-specific component, the vertex positivity, is strictly stimulus-related. This observation is reinforced in the present study by the fact that both the preceding and following components of the VPP were found to be task-sensitive. Secondly, the timing of the VPP and NT components, the topographies and the source localization part of this study strongly suggest that the VPP and the temporal negativities share common generators, probably located in fusiform gyrus regions. Finally, this study demonstrates that, despite high inter-subject variability of the surface characteristics of the ERPs (Fig. 5), source localization can be remarkably constant for the subjects for which a satisfying solution is found (Fig. 6); a result which is very encouraging for further developments of dipole localization and single-subject analysis methods (Fig. 7).

Acknowledgements

The authors are grateful to James Haxby who provided the visual stimulus used in the control task of this study and to two anonymous reviewers for helpful comments on a previous version of this manuscript. The first author is supported by the Belgian National Fund for Scientific Research (F.N.R.S.).

References

Allison T, Ginter H, McCarthy G, Nobre AC, Puce A, Luby M, Spencer DD. Face recognition in human extrastriate cortex. J Neurophysiol 1994;2:821–823.

Barrett SE, Rugg MD, Perret DI. Event-related potentials and the matching of familiar and unfamiliar faces. Neuropsychologia 1988;1:105–117.

Begleiter H, Porjesz B, Wang W, Zhang G. A neurophysiologic correlate of visual short-term memory in humans. Electroenceph clin Neurophysiol 1993;87:46–53.

Bötzel K, Grüsser OJ. Electric brain potentials evoked by pictures of faces and non-faces: a search for 'face specific' EEG potentials. Exp Brain Res 1989;77:349–360.

Bötzel K, Schulze S, Stodieck RG. Scalp topography and analysis of intracranial sources of face-evoked potentials. Exp Brain Res 1995;104:135–143.

Brédart S, Bruyer R. The cognitive approach to familiar face processing in human subjects. Behav Proc 1994;33:213–232.

Bruce V. Influences of familiarity on the processing of faces. Perception 1986;15:387–397.

Bruce V, Young AW. Understanding face recognition. Br J Psychol 1986;77:305–327.

Bruce V, Ellis H, Gibling F, Young A. Parallel processing of the sex and familiarity of faces. Can J Psychol 1987;41:510–520.

Bruyer R. La reconnaissance des visages. Lausanne: Delachaux et Niestlé, 1990.

Campanella S, Gomez C, Rossion B, Delinte A, Debatisse D, Liard L, Dubois S, Bruyer R, Crommelinck M, Guérit J-M. Comparison between grand-average and individual analyses: an ERP study. Neurophysiol Clin, 1999; submitted.

Campbell R, Landis T, Regard M. Face recognition and lip-reading. Brain 1986;109:509–521.

Clark VP, Hillyard SA. Spatial selective attention affects early extrastriate components of the visual evoked potential. J Cogn Neurosci 1996;8:387–402.

Clark VP, Fan S, Hillyard SA. Identification of early visual evoked potential generators by retinotopic and topographic analyses. Hum Brain Mapping 1996;2:170–187.

Clark VP, Parasuraman R, Keil K, Maisog JMa, Ungerleider LG, Haxby JV. fMri studies of attention to color and face identity. Hum Brain Mapping 1995;(Suppl.1):32.

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE. Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. J Neurosci 1991;11:2383–2402.

Corbetta M, Shulman GL, Miezin FM, Petersen SE. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science 1995;270:802–805.

Corbetta M, Miezin M, Dobmeyer S, Shulman G, Petersen SE. Attentional modulation of neural processing of shape, color, and velocity in humans. Science 1990;248:1556–1559.

Dehaene S. The Organization of Brain Activations in Number Comparison: Event-Related Potentials and the additive-Factors Method. Journal of Cognitive Neuroscience, 1996;8:47–68.

Desimone R. Face-selective cells in the temporal cortex of monkeys. J Cogn Neurosci 1991;3:1–8.

Dubois S, Rossion B, Bruyer R, Dejardin S, Bodart JM, Michel C, Roucoux A. functional neuroanatomy of face processing with a PET study and a learning procedure. Neuroimage 1996;(Suppl.)3:270.

Dubois S, Rossion B, Schiltz C, Bodart J-M, Michel C, Bruyer R, Crommelinck M. Effect of ramiliarity on the procession of human races. Neuroimage (1999) in press.

Dupont P, Orban GA, Vogels R, Bormans G, Nuyts J, Schiepers C, De Roo M, Mortelmans L. Different perceptual tasks performed with the same visual stimulus attribute activate different regions of the human brain: a positron emission tomography study. Proc Natl Acad Sci USA 1993;90:10927–10931.

Eason R, Harter M, White C. Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. Physiol Behav 1969;4:283–289.

Etcoff NKL. Selective attention to facial identity and facial emotion. Neuropsychologia 1984;22:281–295.

George N. Etude des bases neurales de la reconnaissance des visages: apport des potentiels evoqués. Thèse de Doctorat de L'Université Paris 6, 1997 (non publiée).

George N, Evans J, Fiori N, Davidoff J, Renault B. Brain events related to normal and moderately scrambled faces. Cogn Brain Res 1996;4:65–76.

Gomez CM, Clark VP, Luck SJ, Fan S, Hillyard SA. Sources of attention-sensitive visual event-related potentials. Brain Topogr 1994;7:41–51.

Grüsser O-J, Landis T, Seeck M. The search for face-responsive components in the visual evoked potentials (EPs) of the human electroencephalogram. In: Grüsser O-J, Landis T, editors. Vision and visual dysfuction, 12. London: MacMillan, 1991.

Halgren E, Baudena P, Heit G, Clarke M, Marinkovic K. Spatio-temporal stages in face and word processing. 1. Depth-recorded potentials in the human occipital and parietal lobes. J Physiol 1994;88:1–50.

Haxby JV, Horwitz B, Ungerleider LG, Maisog JMa, Pietrini P, Grady CL. The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J Neurosci 1994;14:6336–6353.

Heinze HJ, Mangun GR, Burchert W, Hinrichs H, Scholz M, Münte TF, Gös A, Scherg M, Johannes S, Hundeshagen H, Gazzaniga MS, Hillyard SA. Combined spatial and temporal imaging of brain activity during selective attention in humans. Nature 1994;372:543–546.

Hertz S, Porjesz B, Begleiter H, Chorlian D. Event-related potentials to faces: the effect of priming and recognition. Electroenceph clin Neurophysiol 1994;92:342–351.

Jeffreys DA. A face-responsive potential recorded from the human scalp. Exp Brain Res 1989;78:193–202.

Jeffreys DA. evoked potential studies of face and object processing. Vis Cogn 1996;3:1–38.

Jeffreys DA, Tukmachi ESA. The vertex-positive scalp potential evoked by faces. Exp Brain Res 1992;91:340–350.

Jeffreys DA, Tukmachi ESA, Rockley G. Evoked potential evidence for human brain mechanisms that respond to single, fixated faces. Exp Brain Res 1992;91:351–362.

Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 1997;17:4302–4311.

Kendrick KH, Baldwin BA. Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. Science 1987;236:448–450.

Malone DR, Morris HH, McKay M, Levin H. Prosopagnosia: a double dissociation between the recognition of familiar and unfamiliar faces. J Neurol Neurosurg Psychiatry 1982;45:820–822.

Münte TF, Brack M, Grootheer O, Wieringa BM, Matzke M, Johannes S. Brain potentials reveal the timing of face identity and expression judgements. Neurosci Res 1998;30:25–34.

Oldfield RC. The assessment and analysis of handedness: The Edinburgh Inventory. Neuropsychologia 1971;9:97–113.

Perrett DI, Smith PA, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA. Proc R Soc Lond B Biol Sci 1985;223:293–317.

Petersen SE, Fox PT, Snyder AZ, Raichle ME. Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. Science 1990;249:1041–1044.

Puce A, Allison T, Asgari M, Gore JC, McCarthy G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J Neurosci 1996;16:5205–5215.

Raichle ME, Fiez JA, Videen TO, MacLeod AK, Pardo JV, Fox PT, Petersen SE. Practice-related changes in human brain functional anatomy during non-motor learning. Cereb Cortex 1994;4:8–26.

Robertson L, Treisman A, Friedman-Hill S, Grabowecky M. The interaction of spatial and object pathways: evidence from Balint's syndrome. J Cogn Neurosci 1997;3:295–317.

Rugg MD, Milner AD, Lines CR, Phalps R. Modulation of visual event-related potentials by spatial and non-spatial visual selective attention. Neuropsychologia 1987;25:85–96.

Sabbah P, de Schonen S, Salamon G, Briant F, Pascalis O. A fMRI study of face recognition. Human Brain Mapping 1995;S.46.

Scherg M. Fundamentals of dipole source potential analysis. In: Grandori F, Hoke M, Romani M, editors. Auditory evoked magnetic and electric potentials (Adv Audiol, Vol. 6), 6. Basel: Karger, 1990, p. 40.

Seeck M, Grüsser OJ. Category-related components in visual evoked potentials: photographs of faces, persons, flowers and tools as stimuli. Exp Brain Res 1992;92:338–349.

Seeck M, Mainwaring M, Ives J. Differential neural activity in the human temporal lobe evoked by faces of family members and friends. Ann Neurol 1993;34:369–372.

Sergent J, MacDonald B, Zuck E. Structural and functional organisation of knowledge about faces and proper names: a positron emission tomography study. In: Umiltà C, Moscovitch M, editors. Attention and performance XV, Cambridge: MIT Press, 1994, p. 203.

Sergent J, Otha S, Macdonald B, Zuck E. Segregated processing of facial identity and emotion in the human brain: a PET study. Vis Cogn 1994;1:349–369.

Shulman GL, Corbetta M, Buckner RL, Raichle ME, Fiez JA, Miezin FM, Petersen SE. Top-down modulation of early sensory cortex. Cereb Cortex 1997;7:193–206.

Swick D, Kutas M, Neville HJ. Localizing the neural generators of event-related potentials. In: Kertesz A, editor. Localization and neuroimaging in neuropsychology, New York: Academic Press, 1994, p. 73.

Uhl F, Lang W, Spieth F, Deecke L. Negative cortical potentials when classifying familiar and unfamiliar faces. Cortex 1990;26:157–161.

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ. Functional anatomy of a common semantic system for words and pictures. Nature 1996;383:254–256.

Warrington EK, James M. An experimental study of facial recognition in patients with unilateral cerebral lesion. Cortex 1967;3:317–326.

Young AW, Hay DC, Ellis AW. The faces that launched a thousand slips: everyday difficulties in recognizing people. Br J Psychol 1985;76:495–523.