# Enhanced Extrastriate Visual Response to Bandpass Spatial Frequency Filtered Fearful Faces: Time Course and Topographic Evoked-Potentials Mapping

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**Abstract:** We compared electrical brain responses to fearful vs. neutral facial expressions in healthy volunteers while they performed an orthogonal gender decision task. Face stimuli either had a broadband spatial-frequency content, or were filtered to create either low spatial-frequency (LSF) or high spatial-frequency (HSF) faces, always overlapped with their complementary SF content in upside-down orientation to preserve the total stimulus energy. We tested the hypothesis that the coarse LSF content of faces might be responsible for an early modulation of event-related potentials (ERPs) to fearful expressions. Consistent with previous findings, we show that broadband images of fearful faces, relative to neutral faces, elicit a higher global field power of approximately 130 ms poststimulus onset, corresponding to an increased P1 component over lateral occipital electrodes, with neural sources located within the extrastriate visual cortex. Bandpass filtering of faces strongly affected the latency and amplitude of ERPs, with a suppression of the normal N170 response for both LSF and HSF faces, irrespective of expression. Critically, we found that LSF information from fearful faces, unlike HSF information, produced a right-lateralized enhancement of the lateral occipital P1, without any change in the scalp topography, relative to unfiltered (broadband) fearful faces. These results demonstrate that an early P1 response to fear expression depends on a visual pathway preferentially tuned to coarse-magnocellular inputs, and can persist unchanged even when the N170 generators are disrupted by SF filtering. *Hum Brain Mapp 26:65–79, 2005.* © 2005 Wiley-Liss, Inc.

**Key words:** fear perception; P1; band-pass spatial frequency filtering; LSF; HSF; temporal segmentation; extrastriate visual cortex

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## INTRODUCTION

Several EEG or MEG studies in humans have explored the time-course of emotional face processing. In particular, negative facial expressions have been found to modulate the amplitude (sometimes the latency, see Williams et al. [2004]) of various evoked potential components over a large temporal window following face onset, from early perceptual responses [Ashley et al., 2004, Batty and Taylor, 2003; Halgren et al., 2000; Pizzagalli et al., 1999, 2002] through the face-selective N170 [Campanella et al., 2002] or other early occipito-temporal negativity [Sato et al., 2001; Schupp et al., 2004], to the amodal P3 wave [Carretie and Iglesias, 1995; Meinhardt and Pekrun, 2003; Liddell et al., 2004] and other late sustained modulations [Krolak-Salmon et al., 2001].

An early response to negative facial expressions has been observed across several of these studies for the visual P1 component, around 120 ms post-face onset, preceding the subsequent N1 and N170 usually associated with stimulus discrimination or categorization [Itier and Taylor, 2004a; Pizzagalli et al., 1999, 2002; Williams et al., 2004]. The P1 component is an exogenous sensory visual activity that is enhanced by selective attention and presumably generated within extrastriate visual cortex [Clark and Hillyard, 1996]. Increased P1 amplitude during the perception of threat-related (e.g., angry and fearful) relative to positive or neutral expressions might be consistent with behavioral [Pratto and John, 1991] and neuroimaging experiments [Armony and Dolan, 2002; Lang et al., 1998; Vuilleumier et al., 2001] showing that negative emotional events often tend to capture attention in an involuntary reflexive manner [Liddell et al., 2004; Pourtois et al., 2004]. However, such an early effect of facial expression might at first seem paradoxical, given that face detection processes are thought to involve a specialized neural system in inferotemporal cortex that is activated at a later time, around 150–200 ms poststimulus onset, as typically indexed by the face-selective N170 component measured over occipitotemporal electrodes [Bentin et al., 1996; Schweinberger et al., 2002] or by the N200 measured intracranially [Allison et al., 1994; McCarthy et al., 1999; Seeck et al., 2001]. Thus, it remains to be determined what stimulus attribute and/or perceptual process might be responsible for this early response to fearful face expressions, and what underlying neural substrates within the distributed occipitotemporal face network might be involved [Haxby et al., 2000].

In this context, new clues may come from recent fMRI findings [Vuilleumier et al., 2003] showing that the coarse, low spatial-frequency (LSF) information conveyed by faces is crucial to produce an activation to fearful relative to neutral faces in the amygdala, a key structure in emotional processing [LeDoux, 1996; Morris et al., 1999]. Conversely, the finer high spatial-frequency (HSF) information in faces was not found to evoke any differential response to fearful compared to neutral expressions in the amygdala, even though HSF faces generally produced greater activity in occipitotemporal cortex, including face-selective regions in fusiform gyrus [Haxby et al., 2000]. Furthermore, LSF fearful faces, relative to LSF neutral faces, can also produce a greater activation of fusiform cortex [Winston et al., 2003], as previously found for broadband images [Morris et al., 1998; Vuilleumier et al., 2001], whereas no such effect was found for HSF fearful faces, suggesting that an enhanced response in visual cortex for fearful expressions might also be primarily driven by LSF cues. Importantly, neurophysiological data indicate that LSF visual information is mainly carried by magnocellular channels, projecting to the dorsal parietal stream and subcortical structures more than to the ventral temporal stream [Leventhal et al., 1985], and is processed faster than HSF information transmitted by parvocellular pathways to the ventral stream [Bar, 2003; Bullier, 2001; Merigan and Maunsell, 1993]. Taken together, these results raise the hypothesis that LSF components in fearful face expressions might benefit from rapid processing and early access to the amygdala, either through a direct subcortical pathway involving visual pulvinar [Morris et al., 1999; Vuilleumier et al., 2003] or through an initial feedforward sweep of inputs within the visual system [Bullier, 2001; Foxe and Simpson, 2002], allowing a rapid enhancement of ventral temporal activations for fearful stimuli through extensive feedback projections from the amygdala to posterior brain areas [Amaral et al., 2003; Morris et al., 1998; Vuilleumier et al., 2001, 2004]. Such rapid feedback modulation of visual areas based on initial processing of LSF signals in frontal cortex might also play an important role for guiding visual attention [Bullier, 2001] and visual object recognition [Bar, 2003]. Similar mechanisms might thus act to enhance face-processing based on a rapid evaluation of affective value in amygdala, and potentially account for an early increase of occipital P1 responses (at ~120 ms) to negative faces, prior to the face-specific N170 responses (at ~150–170 ms) generated in ventral temporal pathways.

In the present study, we used high-density EEG recording to investigate the time course of emotional face-processing, and compared any differential effects of fearful vs. neutral faces when the critical expression information was presented in an LSF, HSF, or unfiltered image. Although scalp event-related potentials (ERPs) may not be suitable to register activity in deep and close-field structures such as the amygdala, we hypothesized that the high temporal resolution of EEG coupled with a systematic manipulation of emotional cues in different SF bands might enable us to explore the cortical processing of fearful signals from faces based on distinctive LSF cues vs. HSF cues. We predicted that a differential P1 activation within extrastriate cortex for fearful relative to neutral faces [e.g., Batty and Taylor, 2003; Pizzagalli et al., 1999; Williams et al., 2004] might selectively be evoked by LSF, but not HSF images. To control for the possible effects of low-level pictorial differences between LSF and HSF stimuli (e.g., total contrast energy), which might potentially arise when these are presented alone, we adapted a methodology from previous psychophysical work [Schyns and Oliva, 1994, 1999] and created a new type of "hybrid" stimuli by combining the LSF content of a given face (shown upright) with its opposite HSF content presented upside-down, or vice versa [see also Winston et al., 2003].
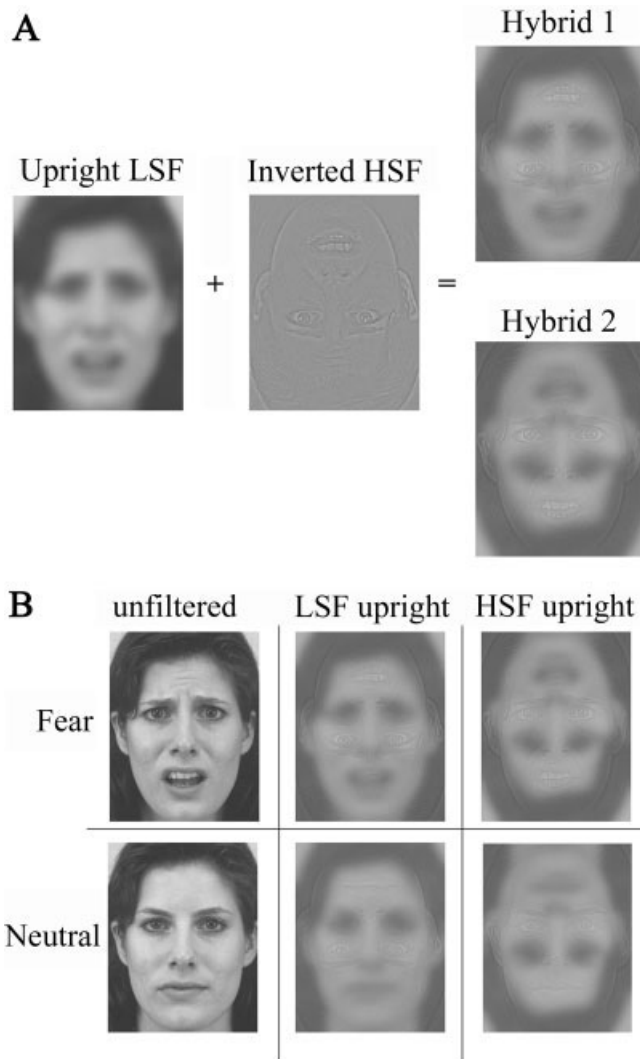
**Figure 1.**

Illustration of stimuli. **A:** Procedure used to create hybrid stimuli, combining the LSF with the HSF band of the same face stimulus, but in opposite plane orientations. With this procedure we created for each face stimulus two different hybrids with either the LSF or HSF in the upright orientation, keeping all low-level pictorial details constant between the LSF and HSF conditions. **B:** The six conditions (2 expressions × 3 spatial-frequency contents) used in our experiment.

This manipulation ensured that the physical properties of all face stimuli were kept constant, while the perception of emotion expression was disrupted by inversion for upside-down faces [Calder et al., 2000; Perrett et al., 1998; Rhodes et al., 1993; Searcy and Bartlett, 1996] but preserved for upright faces (see Fig. 1A,B). The robust advantage in perception for upright relative to inverted faces allowed our participants to perform a gender-decision task on the dominant upright faces and to ignore inverted faces, without the need to control explicitly for any differential allocation of attention

to LSF or HSF content in the stimulus (since two overlapped faces in the same upright orientations might otherwise lead to face perception being unpredictably dominated by either HSF and LSF information on any given trial; see Schyns and Oliva [1999]; Winston et al. [2003]). Based on this well-known advantage of upright faces, an effect of emotional expression in our hybrid stimuli was predicted to result from upright faces (whereas the corresponding stimuli with the same faces presented inverted were predicted to show no effect of expression). As a baseline condition, our participants were also tested on intact broadband images of the same fearful and neutral faces. In addition to a modulation of the lateral occipital P1 as a function of expression in upright faces and LSF content, we also conducted a complementary spatial cluster analysis [Michel et al., 1999] on a larger time window including the face-selective N170, in combination with a distributed source localization approach [Grave de Peralta et al., 2001] providing fine-grained topographic information on neural generators responsible for the observed effects.

## SUBJECTS AND METHODS

### Participants

Participants were 13 right-handed psychology and medical students (nine female, mean age 22 years, SD: 2.5 years) from the University of Geneva. All participants had normal or corrected to normal vision and were free of neurological or psychiatric history. After the EEG session, participants completed the Spielberger State-Trait Anxiety Inventory (STAI) [Spielberger, 1983]. Participants' state anxiety scores ranged from 22–35 (mean = 26.9, SD = 3.6), and their trait anxiety scores ranged from 26–47 (mean = 37.5, SD = 7.3). These scores are within the normal range, corresponding to the low trait and low state anxiety category (between 20 and 39) according to published norms [Spielberger, 1983].

### Materials

We used a large number of standardized fearful and neutral faces (80 different identities, half of each gender), taken from the Karolinska Directed Emotional Faces set (KDEF, D. Lundqvist, A. Flykt, A. Öhman, Dept. of Neurosciences, Karolinska Hospital, Stockholm, Sweden, 1998) and our own stimulus set [similar to Vuilleumier et al., 2003]. All stimuli were black-and-white photographs (256 gray levels), with faces enclosed in a rectangular frame excluding most of the hair and nonfacial contours. Spatial frequency content in the original stimuli (n = 160 faces, 80 for each emotion category) was filtered using a high-pass cut-off > 24 cycles/image for the HSF stimuli, and a low-pass cut-off of < 6 cycles/image for the LSF stimuli [see Vuilleumier et al., 2003]. The mean contrast values were matched across pairs of LSF and HSF images [Schyns and Oliva, 1994]. We then created a pool of 640 different hybrids (Fig. 1A) by combining for each identity and for each emotion category (80 fearful and 80 neutral) the resulting LSF image with its corresponding HSF image

in inverted orientation (total: 320 hybrids, 2 expressions × 80 identities × 2 orientations). Crucially, these combinations of two SF images in opposite orientations (i.e., one SF upright and the other rotated 180 degrees in the picture-plane) were used to produce two different versions of the same hybrid stimuli (Fig. 1B), with either the LSF or the HSF presented in upright orientation, thus resulting in four possible types of hybrids in total (Fig. 1B). This manipulation ensured that the exact same picture was used to study the processing of either LSF or HSF faces, depending on which SF range was presented in the upright orientation (while the concurrent SF range presented inverted in the background was not consistently perceived as a face at the short exposure durations used here, see below). We also created another set of 320 hybrids combining for each face identity the LSF image in one emotion category (either neutral of fearful) with the HSF image for the other emotion of the same face identity. We created this second set of 320 hybrids to allow the repetition of a given face identity within a given SF against two different backgrounds (corresponding to the two emotions categories used), while avoiding the repetition of the same image.

## Procedure

Participants were seated in a shielded room in front of the computer screen (viewing distance: 70 cm). Behavior was monitored by closed-circuit TV. The session began with one practice block of 30 trials, followed by three experimental blocks of 80 trials each, with a brief pause between blocks. Each subject was first presented with 160 different hybrids (i.e., 20 different face identities × 2 SF × 2 expressions × 2 presentations with a different inverted face background), in random order, during the two experimental blocks. Unfiltered faces were presented at the end of the session, during a final third block (the same 20 face identities × 2 emotion expressions × 2 presentations). This order was chosen to avoid uncontrolled interactions due to unequal repetition-priming effects from unfiltered to filtered pictures that might have contaminated the processing of LSF or HSF faces [e.g., George et al., 1999; Vuilleumier et al., 2003].

Each trial began with a fixation cross for 250 ms, followed after a 250-ms delay by a brief presentation of the face stimulus for 250 ms. All stimuli were presented centrally. Following offset of the face pair, a dark screen interval was presented randomly for 850, 900, 950, 1,000, or 1,050 ms, allowing a behavioral response and serving as a variable intertrial interval to minimize any anticipation and/or motor preparation. Reaction time (RT) was recorded from face onset.

Participants were asked to perform a gender categorization task on each upright face (male/female) by pressing one of two buttons of the response box with their dominant hand. They were explicitly told that features from upside-down faces could be ignored. An indirect gender decision task was chosen because previous psychophysical work has shown that behavioral performance on this task is unaffected by the specific spatial frequency content available in the face stimulus (i.e., LSF or HSF), in contrast with emotion

expression judgments or face identification tasks [see Schyns and Oliva, 1999; Vuilleumier et al., 2003].

## Data Acquisition

Visual event-related brain potentials (VEPs) were recorded and processed using a Neuroscan 64 channels (Synamps). Horizontal and vertical EOG were monitored using four facial bipolar electrodes placed on the outer canthi of the eyes and in the inferior and superior areas of the left orbit. Scalp EEG was recorded from 62 Ag/AgCl electrodes mounted in a quickcap (extended 10–20 system) with a linked-mastoids reference, amplified with a gain of 30 K and bandpass filtered at 0.01–100 Hz with a 50-Hz notch filter. Impedance was kept below 5 kΩ. EEG and EOG were continuously acquired at a rate of 500 Hz and stored for offline averaging. EEG was corrected for eye blinks by the subtraction of PCA-transformed EOG components for each electrode, weighted according to VEOG propagation factors [Gratton et al., 1983]. After removal of EEG and EOG artifacts (epochs with EEG or residual EOG exceeding 70 μV were excluded from the averaging), epoching was made for 100 ms prior to visual stimulus onset and 400 ms after stimulus presentation. A baseline correction on the prestimulus interval (–100/0 ms) was computed on each individual epoch prior to averaging. Averaged ERPs were re-referenced offline using a common average-reference [Tucker et al., 1994]. Data were low-pass filtered at 30 Hz.

## Data Analysis

### P1 and global field power (GFP)

First, we performed a traditional waveform analysis [Picton et al., 2000] and analyzed amplitude changes in lateral occipital P1 [see Luck et al., 1990] as a function of emotional expression (either neutral or fearful) and stimulus condition (HSF, LSF, or unfiltered upright face). Because we used an orthogonal gender decision task and concentrated on exogenous stimulus-driven visual responses over occipital regions, we report VEP components pooling across both the correct and the more infrequent incorrect trials (there was no difference in error rates or RTs between the critical LSF and HSF face conditions; see below). Amplitudes of the P1 were quantified in terms of mean voltage within a specified latency window (centered on the component's peak), relative to a 100-ms prestimulus baseline. Latency analyses of the P1 component were also performed. This component was maximal at posterior electrodes PO7/P7 and PO8/P8 in the left and right hemisphere, respectively (mean latency 117.3 ms). These sites were selected in accordance with related emotion effects in previous ERP studies [Batty and Taylor, 2003; Pizzagalli et al., 1999] and with the prominent topographic properties of the current data (see Fig. 2 and next section). For each SF condition (low, high, and broadband), emotional effects were tested by comparing the mean amplitude of the P1 component evoked by a fearful vs. neutral expression in the upright face. Repeated-measures analyses of variance
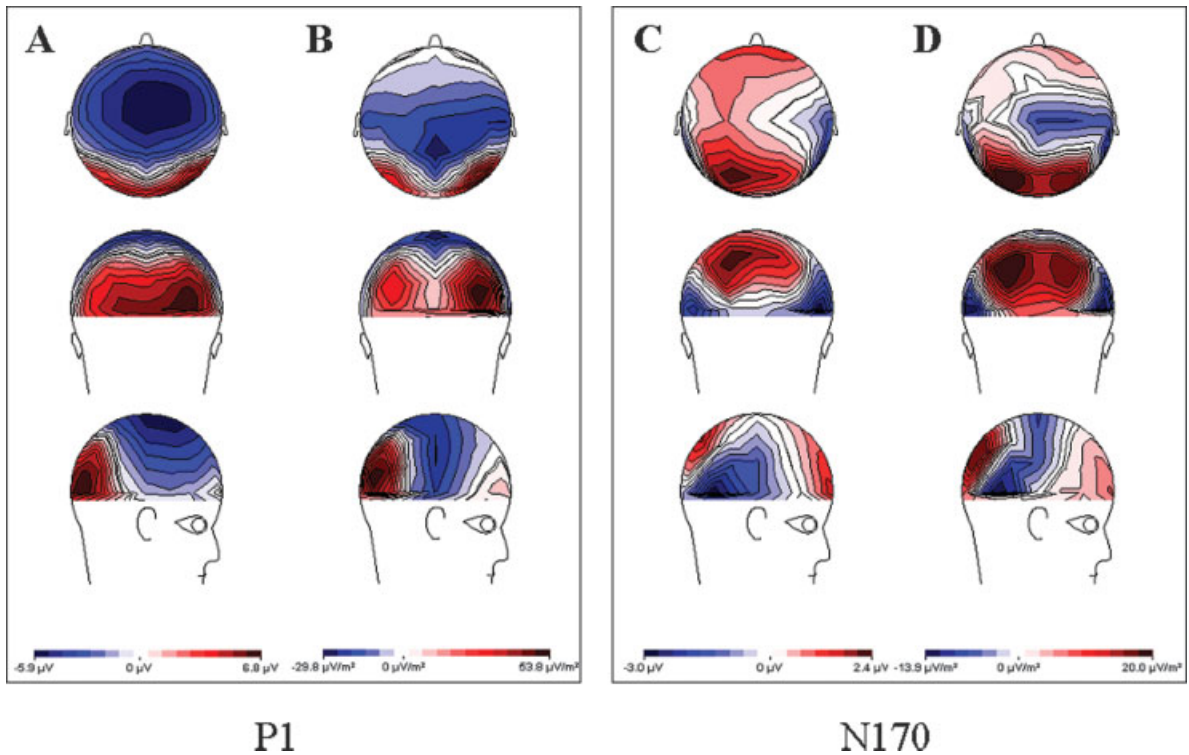
**Figure 2.**
Scalp electrical topographies. **A,C:** Voltage maps and (**B,D**) scalp current densities [Perrin et al., 1989] of the P1 (110 ms) and N170 (170 ms) components, respectively, in the baseline unfiltered face condition (averaged across fear + neutral expressions). Top, back, and right views are presented. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

(ANOVAs) were used, with a Greenhouse–Geisser correction for nonsphericity when required.

As a complement to the P1 waveform analysis, we also determined global changes in electric field strength by calculating the GFP [see Lehmann and Skrandies, 1980] for each subject and each condition. GFP is equivalent to the spatial standard deviation of the electric field distributed over the whole scalp, with larger values for stronger electric fields, and is calculated as the square root of the mean of the squared value recorded at each electrode (vs. the average reference). For each SF condition (low, high, and unfiltered), we applied a point-wise paired $t$-test comparing GFP values for fearful vs. neutral faces with a 10-point temporal criterion for significance. Thus, the first time point (from −100 ms to +400 ms) where the $t$-test was significant (with the 0.05 alpha criterion) for at least 10 consecutive data points (i.e., ≥20 ms at 500 Hz digitization rate) was considered as the onset of a genuine GFP change [Guthrie and Buchwald, 1991].

### Topographic pattern and segmentation analysis

A significant waveform or GFP modulation does not exclude the possibility of concurrent changes in electrical field topography that may not be easily detected when examining amplitude changes in particular components at a few predefined electrodes only [Lehmann and Skrandies, 1980;

Michel et al., 1999, 2001]. Such changes in topography provide important additional information about the spatiotemporal dynamic of visual processing, since they may reflect the activation of distinct neural generators. To characterize topographic modulations over time and conditions, we applied a pattern or spatial cluster analysis [Pascual-Marqui et al., 1995], taking into account the evolution of the scalp field configuration on a millisecond basis, from 50 ms poststimulus onset until 400 ms poststimulus. This topographic analysis can efficiently summarize ERP data by a limited number of field configurations, previously referred to as functional "microstates" [Lehmann, 1987; Michel et al., 1999].

As described in detail elsewhere [e.g., Michel et al., 1999, 2001], we first performed a topographic pattern analysis on the group-averaged data over a large temporal window (from 50–400 ms post-face onset) using a spatiotemporal segmentation algorithm (using CARTOOL software, v. 3.0; developed by D. Brunet, Functional Brain Mapping Laboratory, Geneva, Switzerland), and then fitted the segmentation results to individual data for subsequent statistical testing. This spatiotemporal segmentation algorithm is derived from spatial cluster analysis by the K-means method [Pascual-Marqui et al., 1995] and allows identification of the most dominant scalp topographies appearing in the ERPs from each condition and over time. The optimal number of topo-

graphic maps explaining the whole dataset is determined objectively by a cross-validation criterion [Pascual-Marqui et al., 1995]. Since only landscape differences are of interest, the maps are first scaled to unitary strength by dividing the voltage at each electrode by the GFP. The dominant scalp topographies (identified in the group-averaged data) are then fitted to the ERPs of each individual subject using spatial fitting procedures, to quantify their representation across subjects and conditions. The global explained variance (or goodness of fit) provides a critical index of the significance of a given topography. It represents the sum of the explained variance weighted by the GFP at each moment in time. This procedure can thus provide fine-grained quantitative values regarding the timing, size, relative variance, and field strength of the different scalp topographies, not available otherwise using a classical component analysis [Michel et al., 1999]. Global explained variance values obtained from this analysis were entered in a repeated-measure ANOVA to compare the different experimental conditions.

### Source localization

Finally, to estimate the likely neural sources underlying the electrical field configurations identified by the previous analyses, we used a distributed linear inverse solution based on a local auto-regressive average (LAURA) model for the unknown current density in the brain [Grave de Peralta et al., 2001]. This source localization technique provides a linear distributed inverse solution, using a realistic head model with a solution space of 4024 lead field nodes, selected from a $6 \times 6 \times 6$ mm grid equally distributed within the gray matter of the Montreal Neurological Institute (MNI) template brain. Unlike dipole solutions, LAURA computes multiple simultaneously active sources without any a priori assumption on the number and position of the underlying cortical generators. When topographies differed between conditions within the 100–200 ms poststimulus interval, including the P1 and N170 components, the corresponding periods in ERP data were averaged over time to generate a single time point of data in order to compare sources estimated for the different conditions at this time point. LAURA has previously been shown to provide reliable source estimation in a variety of clinical or cognitive studies [see Grave de Peralta et al., 2001; Michel et al., 2001].

## RESULTS

### Behavioral Results

As anticipated, the gender decision task was more difficult with hybrids than with broadband stimuli, although after some practice all of our participants could accurately perceive an upright face from either blurred (LSF) or finer (HSF) traits presented in the upright stimulus. An ANOVA with two within-subjects factors (Conditions and Expression) was performed on the mean error rate for the gender judgments, and confirmed a significant effect of Condition ($F(2,24) = 59.51$, $P < 0.001$) due to higher accuracy on

unfiltered faces (mean % correct: 95.6) than on LSF and HSF faces (mean % correct: 65.2 and 70.0, respectively), but importantly the two SF-filtered conditions did not differ from each other ($t(12) = 0.10$, $P = $ ns), and there was no effect or interaction involving emotion expression ($F(2,24) = 1.46$, $P = $ ns). Similarly, an ANOVA on the median RTs for correct responses revealed a significant effect of Condition ($F(2,24) = 59.51$, $P < 0.001$), but no main effect of Expression ($F(1,12) = 0.06$, $P = $ ns) and no interaction ($F(2,24) = 0.51$, $P = $ ns), indicating that gender decisions were overall faster for unfiltered faces (mean: 492.2 ms) than for both types of SF-filtered stimuli (mean for LSF: 663.7 ms; for HSF: 663.4 ms), while these two conditions were not significantly different from each other ($t(12) = 0.003$, $P = $ ns). These behavioral results show that participants were able to make reliable gender judgments on faces presented upright in hybrid stimuli without any significant differences when the upright face was defined by LSF or HSF features, whereas performance was unsurprisingly more accurate and faster on unfiltered faces. Moreover, performance was unaffected by emotion expression in all stimulus conditions.

## ERP Results

### Waveform analysis of P1 and GFP

We first examined ERPs in the "baseline" condition with unfiltered faces. In keeping with previous studies [Luck et al., 2000], we found a conspicuous visual P1 response over lateral occipital electrodes as well as a conspicuous N170 over posterior temporal sites (Figs. 2, 3). Furthermore, as predicted based on previous findings [Batty and Taylor, 2003; Pizzagalli et al., 1999; Williams et al., 2004], fearful faces elicited a larger occipital P1 than neutral faces ($F(1,12) = 4.81$, $P < 0.05$), without any difference in the latency or scalp-configuration topography (see also following section).

As can be seen from Figure 3, these effects were strongly modulated by the spatial frequency content of hybrid stimuli. The P1 component, peaking at 111.5 ms at lateral occipital electrodes in the unfiltered condition, was significantly delayed ($F(2,24) = 7.55$, $P = 0.003$) in the two SF-filtered face conditions (mean latency of 118.5 ms and of 121.8 ms for LSF and HSF faces, respectively). However, there was no significant latency difference between these two SF conditions ($F(1,12) = 1.62$, $P = $ ns). In addition, SF-filtered faces not only delayed the P1 but also significantly reduced its amplitude ($F(2,24) = 3.57$, $P < 0.05$). Whereas the mean amplitude of P1 was 6.1 µV for unfiltered faces, it was 5.1 µV and 5.4 for LSF and HSF faces, respectively (no significant amplitude difference between these two conditions; $F(1,12) = 3.58$, $P = $ ns).

Next, for each condition (unfiltered, LSF, and HSF) we tested the effect of emotional expression (in upright faces) on the amplitude of P1 using a 2 (Expression) $\times$ 2 (Electrode Position) $\times$ 2 (Hemisphere) ANOVA.

For unfiltered faces, this analysis revealed a significant effect of Expression ($F(1,12) = 4.81$, $P < 0.05$) indicating a larger P1 amplitude for fearful (mean: 4.8 µV) relative to
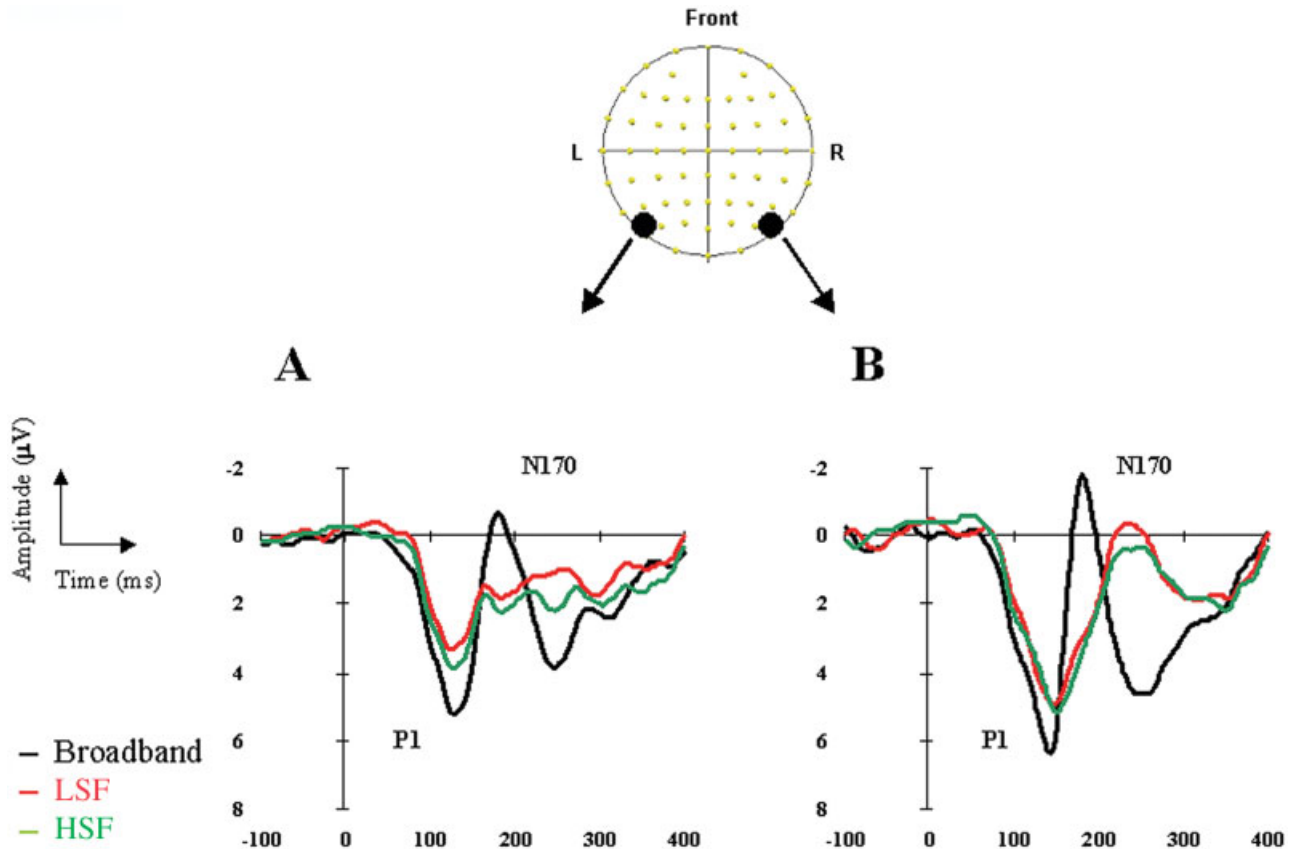
**Figure 3.**

Effects of SF filtering. Grand average waveforms in the unfiltered (black), LSF (red/dark gray), and HSF (green/light gray) face conditions (averaged across fear + neutral expressions) at two different electrode positions (**A:** PO7, left side; **B:** PO8, right side). Evoked potentials for LSF and HSF stimuli were significantly reduced relative to unfiltered faces, but a P1 component was still clearly visible in all three face conditions (**A,B**), accompanied by a concurrent negativity at central sites (not shown here). The N170 component was practically abolished in both the LSF and HSF conditions. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

neutral faces (mean: 4.0 $\mu$V), irrespective of the hemisphere ($F(1,12) < 0.05$, $P$ = ns). This ANOVA also disclosed a significant effect of Electrode Position ($F(1,12) = 59.68$, $P < 0.001$), indicating larger P1 amplitude for posterior (PO8/PO7; mean: 5.7 $\mu$V) than more anterior electrodes (P8/P7; mean: 3.0 $\mu$V). Post-hoc paired $t$-tests (one-tailed) confirmed that the P1 was larger for fearful compared to neutral faces at three positions out of the four preselected electrode sites (PO7, $t(12) = 2.0$, $P < 0.05$; PO8, $t(12) = 1.86$, $P < 0.05$; P7, $t(12) = 1.80$, $P < 0.05$; P8, $t(12) = 1.04$, $P$ = ns).

By contrast, P1 responses evoked by hybrid stimuli showed a modulation by emotional expression for the LSF upright faces only, but not for the HSF upright faces (Fig. 4). This was confirmed by two further ANOVAs performed on the mean amplitude of P1. For LSF faces, this analysis revealed a significant Expression × Hemisphere interaction ($F(1,12) = 6.67$, $P = 0.03$), due to the fact that the emotional effect on P1 was not significant over the left hemisphere (PO7, $t(12) = 0.76$, $P$ = ns; P7, $t(12) = 0.79$, $P$ = ns), while it was significant at two predefined electrode positions over the right hemisphere (PO8, $t(12) = 2.2$, $P < 0.05$; P8, $t(12) = 2.6$, $P < 0.01$), with higher P1 for fearful (mean: 4.8 $\mu$V) than neutral faces (mean: 3.7 $\mu$V). This ANOVA also revealed a significant effect of Electrode Position ($F(1,12) = 45.9$, $P < 0.001$), indicating larger P1 amplitude for posterior (PO8/PO7; mean: 4.8 $\mu$V) relative to anterior electrodes (P8/P7; mean: 2.6 $\mu$V).

For the exact same stimuli in which LSF faces were presented upside-down, and upright HSF faces now preferentially processed, an ANOVA with the same factors as above did not reveal any effect of Expression in HSF ($F(1,12) < 0.05$, $P$ = ns), nor any interaction of Expression with Hemisphere ($F(1,12) = 1.05$, $P$ = ns) or with Electrode Position ($F(1,12) < 0.1$, $P$ = ns). There was only a significant effect of Electrode Position ($F(1,12) = 35.9$, $P < 0.001$), indicating a larger P1 amplitude at posterior (PO8/PO7; mean: 5.1 $\mu$V) than anterior electrodes (P8/P7; mean: 2.9 $\mu$V), as observed for unfiltered and LSF faces. Taken together, these results show that an early P1 effect
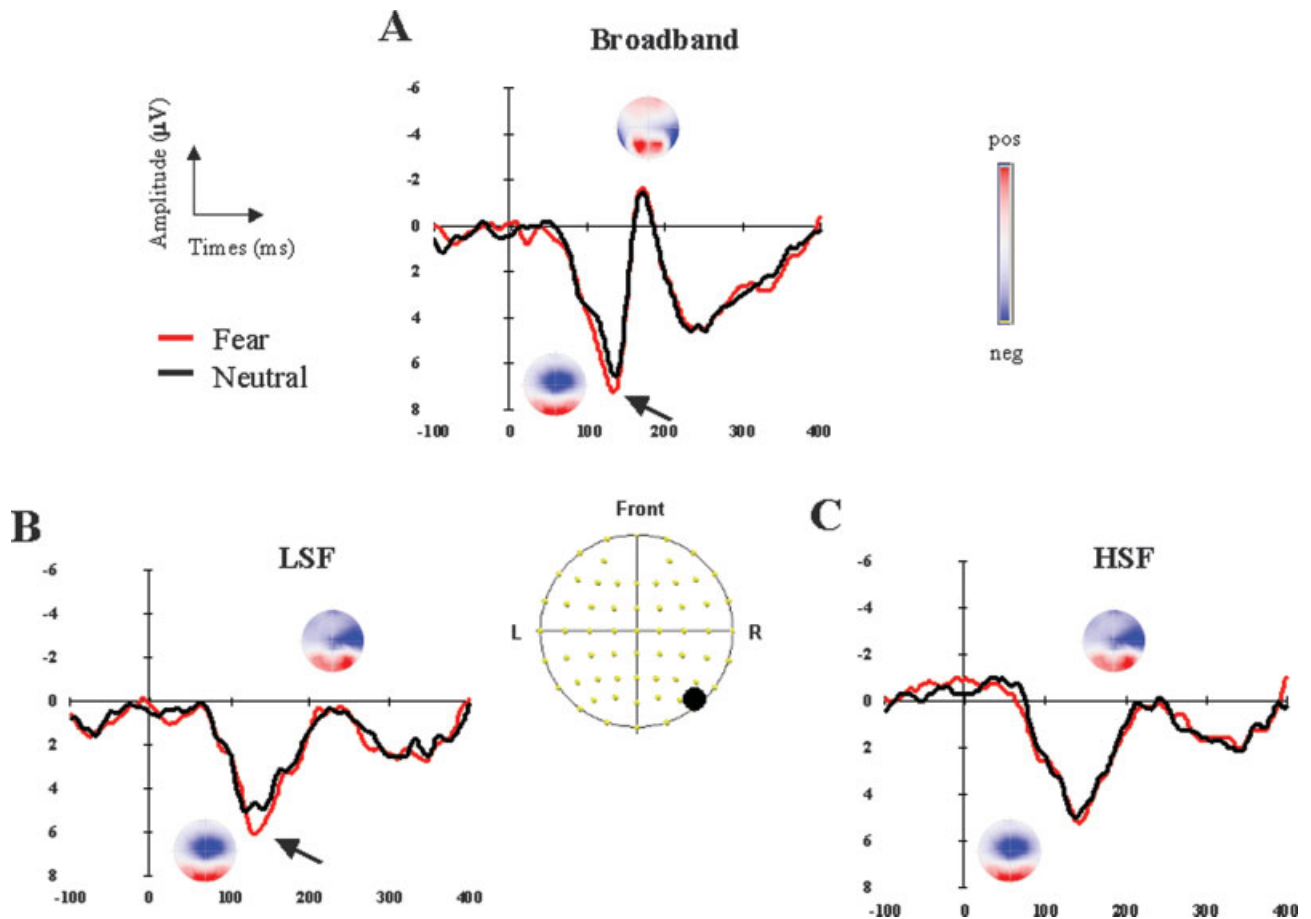
**Figure 4.**

Effects of emotional face expression. **A:** Grand average waveforms at PO8 in the baseline condition with unfiltered faces (fearful expression, red/gray; neutral expression, black), showing a P1 component followed by a N170 component, as expected. There was a selective increase in P1 amplitude for fearful (red/gray) relative to neutral faces (black) with these unfiltered stimuli, whereas the subsequent N170 amplitude was unaffected by expression. Corresponding scalp topographies (scaled to unitary strength by dividing the voltage at each electrode by the GFP) are displayed for the P1 and N170. **B:** Grand average waveforms at PO8 in the LSF face condition showing that a selective increase in P1 amplitude was still found for fearful (red/gray) relative to neutral expressions (black), whereas the N170 was suppressed and replaced by a smaller and delayed negativity. **C:** Grand average waveforms at PO8 in the HSF face condition for fearful (red/gray) and neutral expression (black), showing no amplitude modulation at the level of the P1 component or later, with the same suppression of N170 as in the LSF face condition. [Color figure can be viewed in the online issue, which is available at www. interscience.wiley.com.]
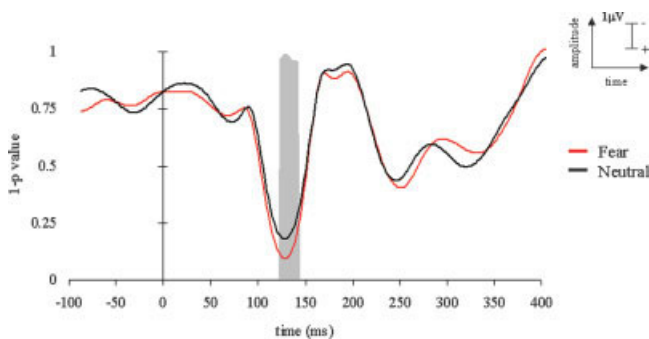


**Figure 5.**

Time-course of global field power changes. Significance level (1–P value, plotted by the light gray area) for the 250 consecutive t-tests (from −100 ms to +400 ms) between fearful and neutral trials performed on the global field power in the unfiltered face condition (the vertical line indicates face onset). Significant t-tests arose from 124 ms until 144 ms. The GFP time-course (fearful unfiltered in red/gray and neutral unfiltered in black) is superimposed on the t-test results to highlight the tight temporal overlap between GFP changes and the occipital P1. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

in response to fearful faces was primarily elicited by LSF rather than HSF face cues.

Note that following the P1, the N170 component showed an almost complete suppression in amplitude for *both* the HSF and LSF face conditions at the same electrode sites (Figs. 3, 4). These observations indicate a profound disruption of face-processing at the level of N170 for the SF-filtered stimuli, as confirmed below by the spatial cluster analysis taking into account topographic changes in the global electric field configuration (see next section).

In a complementary analysis of GFP, reflecting the general field strength at all 62 channels simultaneously, a significant effect of emotional expression was also found for fearful vs. neutral expressions in unfiltered faces (Fig. 5). A point-wise statistical comparison of the GFP from 100 ms prior to stimulus onset until 400 ms poststimulus onset disclosed a unique stable period of significant difference between the two emotion conditions, arising from 124–144 ms (i.e., 20 ms stability). These significant GFP changes precisely overlapped with the P1 waveform latency (Fig. 5), and reflected a higher field strength for fearful (4.97 μV) than neutral faces (4.55 μV). However, a point-wise comparison of the GFP in SF-filtered conditions did not reveal a stable difference between fearful vs. neutral for either LSF or HSF faces, either during the time-range of P1, earlier, or later. Thus, LSF fearful faces elicited a significantly higher P1 compared with LSF neutral face, but this effect was restricted to the posterior lateral electrode positions in the right hemisphere, and not associated with a global change in field strength as observed for unfiltered faces, indicating a more local modulation of occipital responses. Note also that GFP was generally reduced for SF-filtered relative to unfiltered stimuli.

### Temporal segmentation

The temporal segmentation analysis addressed two specific questions regarding the topography of VEPs generated within the first 400 ms poststimulus. First, we tested whether the P1 evoked by SF-filtered faces, although reduced in amplitude (Fig. 3), showed the same topographic properties as the P1 evoked by unfiltered faces. This allowed us to determine whether a similar pattern of neural generators might underlie this exogenous visual response sensitive to fearful expression in unfiltered and LSF faces. Second, we also explored how SF-filtered faces affected the topography of electrophysiological events subsequent to P1, particularly the face-selective N170 component.

The temporal segmentation was performed for each condition from 50–400 ms poststimulus onset. Spatial cluster analysis revealed that the ERP data could reliably be modeled by a solution of eight different maps (Figs. 6, 7) across the six experimental conditions, explaining 95% of the total variance. However, as can be seen from Figures 6 and 7, the temporal organization of these dominant maps differed in the four SF-filtered face conditions relative to the two unfiltered face conditions. Crucially, this difference started only at the time of map 3 (and for subsequent maps 4 to 6), i.e., immediately following the map corresponding to the P1

(map 2), whereas the P1 topography map itself was common to all six conditions (as well as the preceding map 1).

The map 3 identified by this cluster analysis corresponded to the N170 (i.e., dipolar complex with a centro-parietal positivity, previously referred to as the vertex positive potential, VPP; see Jeffreys and Tukmachi [1992]; and a bilateral occipito-temporal negativity, larger in the right than left hemisphere, corresponding to the N170 proper; see Bentin et al. [1996]). This N170-related map was therefore selectively evoked by unfiltered faces (Fig. 6) but markedly disrupted in both filtered face conditions (LSF and HSF, Fig. 7). Importantly, none of the four filtered face conditions showed this topography (map 3) from 50–400 ms poststimulus onset (Fig. 7), suggesting that the N170-related processes in temporal cortical areas were suppressed for all SF-filtered hybrid stimuli equally (and replaced by two different maps 7 and 8, see Fig. 7). These data suggest that the neural generators underlying the scalp-N170 failed to be effectively activated in all of the four SF conditions, in line with the participants' behavioral difficulties in face perception and gender judgments for all of these hybrid stimuli. By contrast, the topography of P1 (map 2) was unaffected by SF condition, indicating similar generators across conditions, even though the *amplitude* of this activity was still significantly modulated by emotional expression in the LSF condition (not in the HSF condition), independent of the concurrent suppression of N170 in both the LSF and HSF conditions. These data therefore indicate a dissociation between a loss of the N170 topography for all SF hybrids, as compared with intact faces, and a preserved effect on the P1 amplitude produced by fearful expression in LSF upright faces, but not by HSF faces.

These observations were confirmed by direct statistical analyses. The eight dominant scalp topographies were fitted to the ERPs of each individual subject using spatial fitting procedures [Pascual-Marqui et al., 1995]. Then, a 3 (Condition) × 2 (Expression) ANOVA was performed on the global explained variance (GEV) corresponding to the P1 segments (map 2). This did not reveal any significant main effect or interaction due to these two factors (Condition, F(2,24) = 0.38; Expression, F(1,12) < 0.01; Condition × Expression, F(2,24) = 1.50; all P = ns), indicating a shared scalp topography between all six experimental conditions. A 2 (Map) × 3 (Condition) × 2 (Expression) ANOVA was also performed on the GEV corresponding to the scalp topography immediately following P1 (i.e., in the N170 range for the baseline unfiltered face condition). This analysis revealed a highly significant Map × Condition interaction (F(2,24) = 30.7, P < 0.001) that was not modulated by the factor Expression (F(2,24) = 3.27, P = ns). This interaction indicated larger GEV values for the N170 scalp topography with unfiltered faces (mean GEV = 0.15; no differences between these two conditions, t(12) = 1.68, P = ns), relative to the filtered face conditions where this topography was not reliably found (mean GEV = 0.03; no difference between each of the four SF conditions, F(1,12) = 1.93, P = ns). For the latter SF conditions, a distinct scalp topography was evoked during the same time range and beyond (maps 7 and 8), unaffected by emotion.
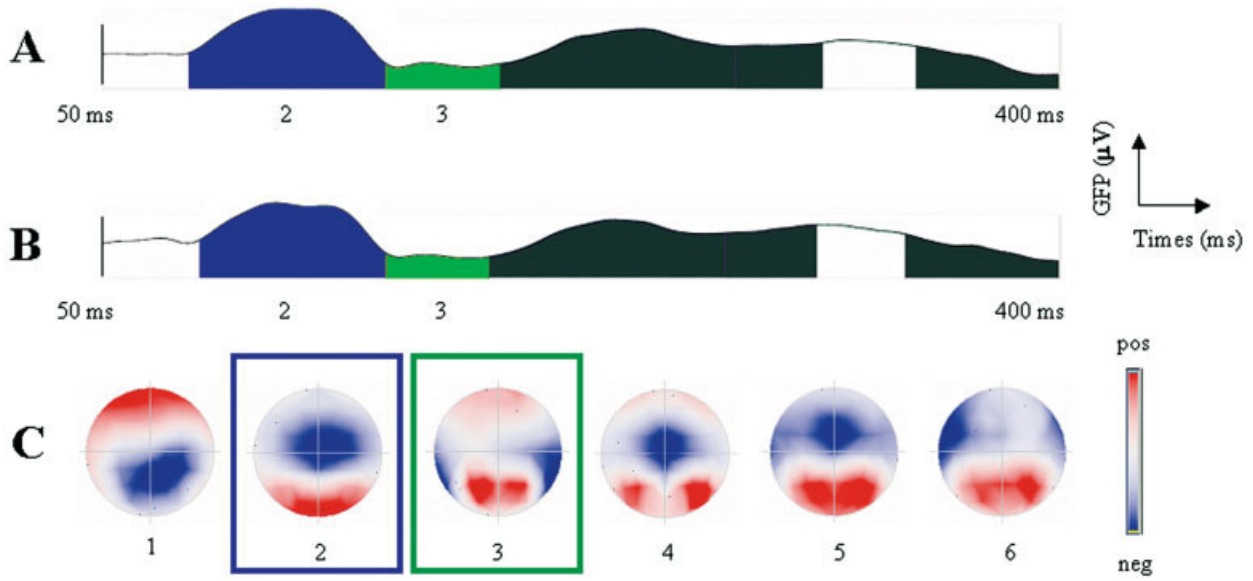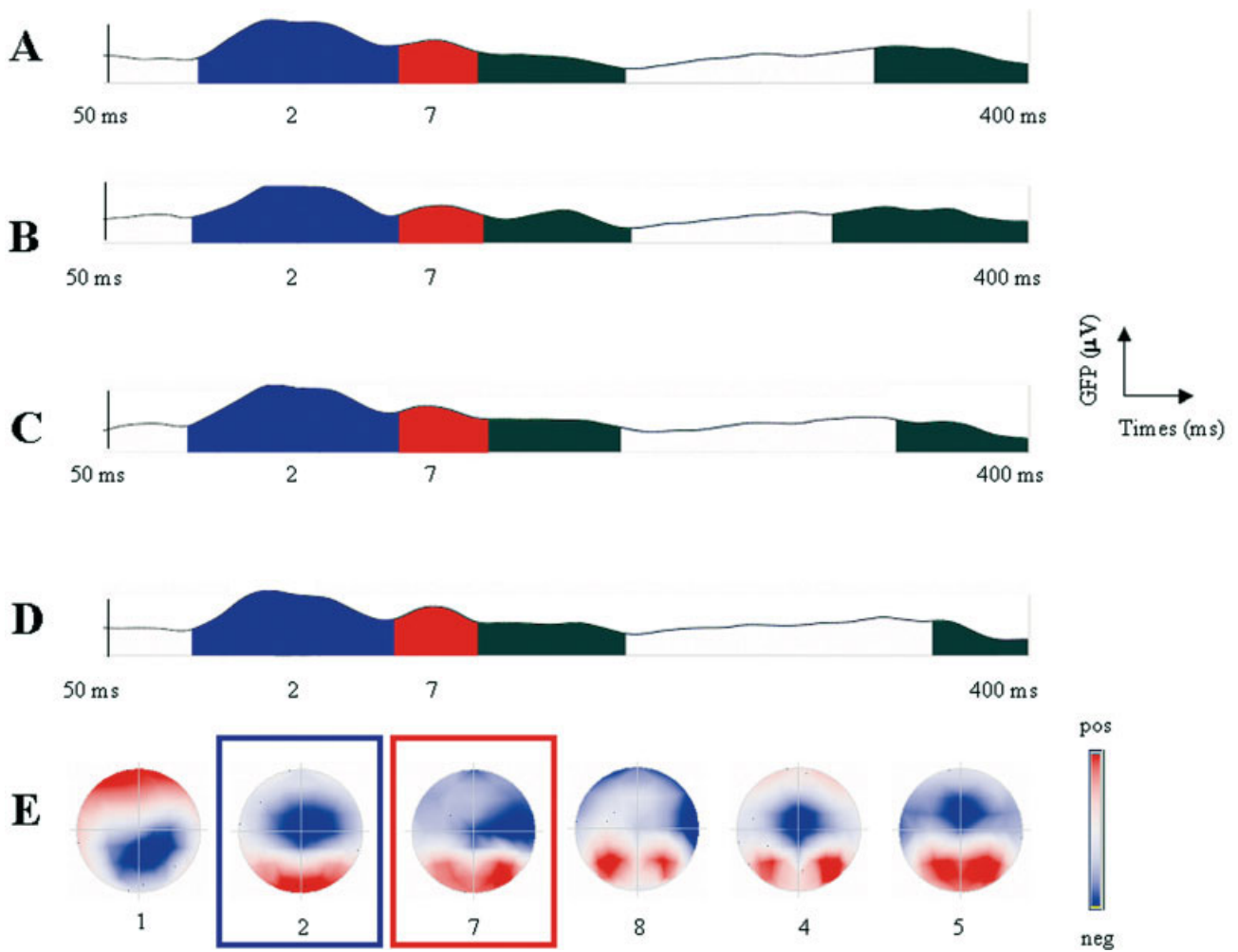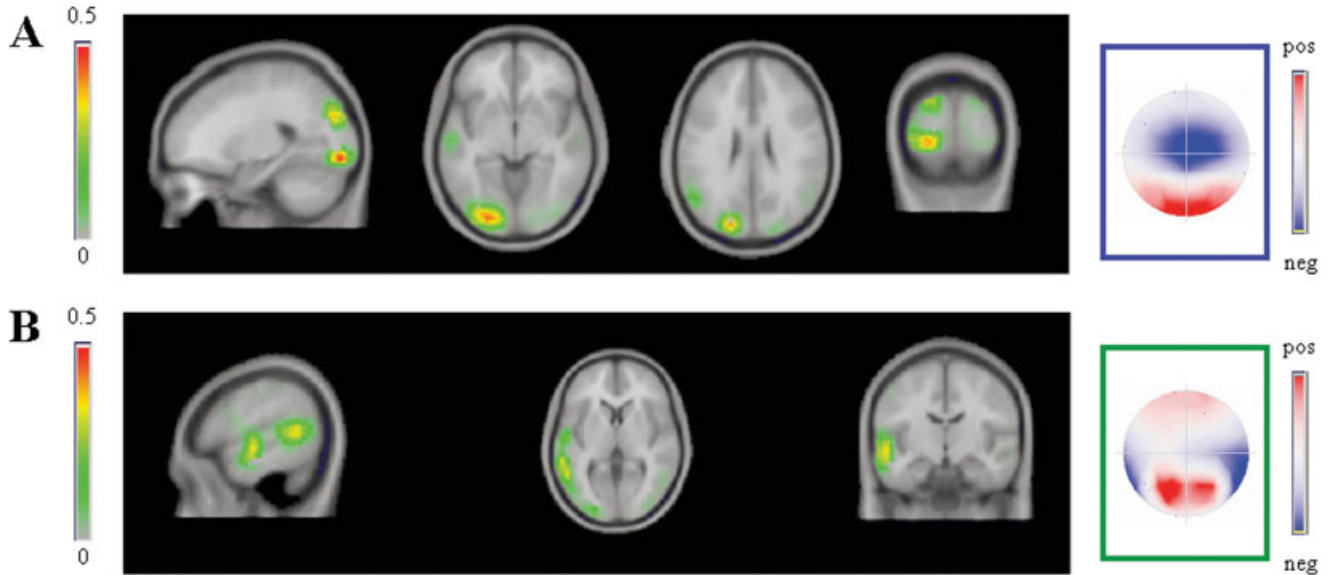
**Figure 6.**



**Figure 7.**

**Figure 8.**

Source estimations. **A:** LAURA solution for sources activated during the time segment corresponding to the P1 topography (common to all six conditions, map 2, top right, in blue), showing two dominant clusters within left extrastriate visual cortex. **B:** LAURA solution for sources activated during the time segment corresponding to the N170 topography (found in the two broad-band face conditions only, map 3, bottom right, in green), showing two dominant clusters within the lateral temporal cortex near the superior temporal sulcus. Scalp topographies were scaled to unitary strength by dividing the voltage at each electrode by the GFP. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

### Source localization

Finally, we used the topographic results from our spatial cluster analysis to define the temporal window of source estimations, calculated by the inverse distributed solution in LAURA. These source estimations were first applied to the P1 (120–150 ms poststimulus) and N170 (160–190 ms poststimulus) topographies from the baseline condition with unfiltered faces, and then to the chronologically corresponding time segment in the filtered face conditions (Fig. 8).

For the P1 scalp topography (common to all six conditions), LAURA found two predominant clusters in extrastriate visual cortex of the left hemisphere (Fig. 8A). These two clusters were located most probably within the left inferior/middle occipital gyrus and left posterior parietal cortex, and thus fully accord with previous reports on the neural generators of this early visual component in extrastriate visual cortex [see Clark et al., 1995; Di Russo et al., 2002]. For the N170 time segment, LAURA disclosed two different sources,

**Figure 6.**

Results of the temporal segmentation (from 50 to 400 ms poststimulus onset) in the baseline conditions with unfiltered faces. This analysis revealed a six-maps solution for (**A**) fearful and (**B**) neutral faces. Black and white colors indicate when a significant topographic change occurred in temporal segmentation. Each stable topography is represented by a number (1–6). **C:** The scalp configuration (scaled to unitary strength by dividing the voltage at each electrode by the GFP) corresponding to each map is shown below. The second time segment identified by the cluster analysis corresponds to the topography of P1 (map 2, in blue), whereas the third time segment corresponds to the typical scalp topography of the N170 (map 3, in green; compare with Fig. 7). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

**Figure 7.**

Results of the temporal segmentation (from 50 to 400 ms poststimulus onset) in the SF-filtered conditions. A six-maps solution was found for (**A**) LSF fear, (**B**) LSF neutral, (**C**) HSF fear, and (**D**) HSF neutral face conditions. Black and white colors indicate when a significant topographic change occurred in the temporal segmentation. The spatiotemporal organization was common to all four conditions. Each stable topography is represented by a number. **E:** The scalp configuration (scaled to unitary strength by dividing the voltage at each electrode by the GFP) corresponding to each map is shown below. The third time segment (map 7, in red) corresponding to the topography of N170 was the first to differ between the unfiltered and SF-filtered face conditions, whereas the scalp topography corresponding to the preceding P1 component (map 2 in blue) was identical in all conditions (compare with Fig. 6). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

mainly located in the anterior part of the lateral temporal cortex of the left hemisphere [Itier and Taylor, 2004b], close to the superior temporal sulcus (STS; see Fig. 8B). Although this left hemispheric lateralization may seem unexpected, since the right hemisphere is usually thought to be dominant in face-processing [Farah, 1990; Sergent, 1995; but see Indersmitten and Gur, 2003; Magnussen et al., 1994], such "paradoxical" asymmetries in source localization [Kawashima et al., 1996] are not always reliable in healthy individuals and can have various origins, including spurious field strength irregularities in group-averaged data. Nevertheless, our most critical result here concerned the distinct sources found within temporal cortex for the two successive maps evoked in the P1 and N170 time range, involving the posterior extrastriate areas and more lateral temporal areas, respectively.

## DISCUSSION

In our study we exploited recent findings from an event-related fMRI study [Vuilleumier et al., 2003] suggesting that visual processing of fearful expression in faces might be distinctively tuned to coarse LSF cues, provided by magnocellular inputs to the amygdala through subcortical (and perhaps also cortical) visual pathways [see also Morris et al., 1999, 2002]. Since LSF information is transmitted faster than HSF information throughout the visual system [Bullier, 2001], we predicted that an early differential response to fearful expressions might be selectively elicited by LSF cues in faces, rather than by HSF cues. A number of important results emerged from the current study and confirmed our prediction that early visual responses to fearful faces might specifically be driven by LSF cues: (1) We found that fearful relative to neutral faces, in the baseline condition with intact stimuli, elicited a significantly higher amplitude of the exogenous visual P1, ~130 ms poststimulus onset. (2) More importantly, fearful expression in hybrid stimuli containing an LSF upright face also elicited a larger P1, relative to those containing a neutral LSF upright face. (3) This early emotional effect was not observed for HSF fearful expressions in the upright faces, although these stimuli were the exact same hybrid images as those used in the LSF condition but inverted, allowing us to rule out that early P1 effects were simply driven by differences in low-level visual features. (4) In addition to classical component analysis, segmentation analyses indicated that the electric field topographies corresponding to P1 responses did not differ for fearful relative to neutral expressions, but rather were modulated in their amplitude, suggesting a local gain control on these visual responses due to emotion rather than an activation of distinct neural generators. It must be emphasized here that the absence of a reliable topographic difference between fearful and neutral faces in the LSF condition is not incompatible with the reliable emotion effect on P1 amplitude found in this LSF condition (unlike in the HSF condition), but corroborates the fact that topography analyses provide complementary results to more classical ERPs analyses [see Lehmann and Skrandies, 1980; Michel et al., 1999, 2001, for methodological discussions]. (5) A preserved P1 response to emotion in LSF but not HSF faces arose despite the fact that both types of SF-filtered faces produced profound changes in the latency and amplitude of the face-sensitive N170 component, and both equally disrupted the sequence of field topographies subsequent to the P1, regardless of the emotion and/or spatial frequency in upright faces. In particular, the scalp topography associated with N170 in the unfiltered baseline condition was not reliably detected in either hybrid condition during a 350 ms time window poststimulus onset. This loss of N170 responses paralleled the reduced accuracy in behavioral performance for all types of hybrid faces, but contrasted with the preserved emotion effect on P1 produced by LSF faces, suggesting a differential sensitivity of N170 and P1 to our SF manipulation. (6) Finally, source estimation using LAURA confirmed a reliable difference between the dominant neural generators of the P1 and N170 components observed here, involving occipital and more lateral temporal cortical regions, respectively [Itier and Taylor, 2004b].

Our results thus confirm recent reports that facial expressions of negative emotions may produce early visual responses at the level of the P1 [Pizzagalli et al., 1999, 2002; Batty and Taylor, 2003; Williams et al., 2004], but also extend these previous findings by showing for the first time that this effect is selectively driven by LSF cues in faces, and that it is independent from neural activity associated with the face-sensitive N170 component [Bentin et al., 1996; Haxby et al., 2000]. We found distinct effects of SF-filtered faces on P1 and N170 for both the waveform and the topography analyses, with a differential effect of emotional expression on P1 still being observed for the LSF face condition (but not HSF), even though N170 responses were severely disrupted for all types of filtered stimuli. In addition, we did not observe any emotion effect on N170, consistent with previous ERP studies of emotional face-processing [Ashley et al., 2004; Eimer and Holmes, 2002; Pizzagalli et al., 1999]. Although N170 might be more sensitive to configural facial cues in LSF than HSF when either SF band is presented alone [Goffaux et al., 2003], a suppression of N170 by both types of hybrids in our study (i.e., with either LSF or HSF in upright faces) suggests that these overlapping stimuli might have disrupted featural or configural processes associated with this particular ERP component [Williams et al., 2004]. Since our participants showed worse behavioral performance in the gender judgment task on hybrid stimuli, the suppressed N170 in these conditions may also reflect an increased perceptual uncertainty about hybrid faces in our task, consistent with the view that N170 activity probably indexes general perceptual processes necessary to recognize facial traits [Carmel and Bentin, 2002; Williams et al., 2004]. Importantly, however, this general behavioral difference between broadband and SF filtered conditions did not confound the critical emotional effects, since the latter concerned the just preceding P1 segment whose amplitude was still modulated by LSF fearful faces (providing impoverished visual information as compared with broadband faces), and not by HSF faces (yielding similarly poor visual information and suppressed N170). Taken together, this dissociation between P1 and N170 clearly indicates that these two successive visual components reflect distinct stages in face-processing [see Itier and Taylor, 2004a], with a different sensi-

tivity to different types of visual information in the faces. Furthermore, this functional dissociation between P1 and N170 was further supported by the distinct neural sources found by LAURA, involving posterior occipital and more lateral temporal areas, respectively.

P1 activity is probably generated at several extrastriate sites within posterior visual cortex [Clark et al., 1995], and is typically modulated by spatial attention in a variety of visual tasks using many different types of stimuli [see Luck et al., 2000, for a review]. A P1 modulation may also arise with nonspatial, object-based attention effects [e.g., Taylor, 2002]. Increased P1 responses to fearful vs. neutral faces might therefore indicate a greater allocation of attentional resources to emotionally significant stimuli, in agreement with evidence from behavioral [Bradley et al., 1997], neuropsychological [Anderson and Phelps, 2001], and neuroimaging studies [Vuilleumier et al., 2001] that threat-related visual stimuli can draw and/or hold attention to their location more strongly than neutral visual stimuli. In addition, it has also been suggested that an enhanced P1 for emotional relative to neutral faces might reflect an effect of emotional expressions on configural face processing, preceding face recognition stages associated with N170 [Batty and Taylor, 2003]. The present findings that emotional effects on P1 are contingent on LSF face cues might thus indicate a more efficient extraction of configural expressional information from LSF than HSF cues [Calder et al., 2001; Schyns and Oliva, 1999]. However, it remains to be determined whether these emotional enhancements in P1 reflect face-specific processes or a more general influence of threat signals on visual processing, which might boost early extrastriate activity based on a rapid extraction of the stimulus emotional significance or arousal, irrespective of object category [Lang et al., 1998; Schupp et al., 2003]. Moreover, our combined use of waveform and segmentation analyses allowed us to establish that P1 effects evoked by fearful faces corresponded to a modulation of amplitude, but were not caused by concurrent changes in scalp topography. This pattern shows that differences in the amplitude of visual responses over occipital electrodes may not necessarily correspond to different scalp topographies [Lehmann and Skrandies, 1980]. Rather, these data suggest that similar neural generators were activated at this latency by LSF cues from both fearful and neutral faces, but that the gain of these responses was locally amplified over posterior electrode sites for fearful relative to neutral faces. This converges with a previous proposal that P1 modulation by visual attention might involve gain control mechanisms exerted on extrastriate cortex, without topography changes [Clark and Hillyard, 1996]

These increased extrastriate response to fearful faces, as indexed by the P1 amplitude and source topography in our study, might reflect the effects of direct modulatory feedback signals on visual areas from the amygdala, which is known to be critical for rapid processing of threat-related stimuli [LeDoux, 1996; Öhman and Mineka, 2001] and has extensive back-projections to many posterior cortical regions, including early striate and extrastriate visual areas

[Amaral et al., 2003; Catani et al., 2003]. Both neurophysiological studies in animals [Armony et al., 1998; Sugase et al., 1999] and imaging studies in humans [Morris et al., 1998; Vuilleumier et al., 2004] suggest that such feedback projections from the amygdala might serve to enhance processing of emotional stimuli in visual cortex. Furthermore, the selective effect of LSF emotion cues on P1 (without any effect of HSF cues) converge with previous fMRI findings that LSF information in faces is critical to produce a differential activation to fearful vs. neutral faces in the amygdala [Vuilleumier et al., 2003] as well as to enhance activation of face-selective regions in fusiform cortex [Winston et al., 2003]. Since LSF cues might be transmitted rapidly to the amygdala by magnocellular visual pathways either through the pulvinar and superior colliculus [Morris et al., 1999; Vuilleumier et al., 2003], or through fast cortical channels [e.g., Bullier, 2001; Bar, 2003; Catani et al., 2003], feedback signals from the amygdala might then allow a rapid enhancement of extrastriate visual responses to faces at the P1 latency, as observed here, and as similarly observed for the modulatory effects of spatial attention in other visual tasks [Luck et al., 2000; Martinez et al., 1999]. Importantly, our temporal segmentation analysis allowed us to establish that the emotional effects of LSF faces on P1 occurred during the same topographic event as the enhancement seen for unfiltered faces, and that it corresponded to an increase in amplitude rather than to a change in topography, relative to the P1 evoked by neutral faces. Our data are therefore consistent with a modulatory influence on P1 generators in extrastriate cortex, rather than an activation of distinct cortical systems, and suggest that the LSF content in faces might be responsible for the early negative emotion effect observed in visual cortex for the intact broadband fearful faces.

We conclude that enhanced processing of emotional faces based on the extraction of LSF information from visual inputs might reflect a general principle of organization within the visual system, whereby rapid (possibly subcortical) pathways with low resolution but fast responsiveness might provide critical signals to guide slower but finer perceptual processing in cortical areas [Bar, 2003; Bullier, 2001; Vuilleumier et al., 2003]. The critical role of LSF visual cues in extracting fear-related signals might allow a fast adjustment of processing resources, as reflected by the enhanced visual P1 responses. Further ERPs studies are needed to establish whether a similar role of LSF face information is involved in modulating visual responses to other facial expressions [see Batty and Taylor, 2003], or to other types of emotional stimuli, and whether magnocellular LSF inputs are also critical to modulate frontoparietal networks generally involved in selective attention.

## ACKNOWLEDGMENTS

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