

## Fearful faces impact in peripheral vision: Behavioral and neural evidence

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### ABSTRACT

Many studies provided evidence that the emotional content of visual stimulations modulates behavioral performance and neuronal activity. Surprisingly, these studies were carried out using stimulations presented in the center of the visual field while the majority of visual events firstly appear in the peripheral visual field. In this study, we assessed the impact of the emotional facial expression of fear when projected in near and far periphery. Sixteen participants were asked to categorize fearful and neutral faces projected at four peripheral visual locations (15° and 30° of eccentricity in right and left sides of the visual field) while reaction times and event-related potentials (ERPs) were recorded. ERPs were analyzed by means of spatio-temporal principal component and baseline-to-peak methods. Behavioral data confirmed the decrease of performance with eccentricity and showed that fearful faces induced shorter reaction times than neutral ones. Electrophysiological data revealed that the spatial position and the emotional content of faces modulated ERPs components. In particular, the amplitude of N170 was enhanced by fearful facial expression. These findings shed light on how visual eccentricity modulates the processing of emotional faces and suggest that, despite impoverished visual conditions, the preferential neural coding of fearful expression of faces still persists in far peripheral vision. The emotional content of faces could therefore contribute to their foveal or attentional capture, like in social interactions.

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### 1. Introduction

In an evolutionary perspective, the particular value of emotions is unquestionable and much specificity associated with emotional processing has been demonstrated through behavioral and brain imagery studies. Compared to neutral stimulations, stimuli with emotional content are faster detected (Öhman, Flykt, & Esteves, 2001), better remembered (Buchanan, 2007) and drive more attentional resources (Schupp, Junghöfer, Weike, & Hamm, 2003a; Schupp, Junghöfer, Weike, & Hamm, 2003b; Smith, Cacioppo, Larsen, & Chartrand, 2003; Vuilleumier, Armony, Driver, & Dolan,

2001). However, one underestimated factor in studies on the processing of emotional stimulations is the influence of their position in the visual field. This is surprising that the majority of observations concerning emotional modulations of visual processing relies on studies focused on stimulations projected to the center of the visual field while the main part of visual information appears outside this center. The main topic of this study is thus to investigate how emotional information appearing at eccentric locations is processed.

The central and the peripheral retina respectively subtend central (CV) and peripheral vision (PV), and, even if it is difficult to precisely locate the boundary between these two parts of the retina (Rossi & Roorda, 2010), their distinct anatomical and functional properties are widely demonstrated. Indeed, classical anatomical data show that the distribution, morphology and connections of the retinal photoreceptors change across eccentricity (Bullier, 2001). Furthermore, data suggest that central and peripheral retina are at the origin of parvocellular and magnocellular systems, respectively, which convey visual information across two parallel retino-geniculo-cortical pathways (Kaplan, 2004; Virsu, Lee, & Creutzfeld, 1987). Although these data are reconsidered by recent works which found connections between parvo- and magnocellular systems in the retina (Masland, 2001, 2004) and in the early visual areas (see Sincich & Horton, 2005), it appears that periph-

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eral vision is mainly related to the magnocellular system. Indeed, connections between rods and magnocellular cells (see Grünert, 1997; Lee, Smith, Pokorny, & Kremers, 1997; Purpura, Kaplan, & Shapley, 1988; Virsu et al., 1987) as well as relations between peripheral vision and dorsal pathway versus central vision and ventral pathway (see Baizer, Ungerleider, & Desimone, 1991; Stephen et al., 2002; Zeki, 1980) were found. Functionally, the decrease of acuity from CV to PV has been supported by several studies using letters, digits, sinusoidal gratings or compound Gabor patterns (Anderson, 1996; Chung, Mansfield, & Legge, 1998; Näsänen & O'Leary, 1998) and could be related to the spacing between retinal ganglion cells, which has been shown to increase in a roughly linear way with eccentricity (Thorpe, Gegenfurtner, Fabre-Thorpe, & Bulthoff, 2001).

Despite the strong decrease of visual performance with eccentricity, most visual events occur in the peripheral visual field and cause saccades which displace targets of interest into CV where detailed visual analysis can be performed (Liversedge & Findlay, 2000). This implies that some features are processed and selected in PV for saccadic capture. In agreement with this, several studies, using ecological or complex stimuli such as objects or natural scenes presented at very high eccentricities (up to 80°), showed unexpected good performances in object recognition (Jebara, Pins, Despretz, & Boucart, 2009), in colour detection (Naili, Despretz, & Boucart, 2006) or in categorization (Thorpe et al., 2001). In particular, Thorpe and colleagues interpreted the high performance in categorization of animal pictures as a phylogenetic advantage for species adaptation and individual survival. Given the high adaptive value of emotional information in terms of survey, the processing of emotional-laden information in PV is likely, even at far eccentric points of the visual field, despite the high decrease of acuity. This assumption is in line with other studies showing that emotional stimulations are still processed in experimentally deteriorated visual conditions like liminal central presentations (e.g., Gläscher & Adolphs, 2003; Kiss & Eimer, 2008; Phillips et al., 2004; Williams et al., 2006) or binocular rivalry (Alpers & Gerdes, 2007; Alpers, Ruhleder, Walz, Mühlberger, & Pauli, 2005; Williams, Morris, McGlone, Abbott, & Mattingley, 2004).

The processing of emotional information as a function of eccentricity in visual field has already been investigated but mostly in parafoveal positions, around 5° of eccentricity (Bayle, Henaff, & Krolak-Salmon, 2009; Calvo, 2006; Gutiérrez, Nummenmaa, & Calvo, 2009). Only a few studies presented emotional scenes in more eccentric positions. Thus, Calvo and Lang (2005) presented at 10° of eccentricity pairs of pictures of natural scenes, one neutral and one emotional, and observed that the first saccade of the participants was preferentially directed towards the emotional picture. They also showed that emotional pictures were better remembered than neutral, even when the pairs of pictures were briefly presented (150 ms). Two recent studies investigated the neural correlates of the processing of affective natural scenes projected in peripheral vision (De Cesare, Codispoti, & Schupp, 2009 at 16°; Rigoulot et al., 2008 at 30°) and found affective modulation of early ERP components for both centrally and peripherally presented scenes.

However, these rare studies focused on how emotional information is processed in natural scenes leaving unexplored the case of emotional facial expressions. Yet, faces have an obvious simpler spatial configuration and are more homogeneous than natural scenes. Moreover, faces are known to play an important role from an evolutionary perspective (e.g., Darwin, 1872; Öhman & Mineka, 2001). Humans developed special sensitivity for faces (Yarbus, 1967) and quick analysis of facial expression is crucial in social communication (Adolphs, 2003). Moreover, electrophysiological studies confirmed this special status as they showed that the emotional expression of faces can modulate early (Batty & Taylor, 2003; Eger, Jedynak, Iwaki, & Skrandies, 2003; Pizzagalli, Regard, &

Lehmann, 1999; Pourtois, Grandjean, Sander, & Vuilleumier, 2004) and late evoked components (Ashley, Vuilleumier, & Swick, 2004; Campanella et al., 2004; Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003; Krolak-Salmon, Fischer, Vighetto, & Mauguier, 2001; Sato, Kochiyama, Yoshikawa, & Matsumura, 2001; Schupp et al., 2004). The data are less homogeneous concerning the classical N170 component indexing specific face processing (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996; Itier & Taylor, 2004). Some studies found no emotional modulation (Eimer & Holmes, 2002, 2007; Herrmann et al., 2002; Krolak-Salmon et al., 2001), while others showed differences of amplitude and latency according to the emotional expression of faces (Batty & Taylor, 2003; Eger et al., 2003; Pizzagalli et al., 2002).

As a whole, these studies performed in CV showed that emotional facial expressions engage a specific brain network. However, very few studies explored whether emotional facial expressions are still processed in far eccentric positions. Only two recent studies using magnetoencephalography (Bayle et al., 2009; Liu & Ioannides, 2010) observed increased cerebral activations in amygdala and fusiform gyrus in response to fearful and happy expressions when they were presented at 5° of eccentricity for the former study and at 10° for the latter, in line with the role of these structures in the processing of emotional expressions (Adolphs, 2002).

Among the emotional facial expressions, fear is a significant biological indicator of potential threat in the environment and allows a rapid behavioral response to danger (Eccleston & Crombez, 1999; Mathews & Mackintosh, 1998; Öhman & Soares, 1993). Moreover, a recent study (Bocanegra & Zeelenberg, 2009) showed that fearful faces could improve behavioral performance in a tilt-detection task of low spatial frequencies (LSF) Gabor patches but not of high spatial frequencies (HSF) ones, in agreement with studies suggesting that the processing of emotional facial expression would be supported by LSF rather than by HSF (Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Vlamings, Goffaux, & Kemner, 2009; Vuilleumier, Armony, Driver, & Dolan, 2003). Given that LSF information is conveyed by the visual magnocellular pathway and that peripheral vision is mainly related to this pathway, these results suggest that PV processes could be specifically modulated by the emotional expression of fear.

Consequently, our hypothesis is that the enhancement of electrophysiological responses to fearful faces, well-documented in CV, persists in PV even at large eccentricities. Accordingly, the behavioral and neural impact of fearful and neutral faces, presented in near and far locations in peripheral vision, was evaluated by means of reaction times and ERPs recordings. Considering the rare available electrophysiological data related to peripheral vision, particularly the processing of faces at far eccentricities, we conducted a spatio-temporal principal component analysis (PCA) to investigate ERPs data without *a priori* hypotheses (see Pourtois, Delplanque, Michel, & Vuilleumier, 2008). In addition, PCA techniques have already demonstrated their relevance to analyze ERPs in response to emotional stimuli (Delplanque, Lavoie, Hot, Silvert, & Sequeira, 2004; Delplanque, Silvert, Hot, & Sequeira, 2005; Delplanque, Silvert, Hot, Rigoulot, & Sequeira, 2006; Hot, Saito, Mandai, Kobayashi, & Sequeira, 2006; Kayser & Tenke, 2003; Rigoulot et al., 2008).

## 2. Methods

### 2.1. Participants

Sixteen right-handed women were included in the study (mean age: 19.1 ± 3.5 years). Only women were included in this study because they are known to be more reactive to emotional information than men (Larsen & Diener, 1987), especially to threatening information (Bradley, Codispoti, Sabatinelli, & Lang, 2001; Collignon et al., 2010; Kring & Gordon, 1997). They all had normal or corrected to normal vision. Prior to the experiment, participants were given a questionnaire in order to get their consent and another to test their handedness (Hécaen, 1984). They also filled a

form intended to check that they had no history of neurological illness, psychiatric disorder, or drug consumption. They were paid twenty Euros for their participation. The study was approved by the national ethics committee of the Centre National de la Recherche Scientifique (CNRS).

## 2.2. Apparatus and stimuli

Participants were seated in a chair in front of a panoramic screen in a dimly lit room where three projectors (SONY CS5, Tokyo, Japan) displayed the stimuli on a panoramic semi-circular light-grey ( $68 \text{ cd/m}^2$ ) screen covering almost the entire visual field ( $180^\circ$ ). The projectors were connected to the computer devoted to the presentation of the stimuli (Hewlett-Packard Pentium III 1000 MHz).

In a preliminary experiment, faces from Nim Stim (MacBrain Face Stimulus Set; Tottenham et al., 2009) and KDEF (Karolinska Directed Emotional Faces System; Lundqvist, Flykt, & Öhman, 1998) datasets were projected in central vision of twenty-two female participants (mean age:  $22.5 \pm 2$  years). For each face, participants had to assess the emotional expression they perceived (free answer) and the certainty of their answer (on a 0–10 scale). We selected two sets of 24 faces evaluated as either expressing fear or without expression (neutral), by at least 70% of the subjects, with a median of certainty at least equal to 7 (percentage of correct recognition: fear =  $84 \pm 6\%$ ; neutral =  $86 \pm 7\%$ ; median of certainty: fear =  $8.17 \pm 0.5$ ; neutral =  $8.14 \pm 0.5$ ); no significant difference was found between both sets of pictures for these two measures ( $F(1,47) = 1.06$ ;  $p = 0.306$  for percentage of correct recognition;  $F(1,47) = 0.02$ ;  $p = 0.882$  for median of certainty). Both sets included the same number of male and female faces.

The mean luminance and colour saturation (for red, green and blue) were measured for each picture and these values were adjusted for some pictures in order to maintain homogeneity between fearful and neutral sets (Adobe Photoshop software, see Calvo & Lang, 2005). Separate analyses of variance (ANOVAs) performed on the mean luminance, the colour saturation and the standard deviation of luminance values (i.e. a contrast index) did not reveal any significant difference between fearful and neutral groups (all  $F_s(1,46) < 0.57$  and  $p_s > 0.40$ ).

## 2.3. Procedure

Each picture ( $640 \times 822$  pixels; size:  $15.6^\circ \times 20^\circ$ ; distance: 2.1 m) was projected on the panoramic screen, at four different spatial positions:  $-30^\circ$  and  $-15^\circ$  (high and low periphery in the left visual field);  $+15^\circ$  and  $+30^\circ$  (low and high periphery in the right visual field). The angular size of the faces was kept constant across the different peripheral positions of the stimuli. For faces centered at  $15^\circ$  of eccentricity, the inner border of the pictures was at  $7.2^\circ$  of eccentricity and the outer border at  $22.8^\circ$ . For faces centered at  $30^\circ$ , the inner border was at  $22.2^\circ$  and the outer border at  $37.8^\circ$  of eccentricity. Indeed, large faces were used in order to help us to maximize electrophysiological responses of PV where the density of neurons, as previously indicated, decreases with the eccentricity.

The whole dataset was organized into four blocks of 48 pictures (24 F and 24 N). Each picture was presented once per block and was repeated four times across blocks in such a way that, at the end of the experiment, all the pictures had appeared at the four spatial positions. The order of presentation of the pictures was counterbalanced to avoid possible confusion with effects of laterality (first presentation of pictures in right or left visual field) and of degree of eccentricity (first presentation of pictures in near or far periphery).

For each trial, participants first had to fixate their eyes on a central cross. Pictures were then projected at one of the four possible spatial positions for 300 ms and, as soon as a picture appeared, participants had to categorize it according to its emotional content (fear or neutral) with the help of a two-button response box (Fig. 1). The inter-stimulus interval randomly varied between 2.5 and 4 s. The buttons and hands were counterbalanced across participants. Before the experiment, participants were trained with a small set of different pictures.

## 2.4. Electroencephalogram (EEG) recording and signal processing

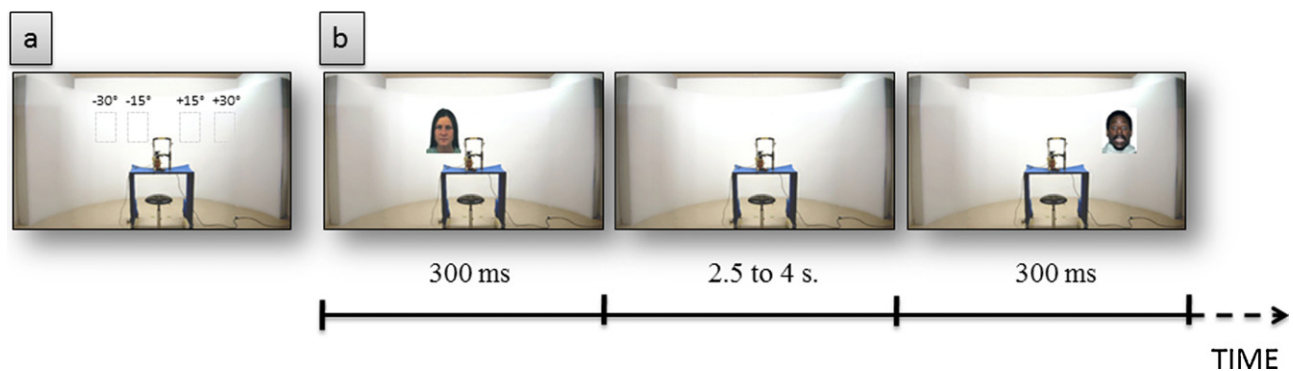
The EEG system was composed of 128 electrodes cap (Electrocap), an amplifier (Advanced Neuro Technology, ANT) and a recording computer. Electroencephalographic activity (EEG, ANT system) was recorded at 63 electrode sites (Fpz, Fp1, Fp2, AFz, AF3, AF4, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FCz, FC1, FC2, FC3, FC4, FC5, FC6, FT9, FT10, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, TP9, TP10, A1, A2, Pz, P1, P2, P3, P4, P5, P6, P7, P8, POz, PO3, PO4, PO7, PO8, Oz, O1, and O2) of the extended 10–20 system using tin electrodes inserted in an elastic nylon cap (Electrocap International) with an online averaged reference and a forehead ground. Seven additional electrodes were placed, one at the nasion (usual reference) and six others for vertical and horizontal electro-oculograms recordings: two at the outer canthi of eyes and one above and below each eye. The impedance for all the electrode sites was kept below 5 k $\Omega$ . The EEG was digitized at 1024 Hz in continuous. After the recording, a bandpass was offline set between 0.016 and 30 Hz. All trials with artifacts exceeding  $\pm 100 \mu\text{V}$  were excluded from the analysis. Moreover, all trials containing eye movements within the first 300 ms after the presentation of the stimulus were rejected to exclude the possible saccades towards the location of visual stimulus (Rayner, 1998). Across all conditions, 8.2% of the trials were rejected. Average referenced EEG epochs ( $-100$  to  $800$  ms) were time-locked to the stimulus onset, baseline corrected ( $-100$  to  $0$  ms) and averaged offline according to the spatial position and the emotional category of faces.

## 2.5. Data analyses

Behavioral data concerned the accuracy and the reaction times of the participants. A Greenhouse–Geisser corrected repeated measures analysis of variance (ANOVA) with the degree of eccentricity ( $15^\circ$ ,  $30^\circ$ ), side (left, right) and emotional facial expression (fear and neutral) as within-subject factors was performed on the percentage of correct responses and on the reaction times of correct responses of participants. A significance level of 5% (two-sided) was selected.

Spatio-temporal PCA (st-PCA) consists of two successive PCAs computed on EEG waveforms, providing scores that reflect ERP amplitude at specific localizations (spatial factors, or SFs, extracted during spatial PCA) and specific latencies (temporal factors, or TFs, extracted during temporal PCA; detailed EEG procedures are reported in Spencer, Dien, & Donchin, 1999; Spencer, Dien, & Donchin, 2001). In a first step, we performed a spatial PCA with 63 electrode sites as dependent variables and time points, participants (16) and conditions (four spatial positions and two emotional facial expressions) as observations (Varimax rotation, SPSS V. 15 software; Pourtois et al., 2008). Each SF represents a specific spatial configuration of brain activation and the factor loading corresponds to the SF's contribution to the original variables (i.e. how much the spatial factor accounts for the voltage recorded at each electrode). These spatial configurations can be visualized by topographic maps of factor loadings (Cartool software, Denis Brunet, <http://brainmapping.unige.ch/Cartool.htm>), and are usually defined by considering electrodes with the highest factor loadings (D'Hondt et al., 2010; Rigoulot et al., 2008). In a second step, SF scores were considered as "virtual electrodes", and their corresponding time series (818 time points, 800 ms duration at 1024 Hz sampling rate) were subjected to temporal PCA (tPCA), with emotional conditions, experimental blocks, and participants as observations. Temporal PCA identifies groups of highly correlated points in time and redistributes them into hypothetical and unobserved variables (i.e. temporal factors). Temporal PCA loadings correspond to the TF's contribution to each SF at each time point. Thus, TFs determine SF activity at specific latencies, usually by taking into account the highest factor loadings (D'Hondt et al., 2010; Rigoulot et al., 2008). For each couple composed by a spatial and a temporal factor, temporal factor scores reflect the activity of a "virtual electrode" at a specific time. Thus, an ANOVA with eccentricity, side and emotional facial expression as within-subject factors was performed on the individual temporal factor scores provided by the complete st-PCA procedure.

Moreover, in order to investigate the early occipital activity in response to peripherally faces, we first conducted a baseline-to-peak analysis (seeking for max-



**Fig. 1.** Illustration of the panoramic screen and trials of pictures presentation. (a) Spatial positions ( $-30^\circ$ ,  $-15^\circ$ ,  $+15^\circ$ , and  $+30^\circ$ ) for pictures' projection on the panoramic screen. (b) Duration of each picture presentation (300 ms) and inter-stimulus interval (ISI; from 2.5 to 4 s) during two successive trials.

imum amplitude and latency) between 140 and 240 ms for two parieto-temporal electrodes (P7 and P8), corresponding to the onset of the classical component evoked by faces when they are displayed in central vision, the N170. These time window and electrodes were defined after examination of the grand average of the data and were equivalent to those used in other studies (Ashley et al., 2004; Batty & Taylor, 2003). A Greenhouse–Geisser corrected repeated measures ANOVA with eccentricity, side and emotional facial expression as within-subject factors was performed on the amplitudes and latencies obtained from the baseline-to-peak analysis.

### 3. Results

#### 3.1. Behavioral data

The overall percentage of faces correctly categorized was high overall ( $91\% \pm 1$ ). The analysis on the accuracy of participants revealed an influence of the degree of eccentricity and of the emotional content of faces. First, a significant effect of eccentricity ( $F(1,15) = 18.93$ ;  $p < 0.001$ ) was obtained as the accuracy was higher when faces were projected at low eccentricities than at high eccentricities ( $-30^\circ = 87\% \pm 1$ ;  $-15^\circ = 95\% \pm 1$ ;  $+15^\circ = 94\% \pm 1$ ;  $+30^\circ = 90\% \pm 1$ ;  $F(1,15) = 17.34$ ;  $p < 0.001$ ). The effect of the degree of eccentricity was not influenced by any other factor, be it the emotional content of faces or the side of the visual field.

Second, as for the influence of the emotional content, many participants reported, after the experimental session, that they experienced some difficulties to identify the emotional expression of faces and selected the fear button only when they felt “aroused” enough. Accordingly, the accuracy appeared higher ( $F(1,15) = 17.39$ ;  $p < 0.001$ ) for neutral faces ( $95\% \pm 1$ ) than for fearful faces ( $88\% \pm 1$ ). The parameters  $d'$  and  $\beta$  from the signal detection theory were also computed:  $d'$  reached 2.81 and  $\beta$  ( $= 1.86$ ) confirmed the bias favoring neutral responses. This hold true for  $\pm 15^\circ$  ( $d' = 3.23$ ,  $\beta = 2.44$ ) and  $\pm 30^\circ$  ( $d' = 2.49$ ;  $\beta = 1.63$ ). At both eccentricities,  $\beta$  was clearly  $> 1$ .

The analysis of the participant's mean reaction times revealed an effect of degree of eccentricity ( $F(1,15) = 21.14$ ;  $p < 0.001$ ). The reaction times of the participants were shorter when faces were presented at low eccentricities ( $-30^\circ = 735 \pm 190$  ms;  $-15^\circ = 711 \pm 201$  ms;  $+15^\circ = 697 \pm 224$  ms;  $+30^\circ = 751 \pm 211$  ms;  $F(1,15) = 22.90$ ;  $p < 0.001$ ). Moreover, reaction times to fearful faces were shorter than those to neutral ones ( $F(1,15) = 5.42$ ;  $p = 0.034$ ; see Fig. 2 for correctly categorized faces). The analysis did not reveal any interaction between the degree of eccentricity and the emotional content of faces. Moreover, the side of the visual field did not have any influence on either effect.

#### 3.2. ERP results

##### 3.2.1. Eccentricity effect

The ANOVA performed on the amplitudes of N170 (Table 1) did not reveal an influence of the side ( $p = 0.857$ ) or of the degree of eccentricity ( $p = 0.227$ ) on the peak amplitudes. A similar ANOVA was performed on the latencies of these peaks. This analysis revealed that the onset of peaks was significantly delayed for high eccentricities when compared to low ones ( $F(1,15) = 25.11$ ;  $p < 0.001$ ; see Table 1). Moreover, a significant interaction between the side of projection and the electrode was shown ( $F(1,15) = 12.34$ ;  $p = 0.003$ ). Indeed, when faces were projected in the left visual field, latencies were longer in the left hemisphere (P7) than in the right

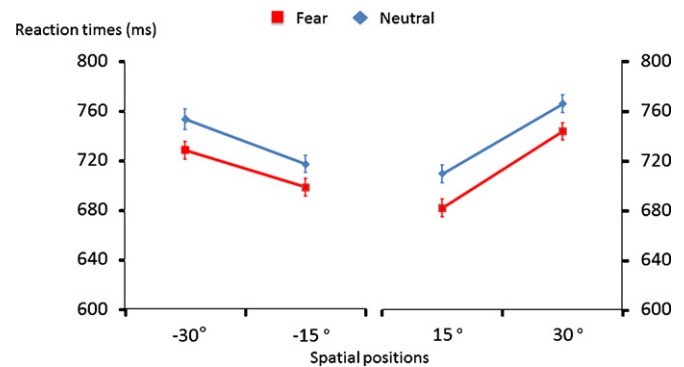


Fig. 2. Averaged reaction times to the presentation of fear and neutral faces at four spatial positions ( $-30^\circ$ ,  $-15^\circ$ ,  $+15^\circ$ , and  $+30^\circ$ ). Error bars represent the standard error of the mean values.

one (P8) while they were shorter when faces were projected in the right visual field (see Table 1 and Fig. 3a).

##### 3.2.2. Emotional effect

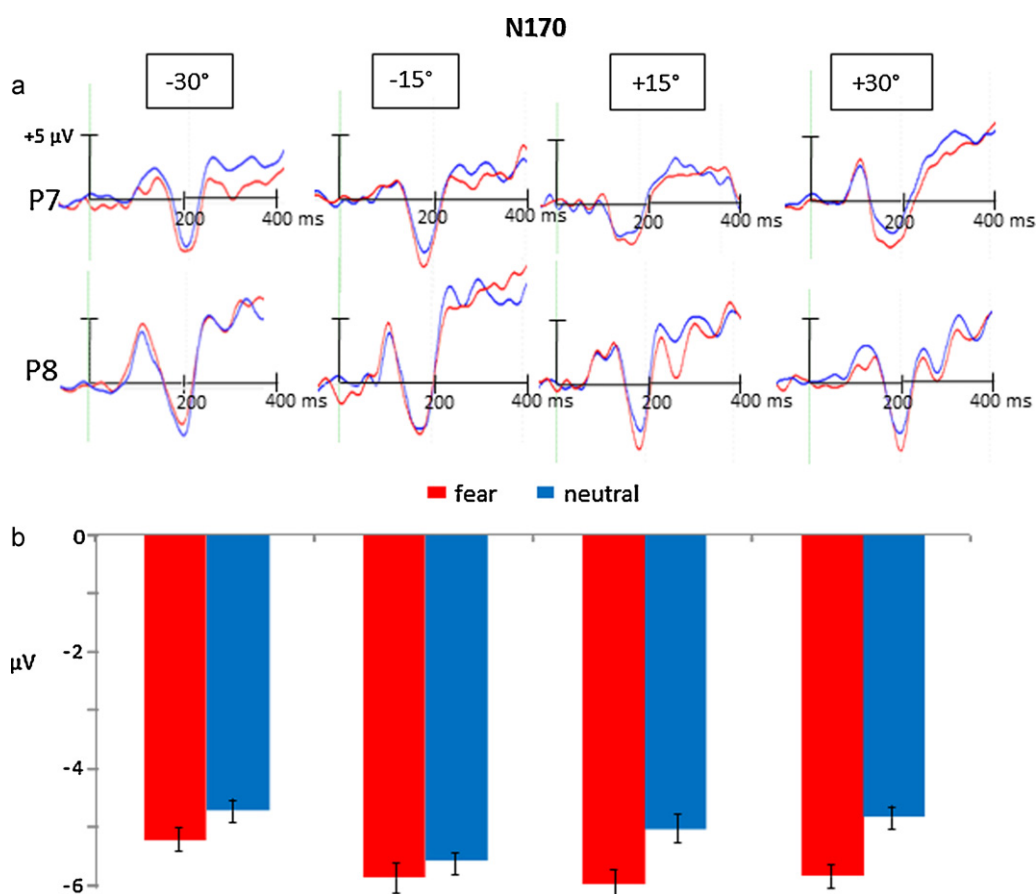
In addition, the baseline-to-peak analysis on the amplitudes of the N170 revealed an emotional effect because the amplitude was more negative for fearful faces than for neutral ones ( $F(1,15) = 6.51$ ;  $p = 0.021$ ; Fig. 3). Analyses did not reveal that this effect varied as a function of the side ( $F(1,15) = 2.93$ ;  $p = 0.11$ ) or of the degree of eccentricity ( $F(1,15) = 0.01$ ;  $p = 0.995$ ).

For better clarity of the results provided by st-PCA procedure, we report only the comparisons that demonstrated significant differences for the emotional content or significant interaction between emotional content and side or eccentricity of the pictures. The first significant effect occurred 150 ms after the onset of the stimulus (as indicated by the maximum of TF7 loadings) mainly on right parieto-occipital areas (as indicated by the maximum of SF3 loadings) with more negative factor scores for fearful faces than for neutral ones ( $F(1,15) = 5.58$ ;  $p = 0.032$ ; Fig. 4). This effect did not depend on the side of presentation or on the degree of eccentricity. The analysis revealed 190 ms after stimulus onset (TF6) in the left temporal areas (SF5) a double significant interaction between emotional content, side of projection and eccentricity ( $F(1,15) = 5.77$ ;  $p = 0.030$ ). This analysis did not reveal any interaction between the emotional content of faces and the degree of eccentricity ( $F(1,15) = 1.68$ ;  $p = 0.215$ ) or the emotional content of faces and the side of the visual field ( $F(1,15) = 0.35$ ;  $p = 0.564$ ). Further detailed analysis showed a significant effect of emotional content only when pictures were presented at  $-15^\circ$ , in the left visual field, the scores being more negative for fearful faces than for neutral ones ( $F(1,15) = 6.92$ ;  $p < 0.019$ ). At 260 ms after stimulus (TF4), analysis revealed a significant effect of emotional content in right parieto-occipital areas (SF3), with higher scores for neutral faces than for fearful ones ( $F(1,15) = 106.13$ ;  $p < 0.001$ ). Later on, at 370 ms (TF2), scores tended to be more negative for fearful faces than neutral ones in left temporal areas (SF5;  $F(1,15) = 4.36$ ;  $p = 0.054$ ). This effect did not depend on the degree of eccentricity or the side of presentation. Finally, 500 ms after stimulus onset (TF3), a significant double interaction between emotional content, side of projection and eccentricity was found in parietal areas (SF1;  $F(1,15) = 6.89$ ;  $p = 0.019$ ). Again,

Table 1

Peak amplitude and latency values for the N170 evoked component as a function of eccentricity and electrodes.

		Amplitude ( $\mu V$ )				Latency (ms)			
		-30	-15	+15	+30	-30	-15	+15	+30
N170	P7	4.60 $\pm$ 1.9	-5.51 $\pm$ 3.1	-5.58 $\pm$ 2.5	-5.24 $\pm$ 2.7	194.83 $\pm$ 16	183.72 $\pm$ 25	176.92 $\pm$ 25	180.94 $\pm$ 22
	P8	-5.25 $\pm$ 4.2	-5.88 $\pm$ 4.7	-5.30 $\pm$ 4.3	-5.41 $\pm$ 3.6	184.73 $\pm$ 18	176.98 $\pm$ 19	186.16 $\pm$ 14	197.45 $\pm$ 18



**Fig. 3.** Emotional effect on latency and amplitude of N170 component. (a) Averaged event-related potentials (ERPs), in response to fearful (red line) and neutral faces (blue line) projected at  $-30^\circ$ ,  $-15^\circ$ ,  $+15^\circ$  and  $+30^\circ$ . ERPs were recorded at left (P7) and right (P8) parietal electrodes. (b) Mean amplitude peaks of the N170, calculated between 140 and 240 ms for both P7 and P8 electrodes, in response to fearful (red) and neutral (blue) faces. Error bars represent the standard error of the mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

this analysis did not reveal any interaction between the emotional content of faces and the degree of eccentricity ( $F(1,15)=0.071$ ;  $p=0.794$ ) or between the emotional content of faces and the side of the visual field ( $F(1,15)=2.34$ ;  $p=0.147$ ). Further detailed analysis showed that fearful faces generated higher scores than neutral ones only when faces were presented at  $-15^\circ$ , in the left visual field ( $F(1,15)=9.13$ ;  $p=0.009$ ).

#### 4. Discussion

The aim of this experiment was to investigate the behavioral and electrophysiological responses in peripheral vision evoked by fearful and neutral faces. More precisely, we hypothesized that the responses would be enhanced by the fearful expression of faces. Firstly, we confirmed that behavioral and neural responses to visual stimuli significantly dropped for far peripheral eccentricities. Secondly, for the first time at such eccentricities, we showed faster reaction times and larger electrophysiological responses in response to fearful faces compared to neutral ones.

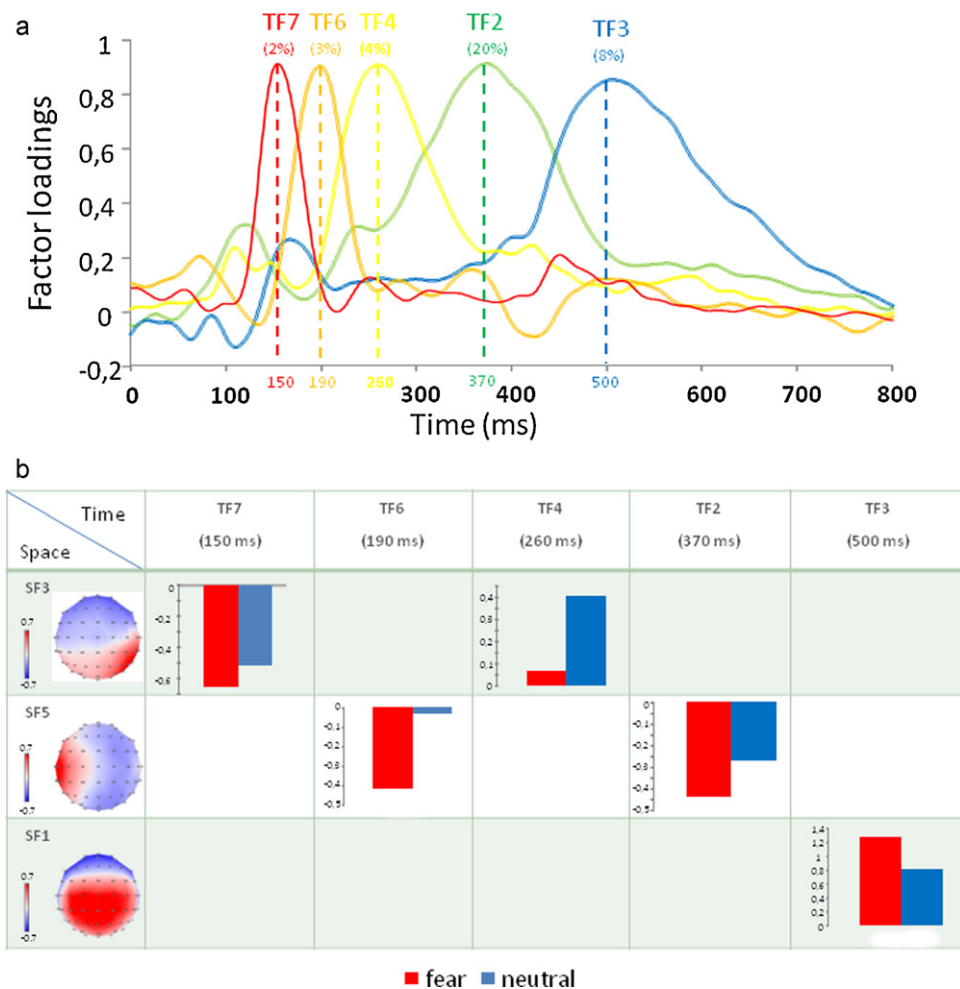
##### 4.1. Eccentricity effects

First, we showed that the behavioral performance declines with eccentricity, in agreement with previous studies (Rigoulot et al., 2008; Thorpe et al., 2001). Also, this decrease appears to be related to the degree of eccentricity, as the performances were worse at  $30^\circ$  than at  $15^\circ$ . In a similar way, Thorpe and coworkers found a linear decrease of behavioral performance in peripheral vision and these authors related their results to the almost linear decrease of

retinal ganglion cells observed in anatomical studies (Curcio & Allen, 1990 in humans; Wässle, Grunert, Rohrenbeck, & Boycott, 1990 in monkeys). This decrease would explain the low acuity of peripheral vision and consequently the degradation of performance in comparison with central vision.

Second, this study constitutes the first investigation of electrophysiological responses of far peripheral vision to faces. We discovered that the projection of faces in far PV evoked the classical N170 (without using cortical magnification factor, see Mäkelä, Näsänen, Rovamo, & Melmoth, 2001) although this result seems contradictory with those reported by Rousselet, Husk, Bennett, and Sekuler (2005). Indeed, these authors found no differences in electrophysiological activity around 170 ms in response to faces and houses presented at  $10^\circ$  of eccentricity which led them to conclude the absence of N170 to faces projected in low periphery. However, their investigation limited to near PV and differences of duration (80 ms *versus* 300 ms), size of pictures ( $3^\circ$  *versus*  $20^\circ$ ) and apparatus (computer screen *versus* panoramic screen) between both experiments could explain the discrepancy with the present results.

Here we observed that the N170 peaked after a longer time for faces at  $30^\circ$  of eccentricity than for those at  $15^\circ$ , in line with the gradual decrease of visual acuity across eccentricity. Further studies using faces both in peripheral and in central vision would be necessary to demonstrate that N170 is significantly delayed in PV. Furthermore, the significant interaction between the side of projection and the position of electrode reveals a maximal contralateral activity for the N170 supporting the persistence of contralateral activity along the visual pathways. These findings are also in line with an fMRI experiment, which found a maximal contralateral



**Fig. 4.** Emotional modulation of ERPs components revealed by spatio-temporal PCA. (a) Temporal factor (TF) loadings as a function of time. The percentage of variance is indicated for each factor. (b) Table illustrating significant modulations on ERP activity induced by emotional content of faces. The structure of the array allows to localize (lines) and to temporally define (columns) emotional modulations. Vertically, topographical representations of spatial factors (SF) loadings. Horizontally, TF are organized according to the onset of their peak loadings, from the earliest in the left to the latest in the right; TF scores are represented as a function of facial emotional expression. The value of the factor scores (y axis) is a unitless dimension.

activity in the fusiform gyrus, known as the cortical generator of the N170 (Hemond, Kanwisher, & Op de Beeck, 2007).

#### 4.2. Emotional effects

As for the accuracy of the participants, no difference was expected between neutral and fearful faces, as an extensive set of criteria constrained our *a priori* selection of pictures. In fact, this selection took into account the rate and the certainty of recognition as well as physical parameters such as luminance, contrast and size. Nevertheless, the correct responses were slightly more frequent for the neutral trials than for fearful ones. Even though this result is counterintuitive, this difference could easily be explained by the response strategy of the participants, like in Rigoulot et al. (2008). Indeed, in case of doubt they pressed the neutral button, which artificially increased the rate of correct responses for neutral pictures, in comparison with emotional ones.

We also provided evidence of faster responses to *correctly categorized* fearful faces than to neutral ones. This effect could be related to a more efficient allocation of resources towards negative stimulations, as already described in other studies (Fox, 2002; Koster, Crombez, Verschuere, & De Houwer, 2004; Öhman et al., 2001; Vuilleumier, 2005). For example, Öhman and colleagues observed in a visual search paradigm quicker detection of fear-relevant pictures than fear-irrelevant ones and suggest that threatening stimuli

are able to capture attention. Öhman and Mineka (2001) proposed that the human brain would be equipped with a fear module subserving modulation of selective attention to evolutionarily prepared threat stimuli. This module could have been activated when fearful faces appeared in PV and explain the quicker responses to fearful faces in comparison with neutral faces.

Electrophysiologically, and at such peripheral eccentricities, we showed for the first time the modulation of evoked responses by emotional expression of faces. This confirms the capacity of PV to analyze high-saliency events, in agreement with recent results (Bayle et al., 2009; De Cesarei et al., 2009; Liu & Ioannides, 2010). These modulations are distributed in early and late temporal windows and primarily represent larger activity in response to fearful faces than to neutral ones.

The first emotional modulation appears around 150 ms after the onset of the stimulus, on right parieto-occipital areas. We argue that this parieto-occipital activity could reflect a delayed and more lateralized P100 (P100-like, see Rigoulot et al., 2008). A similar effect was found in Rigoulot et al. (2008) with unpleasant natural scenes and could reflect an early extraction of emotional content of the stimulations (e.g., Pourtois et al., 2004) favoring adaptive behavioral responses to events announcing danger. Early emotional differentiation was also observed in Liu and Ioannides (2010) who projected emotional faces at 10° of eccentricity and found that the emotions were separated first in the ipsilateral amyg-

dala and contralateral superior temporal sulcus. As the authors found another pattern of activation when faces were presented in central vision, these data and those of Rigoulot et al. (2008) support the idea that peripheral vision engages specific brain networks to process emotional information. This should be noted that earlier modulations have been found with faces presented in CV, between 120 and 150 ms (Batty & Taylor, 2003; Pizzagalli et al., 1999; Pourtois et al., 2004), for the components P100 and N100. In this frame and considering the higher temporal resolution of the magnocellular pathway mostly related to peripheral vision, it seems counter-intuitive that emotional effects appeared earlier in central than in peripheral vision. However, recent data (Sincich & Horton, 2005) showed that magnocellular and parvocellular pathways are not so clearly separated and that many connections exist between them. Thus, it seems premature to conclude that the magnocellular pathways alone would convey the emotional related information. Future studies using moving or low-pass filtered stimuli rather than static pictures containing all the spatial frequencies, could be of great help to shed light on this issue. Moreover, the nature of the task could influence the results as we found with the same experimental design earlier modulations during an implicit emotional categorization (Rigoulot et al., submitted) and De Cesare et al. (2009) observed emotional modulations at 16° of eccentricity only when no instructions were given to the participants.

Later, we found an increase of activation in left temporal areas around 190 ms. Given the timing and the spatial location, this activity likely reflects the activity of the N170, slightly delayed by the display of faces in PV. This seems to be confirmed by the baseline-to-peak analysis which revealed that N170 amplitude was more negative in response to fearful faces. In central vision, while some studies did not show emotional modulations on N170 (Eimer & Holmes, 2002, 2007), others have found differences for fear expression (Batty & Taylor, 2003; Eger et al., 2003). The observed peripheral effect suggests that, first, structural analysis of the face and that of emotional expression could occur concomitantly, in line with Haxby, Hoffman, and Gobbini (2000) and, second, the affective nature of faces could enhance the neuronal activity engaged in face processing, even when they are presented in peripheral vision. Overall, peripheral vision is likely able to sustain mechanisms that detect relevant information and that could have a crucial adaptive role.

Furthermore, it was shown that emotional modulations persist in late temporal windows. First, a negative shift of the ERP amplitude for fearful relative to neutral expressions over lateral temporal scalp was observed starting from 200 ms (TF6) to 370 ms (TF2) post-stimulus in line with other data (Bar-Haim, Lamy, & Glickman, 2005; Eimer et al., 2003; Esslen, Pascual-Marqui, Hell, Kochi, & Lehmann, 2004; Eimer & Kiss, 2007; Luo, Feng, He, Wang, & Luo, 2010; Schupp et al., 2004). Second, the couple SF1-TF3 corresponding to a late component in parietal areas could be identified as the late positive potential (LPP). The LPP has already been found sensitive to emotional pictures (Pastor et al., 2008) as well as threatening faces (Schupp et al., 2004) and increased activations of this component to fearful faces could reflect a sustained attention towards emotional stimulations in comparison with neutral ones. In addition, at 200 and 500 ms, effects appear only when the faces were presented in left visual field. Such a laterality effect was also found in Luo et al. (2010) in the same temporal windows and this is in agreement with emotional effects observed in CV which suggest a right hemispheric dominance in the processing of emotional stimulations, particularly negative ones (Borod, 1992; Borod et al., 1998; Calvo & Avero, 2008; Davidson & Irwin, 1999; Pizzagalli et al., 1999; Sato & Aoki, 2006).

Finally, in Rigoulot et al. (2008), some results challenged the classical view of behavioral and electrophysiological superiority for emotional laden stimuli in comparison to neutral ones. The

use of faces here, instead of natural scenes in the previous study, could have maximized the emotional impact in PV. First, as already mentioned in the introduction, fearful faces have an obvious simpler spatial configuration and are more homogenous than natural scenes (in comparison with the heterogeneity of possible negative scenes). Second, meta-analyses suggest that the amygdala, known to play a key role in facial emotional processing (Adolphs et al., 1999), is more strongly activated by emotional faces than emotional natural scenes (Sergerie, Chochol, & Armony, 2008). The role of the amygdala in social interactions (Adolphs et al., 1999; Brothers, Ring, & Kling, 1990) and its connections with occipito-temporal areas (Lang et al., 1998; Morris et al., 1998) suggest its involvement in the early and late modulations described in this study although this is not possible to show with electrophysiological recordings. Furthermore, some studies (Morris et al., 1998; Vuilleumier et al., 2003) propose that a tecto-pulvo-amygdala pathway could provide quick and coarse (LSF) visual signal about fear-related stimuli and could aid rapid adaptive behavioral responses. Given that PV relies on LSF information, this subcortical pathway could be activated and subtend faster responses to fearful faces appearing in PV. In the end, this study constitutes the first investigation of far eccentric emotional faces processing but the absence of stimulations in central vision limits our exploration and does not allow to clarify how specific is the emotional processing in PV. By using stimulations displayed both in central and peripheral visual fields, further studies certainly will allow to know whether peripheral emotional processing differs from that taking place in central vision.

To conclude, this study shows for the first time the behavioral and neuronal impact of fearful face expressions in far eccentric points of the visual field. Despite the impoverished conditions of vision, a preferential processing of emotional expression of fear persists over neutral faces. This result is in line with those of other studies showing the impact of emotional stimulations even when their perception is reduced or abolished, as in subliminal presentation, binocular rivalry situations, or in clinical cases of parietal neglect and affective blindsight (e.g., Vuilleumier et al., 2002; see also Morris, DeGelder, Weiskrantz, & Dolan, 2001). Futures studies might use the saliency of emotions in neurovisual rehabilitation (Kerkhoff, 2000) to stimulate the PV in patients suffering from reduced acuity in CV (like from Age-related Macular Disease) as clinical studies have shown that sustained attention is a key factor in improving PV capacities (Altpeter, Mackeben, & Trauzettel-Klosinski, 2000).

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