RESEARCH ARTICLE

WILEY

Retinotopy of emotion: Perception of negatively valenced stimuli presented at different spatial locations as revealed by event-related potentials

Luis Carretié¹ | Constantino Méndez-Bértolo¹ | Cristina Bódalo¹ María Hernández-Lorca | Uxía Fernández-Folgueiras | Sabela Fondevila | Tamara Giménez-Fernández¹

Correspondence

Luis Carretié, Facultad de Psicología, Universidad Autónoma de Madrid, 28049 Madrid, Spain. Email: carretie@uam.es

Funding information

Comunidad de Madrid, Grant/Award Number: HUM19-HUM5705; Ministerio de Ciencia, Innovación y Universidades, Grant/Award Number: PGC2018-093570-B-IOO

Abstract

Scarce previous data on how the location where an emotional stimulus appears in the visual scene modulates its perception suggest that, for functional reasons, a perceptual advantage may exist, vertically, for stimuli presented at the lower visual field (LoVF) and, horizontally, for stimuli presented at the left visual field (LeVF). However, this issue has been explored through a limited number of spatial locations, usually in a single spatial dimension (e.g., horizontal) and invariant eccentricities. Event-related potentials (ERPs) were recorded from 39 participants perceiving brief neutral (wheels) and emotional stimuli (spiders) presented at 17 different locations, one foveal and 16 at different peripheral coordinates. As a secondary scope, we explored the role of the magnocellular (M) and the parvocellular (P) visual pathways by presenting an isoluminant/heterochromatic (P-biased) and a heteroluminant/isochromatic version (M-biased) of each stimulus. Emo > Neu effects were observed in PN1 (120 ms) for stimuli located at fovea, and in PN2 (215 ms) for stimuli located both at fovea and diverse peripheral regions. A factorial approach to these effects further revealed that: (a) emotional stimuli presented in the periphery are efficiently perceived, without evident decrease from para- to perifovea; (b) peripheral Emo > Neu effects are reflected 95 ms later than foveal Emo > Neu effects in ERPs; (c) LoVF is more involved than UVF in these effects; (d) our data fail to support the LeVF advantage previously reported, and (e) Emo > Neu effects were significant for both M and P stimuli.

KEYWORDS

emotion, ERPs, perception, spatial location

Luis Carretié and Constantino Méndez-Bértolo contributed equally to this study.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made. © 2019 The Authors. Human Brain Mapping published by Wiley Periodicals, Inc.

¹Facultad de Psicología, Universidad Autónoma de Madrid, Madrid, Spain

²Facultad de Psicología, Universidad Complutense de Madrid, Madrid, Spain

1 | INTRODUCTION

Due to a number of differences from the photoreceptor level, where the presence of cones decreases as eccentricity increases (Strasburger, Rentschler, & Jüttner, 2011), to the visual cortex level, where foveal vision is overrepresented (Azzopardi & Cowey, 1996; Hubel & Wiesel, 1972), acuity of nonfoveal vision is much lower than foveal. Despite this, evolution has favored the nervous system to efficiently detect salient stimuli such as dangerous, appetitive or novel events even when they appear at nonfoveal areas of the visual field. Thus, these emotional events (they inherently trigger physiological, subjective, and/or behavioral emotional responses), such as threatening scenes or facial expressions, elicit differential neural responses with respect to neutral stimuli when they appear in the periphery (Bayle, Henaff, & Krolak-Salmon, 2009; Calvo, Nummenmaa, & Hyönä, 2008; Carretié, Albert, et al., 2013; Rigoulot, D'Hondt, Defoort-Dhellemmes, Despretz, & Honoré, 2011; Rigoulot, D'hondt, Honore, & Sequeira, 2012; but see De Cesarei, Codispoti, & Schupp, 2009). However, this "peripheral capability" to detect emotional elements of the visual context could not be homogeneous: the exact location in the periphery where the emotional stimulus appears could be a crucial factor determining the brain mechanisms involved in its processing and, ultimately, our response to it. Indeed, whereas this issue has not been directly explored vet, some lines of research suggest that verticality (whether the stimulus appears in the upper or in the lower visual hemifields) and horizontality (left vs. right hemifields) may influence the perception of emotional stimuli.

This influence may be exerted at two levels, the first of which is of anatomical nature and the second of functional nature. In the first place, the human (and other species) visual system is retinotopic and contralateral-in terms of left-right hemifields-from the thalamic lateral geniculate nuclei (Schneider, Richter, & Kastner, 2004) to visual cortices (Tootell, Hadjikhani, Mendola, Marrett, & Dale, 1998). This is especially well defined in V1 or primary visual cortex, where left and right primary visual cortices process the information from the contralateral hemifield, while dorsal cuneus (the part above the calcarine fissure) processes the lower part of the visual scene and the ventral cuneus (the bank below the calcarine fissure) processes the upper part (Jeffreys & Axford, 1972a, 1972b). To different extents, retinotopy extends to the visual extrastriate cortices and ventral and dorsal visual pathways (Sereno & Tootell, 2005). This retinotopy is reflected in event-related potentials (ERPs), where the spatial location of the stimulation has a clear and direct reflection in the amplitude and polarity of visual components, particularly in the 80-250 ms interval: C1, P1, N1, and P2 (e.g., Capilla et al., 2016; Clark, Fan, & Hillyard, 1995). This stimulus location-related variability of ERPs has been observed in response to nonemotional (checkerboards) stimuli, so it is independent of emotional load. Therefore, any ERP study on the differential processing of emotional stimuli as a function of the location in which they appear should take into account this level of variability (e.g., by employing nonemotional stimuli as control that allow to subtract this nonemotional retinotopic variability).

Second level, of functional nature, and more relevant to our scopes, would consist of a differential cognitive, and potentially affective, response to each vertical or horizontal hemifield: upper (UVF) and lower (LoVF), or left (LeVF) and right fields (RVF). Thus, UFV and LoVF (i.e., the part of the visual scene which is above and below our fixation point, respectively) have been proposed to be evolutionarily associated with different functional implications and, consequently, with different visual neural circuits. The UVF is usually linked to extrapersonal or "far" space and, consequently, to scanning and recognition of relevant stimuli, whereas the LoVF is often linked to "near" or peripersonal space and, therefore, to physical interaction with our close environment (Previc, 1990, 1998). Ultimately, this (nonabsolute) dichotomy would explain the differential involvement of dorsal and ventral visual processing systems, traditionally related to vision for action and vision for perception, respectively (Goodale & Milner, 1992; Milner & Goodale, 1995), and later confirmed (e.g., Brown, Halpert, & Goodale, 2005). Indeed, the LoVF is mostly processed by the dorsal visual/viso-motor system and the UFV by the ventral visual system (Gallivan, Cavina-Pratesi, & Culham, 2009; Hadjidimitrakis et al., 2011; Pitzalis, Fattori, & Galletti, 2013; Previc, 1990, 1998; Rossit, McAdam, Mclean, Goodale, & Culham, 2013). Importantly to our scopes, some clues suggest a processing advantage of emotional stimuli presented at the LoVF, since an enhanced capability of angry faces to capture attention has been detected when presented in this hemifield, this bias reflecting an enhanced LoVF vigilance to protect peripersonal space according to authors (Petrova & Wentura, 2012). Other clue on the differential processing of emotional stimuli in both hemifields is the perceptual performance for stimuli presented at LoVF and UVF. Since certain critical stimuli in evolutionary terms, such as threats, tend to appear in the LoVF (Isbell, 2006), stimuli appearing at this hemifield should present certain perceptual advantage (in terms of detection and recognition). Indeed, several studies confirm this LoVF advantage in target detection tasks (e.g., Blini et al., 2018; Losier & Clane, 2004). Other studies exploring several visual attributes show the LoVF advantage is limited to parameters such as of motion, contrast and hue, whereas others, such as distance/ depth, would be better perceived for UFV stimuli (e.g., Levine & McAnany, 2005).

Still at this second, functional level, and with respect to the horizontal dimension, a bias in perception and attention to the LeVF have been reported in response to nonemotional stimuli (see reviews in Brooks, Della Sala, & Darling, 2014; Jewell & McCourt, 2000; but see Hatin, Sykes Tottenham, & Oriet, 2012; this bias is named pseudoneglect due to the relative "neglect" of RVF). Interestingly, when stimuli are emotionally loaded, a LeVF bias has been also reported, as revealed by reaction times in emotional perception/recognition tasks (Alves, Aznar-Casanova, & Fukusima, 2009): performance is reported to be significantly better when emotional stimuli appear in the LeFV. These results are interpreted at the light of the two main theoretical proposals claiming that an asymmetry exists at the cortical level in emotional processing (Alves et al., 2009). On the one hand, some classical proposals suggest that the right hemisphere is more involved in emotional processing—and expression—than the left (Borod, Koff,

Lorch, & Nicholas, 1986; Etcoff, 1986) and, on the other hand, others theorize that the right hemisphere is more involved in negative affect and the left hemisphere in positive emotional processes (Davidson, 1984; Heller, 1993). Since Alves and colleagues found a relative LeVF superiority for both positive and negative stimuli, their data are presented as further supporting the former proposal. Convergently, an earlier emotion discrimination (emotional vs. neutral stimuli differences), as revealed by ERPs, has been reported when emotional stimuli, positive and negative, are presented in the LeVF (Pizzagalli et al., 1999). In sum, this line of research suggests a LeVF advantage in emotional processing.

Since scarce previous data were obtained employing a limited number of spatial locations (usually two), we consider that a systematic exploration of this issue is necessary by increasing the number of coordinates in which emotional stimuli are presented. The main scope of this study is, therefore, to explore how the brain reacts to neutral and emotional stimuli presented at 17 different locations (one foveal and 16 at different peripheral para- and perifoveal coordinates). The ERP components sensitive to the spatial location of visual stimuli mentioned above have all been reported to be sensitive to their emotional content. Thus, C1 (Pourtois, Grandjean, Sander, & Vuilleumier, 2004), P1 (Carretié et al., 2009), N1 (Keil et al., 2001), and P2 (Delplangue, Lavoie, Hot, Silvert, & Segueira, 2004) have variable amplitudes in response to different facial expressions or affective scenes. Importantly, the polarity of these components recorded at a particular scalp point changes depending on the spatial location of the visual scene where the stimulus appears. For example, C1 and P1 present opposite polarity for stimuli appearing in LoVF and UVF, and N1 also varies its polarity for LeVF and RVF locations (Capilla et al., 2016). Therefore, the label "N" or "P" becomes arbitrary when these components are evoked by stimuli presented at different spatial locations, as in the present study. Consequently, the label "PN" will be employed here for those components presenting this space-related positivity/negativity concurrence. Our main hypothesis is that the emotional sensitivity of these visual components appearing in the 80-250 ms interval (labeled here, according to their temporal order, as PN1, PN2, etc.) will be significantly modulated by the spatial location of stimulation. More specifically, we would like to test the proposed LoVF and LeVF advantage in emotional perception previously described.

A secondary scope we considered worth exploring is whether the parvocellular (P) versus magnocellular (M) balance of stimulation modulate the emotional effects that may be observed. Retinal projections to P and M layers of the lateral geniculate nucleus decline to a greater extent in the former case with eccentricity (Brown et al., 2005), resulting in a magnocellular bias for peripheral vision. Thus, peripheral effects (including emotional peripheral effects) on visual perception would be more pronounced for stimuli especially designed to be better processed by the M system than those designed to be better processed by the P system. With the idea of testing this hypothesis in mind, we presented emotional and neutral stimuli under two modalities: isochromatic/heteroluminant stimuli and heterochromatic/isoluminant. These parameters have been

reported to be M and P balanced, respectively (e.g., Livingstone & Hubel, 1988), enhancing the involvement of one visual system (P or M) over the other (but not completely suppressing any, since P and M systems may respond similarly to isoluminant stimuli under certain circumstances: see a review in Skottun, 2013). A recent study (not exploring spatial location) reported that isochromatic/heteroluminant (i.e., M balanced) emotional stimuli presented in the periphery captured attention to a greater extent than both P balanced emotional stimuli and M balanced neutral stimuli (Carretié et al., 2017).

2 | METHODS

2.1 | Participants

Forty-five individuals participated in this experiment, although data from only 39 of them could eventually be analyzed, as explained later (33 women, age range of 18–35 years, mean = 20.21, SD = 3.12). The study had been approved by the Universidad Autónoma de Madrid's Ethics Committee. All participants were students of Psychology, provided their informed consent, and received academic compensation for their participation. They reported normal or corrected-to-normal visual acuity.

2.2 | Stimuli and procedure

Participants were placed in an electrically shielded, sound-attenuated room. They were asked to place their chin on a chinrest maintained at a fixed distance (60 cm) from the screen (VIEWpixx[®], 120 Hz) throughout the experiment. Four types of stimuli were presented to participants (Figure 1): 20 emotional (spiders or S) and 20 neutral (wheels or W), which were either parvocellular-P (red figure over green ground: heterochromatic/isoluminant condition), or magnocellular balanced-M (black figure over gray background: isochromatic/heteroluminant condition). Spiders are among the top five most feared animals (Gerdes, Uhl, & Alpers, 2009), and they cause the most prevalent phobia related to animals (Jacobi et al., 2004). Indeed, spiders are assessed as negatively valenced stimuli by relatively large samples in emotional picture databases (e.g., International Affective Picture System (IAPS): Lang, Bradley, & Cuthbert, 2005; EmoMadrid: Carretié, Tapia, López-Martín, & Albert, 2019). In order to test whether spider silhouettes were also efficient as negatively valenced stimuli, and wheels as neutral, these stimuli were submitted to a questionnaire in which an independent sample of 447 participants (397 women, mean age = 19.51, SD = 1.46) rated their emotional valence through a 7-point Likert scale that ranged from "very negative" (1) to "very positive" (7). Spiders were rated as negative (mean = 1.704, SEM = 0.038) and wheels as neutral (i.e., in the intermediate values of the scale: mean = 3.918, SEM = 0.030). Differences between both stimuli were strongly significant (F(1,446) = 2,557.289, p < .001, $\eta_p^2 = 0.852$).

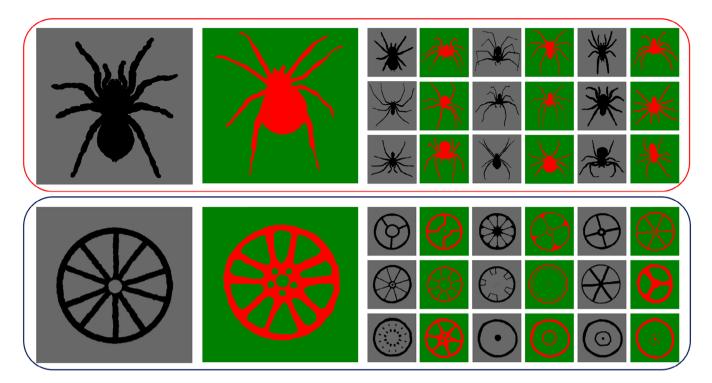


FIGURE 1 Stimuli employed in this experiment. One exemplar per category is presented at the left, and thumbnails of all stimuli are illustrated at the right side

The size of stimuli (figure + ground) was $4.5^{\circ} \times 4.5^{\circ}$ width. Details on the physical characteristics of the spiders and the wheels (i.e., figure-ground luminosities—theoretical/graphical and real as measured through a TES-137® luminance meter—RGB saturations, figure surface against background and spatial frequencies), as well as stimuli themselves, are provided in http://www.psicologiauam.es/CEACO/sup/SpatLoc19.htm. Differences between S and W stimuli regarding both spatial frequencies and figure versus ground surface were not significant (see details in the link above).

Each individual P-mode and M-mode spider and wheel appeared three times in random order in each of the 17 locations depicted in Figure 2. In other words, each stimulus category (SP, SM, WP and WM) was presented 60 times in each location (3x 20 stimuli per category). This resulted in 1,020 trials per category (60×17 locations), and the total number of trials was 4,080 (1,020 \times 4 categories). Each stimulus, whatever its location, was displayed on the screen for 150 ms, and stimulus onset asynchrony was 450 ms. Participants were instructed to look at the fixation dot at the center of the screen all the time (position 17 of Figure 2), which was marked with a gray circle (0.5° radius) during the interstimulus intervals. Participants were instructed to permanently direct their gaze to the fixation dot and to avoid any ocular movement. Total duration of the stimulus sequence was 40.8 min, so it was divided into 10 blocks to provide brief rest periods. In order to facilitate constant attention to stimulation, the inter-stimulus fixation dot randomly changed its color from gray to blue in 60 trials (0.014%), and the participants were instructed to count these changes and report the total number after each block (this sum was different from block to block).

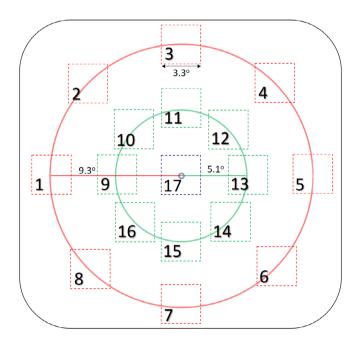


FIGURE 2 Stimulus size and visual locations where stimuli were presented. A single stimulus was presented in one of these 17 locations in each trial. Fixation point was placed over position 17

2.3 | Recording and preprocessing

Electroencephalographic (EEG) activity was recorded using an electrode cap (ElectroCap International) with tin electrodes. Fifty-nine

electrodes were placed at the scalp following a homogeneous distribution and the international 10-20 system. All scalp electrodes were referenced to the nosetip. Electrooculographic (EOG) data were recorded supra- and infraorbitally (vertical EOG) as well as from the left versus right orbital rim (horizontal EOG) in order to detect blinkings and ocular deviations from the fixation point. An online analog high-pass filter was set to 0.03 Hz; analog low-pass filtering was not applied. Recordings were continuously digitized at a sampling rate of 420 Hz. An offline digital Butterworth bandpass filter (order: 4, direction: zero phase forward and reverse—twopass—filter) of 0.3–30 Hz was applied to continuous (preepoched) data using the Fieldtrip software (http://fieldtrip.fcdonders.nl; Oostenveld, Fries, Maris, & Schoffelen, 2011). The continuous recording was divided into 600 ms epochs for each trial, beginning 100 ms before stimulus onset.

EEG epochs corresponding to trials in which the fixation dot changed its color (see previous section) were eliminated, as well as those corresponding to the subsequent two trials, in order to avoid the effect of this control, irrelevant (to our scopes) task. Trials in which ocular horizontal or vertical movements were detected (EOG deviations over 100 µV) were automatically removed. Additionally, blinking-derived artifacts were removed through an independent component analysis (ICA)-based strategy (Jung et al., 2000), as provided in Fieldtrip. After the ICA-based removal process, a second stage of visual inspection of the EEG data was conducted in order to manually discard trials in which any further artifact, ocular (horizontal or vertical motion) or other type, was present. This automatic and manual rejection procedure led to the average admission of 843.5 (SD = 54.6) SP, 844.5 (53.9) WP, 839.9 (59.2) SM, and 840.4 (54.8) WM trials, the difference among stimulus categories being nonsignificant (F(3,114) < 1.395, Greenhouse-Geisser ε corrected p = .25, $\eta_p^2 = 0.342$). The minimum number of trials accepted for averaging was 43 trials per participant and condition (i.e., each category presented in each location). Data from one participant were eliminated since they did not meet this criterion. The rest of nonanalyzed participants (five) presented non solvable anomalies in the recordings of one or more EEG leads (the integrity of all channels was necessary for spatial analyses described later).

2.4 | Data analysis

2.4.1 | Detection, spatiotemporal characterization, and quantification of relevant ERP components

Data reduction preserving most part of the variance resulted necessary to further analyze our Emotion (two levels: S or W) \times Visual Manipulation (two levels: M or P) \times 17 Locations design, taking also into account that recordings consisted of a 59 EEG channels \times 253 digitized voltages or "time points" \times 4,080 trials matrix (this matrix is openly available at https://osf.io/85nu3/). Thus, data reduction was carried out via three-step principal component analysis (PCA), a factorial procedure that, in brief, groups variables which tend to covary,

forming a single "factor" that retains most of the variance of the individual variables that form it. Therefore, PCA reduces the original amount of variables to a smaller one which keeps most of the original variability. The decision on the number of factors to select in the three PCAs was based on the scree test (Cliff, 1987), and extracted factors were submitted to promax rotation also in all cases (Dien, 2010). This three-step procedure is summarized in Figure 4, which also shows its main results.

Data reduction in the time domain: temporal PCA

First, detection and quantification of prominent perception-related temporal components was carried out through a covariance-matrixbased temporal PCA (tPCA), a strategy that has repeatedly been recommended for these purposes (e.g., Chapman et al., 2004; Chapman & McCrary, 1995; Dien, 2010). In brief, tPCA computes the covariance between all ERP time points, which tends to be high between those involved in the same component and low between those belonging to different components. The matrix submitted to tPCA was formed by voltages as variables (i.e., 252 voltages corresponding to 500 ms at 420 Hz: see Section 2.3) and participants x stimulus category x stimulus location \times channels (i.e., $39 \times 4 \times 17 \times 59 = 156,468$) as cases. Among the resulting temporal factors (TFs) selected through the scree test previously mentioned, only those comprised in the 80-250 ms interval (see Section 1) were selected and, among them, those most prominent in grand averages. As later explained in Section 3, these components were PN1 and PN2. The TF scores, which consist of a single value per TF (involving several time points) and are linearly related to amplitudes, were submitted to the next PCA.

Data reduction in the topography domain: scalp map PCA

Second, both PN1 and PN2 TF scores resulting from the previous tPCA were submitted to scalp map PCA (sPCA). This PCA provides a reliable division of the scalp into the different regions or scalp factors (SFs) in which each TF is distributed. Basically, each scalp map factor (e.g., a frontal or a posterior factor) is formed with the scalp points (i.e., electrode locations) where recordings tend to covary. Each input matrix (one for PN1 and another for PN2) consisted of 59 variables (i.e., EEG channels) and 2,652 cases (i.e., participants × stimulus category × stimulus location). In this case, no restrictions were introduced for factor selection besides the scree test, since some relevant components may present both anterior and posterior scalp maxima for different stimulus locations (e.g., P2: Capilla et al., 2016). PN1 and PN2 SF scores, which consist of a single value per SF (involving several electrodes) and are linearly related to amplitudes, were then submitted to a subsequent PCA.

Data reduction in the stimulus location domain: visual location PCA

Third, a visual location PCA (vPCA) was performed in order to detect the stimulus locations in which PN1 and PN2 SF amplitudes (or SF scores) covaried, grouping these locations into a reduced number of "visual location factors" (VFs) explaining most of the original variance. Each matrix introduced in vPCAs (one for each SF in which PN1 and PN2 were decomposed) consisted of 17 variables (stimulus locations) and 156 cases (participants × stimulus category). Regarding the selection criteria, the scree test was used except if it did not include a foveal VF. If this occurred, the number of selected factors was increased up to the first foveal factor to ensure that subsequent analyses (see next section) allowed to test both foveal and peripheral effects in every relevant ERP temporal and SF. The resulting VF scores consist of a single value per VF (involving several stimulus locations) and are linearly related to amplitudes, were those submitted to the analyses described in the next section.

2.4.2 | Analyses of experimental effects

Experimental effects on PN1 and PN2 were tested by introducing Emotion (two levels: S and W) and Visual Manipulation (two levels: P and M) as within-subject factors in repeated-measures analysis of variances (ANOVAs) carried out for VF scores. As explained above, each VF score summarizes the amplitude of a particular PN1 or PN2 spatial factor in response to a group of visual locations which tend to elicit similar (covariating) responses. Effect sizes in these ANOVAs were computed using the partial eta-square (η_p^2) method. Post hoc comparisons to determine the significance of pairwise contrasts in potential interactions were performed using the Bonferroni correction procedure.

3 | RESULTS

3.1 | Detection, spatiotemporal characterization and quantification of ERP components

Figure 3 shows a selection of grand averages after subtracting the baseline (prestimulus) activity from each ERP. These grand averages correspond to medial and lateral parieto-occipital areas, where the experimental effects, discussed later, were most prominent. An important pattern of response already observable in the grand averages is worth mentioning at this point: PN1 and PN2 are the most prominent components within the 80–250 ms window in most grand averages and are those that appear to be sensitive to the experimental manipulation. They are labeled "PN" since they present opposite polarity at parieto-occipital areas in response to stimuli presented in UVF and LoVF, being therefore "both" positive and negative.

Figure 4 summarizes main results (see also Section 2.4). First analytical step consisted in detecting and quantifying these components through a tPCA. Seven TFs were extracted by tPCA and submitted to promax rotation. Factor peak-latency and topography characteristics revealed TF6 and TF4 as the critical components, since the former was associated with PN1 (peak latency \simeq 120 ms) and the latter with PN2 (\simeq 215 ms). Next, sPCAs applied to these two relevant TFs decomposed PN1 into five SFs or regions and PN2 into three SFs. In all cases, the SF scores (equivalent to the global amplitude of a scalp

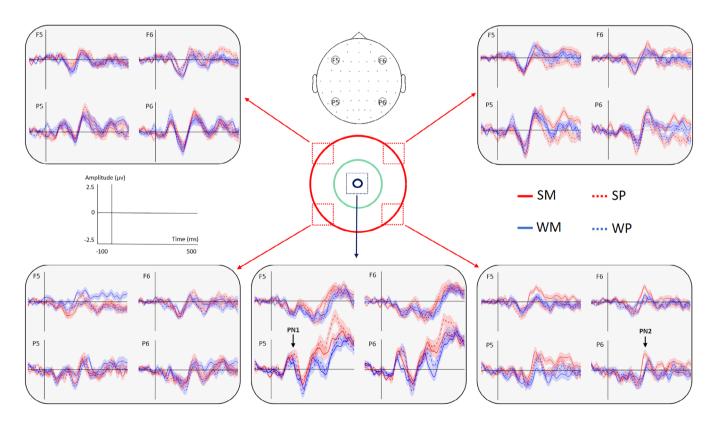


FIGURE 3 Grand averages at two anterior (F5 and F6) and two posterior (P5 and P6) electrodes in response to stimuli presented at fixation and at four peripheral positions (UVF-LeVF, UVF-RVF, LoVF-RVF). "Shadows" surrounding lines represent the standard error of means

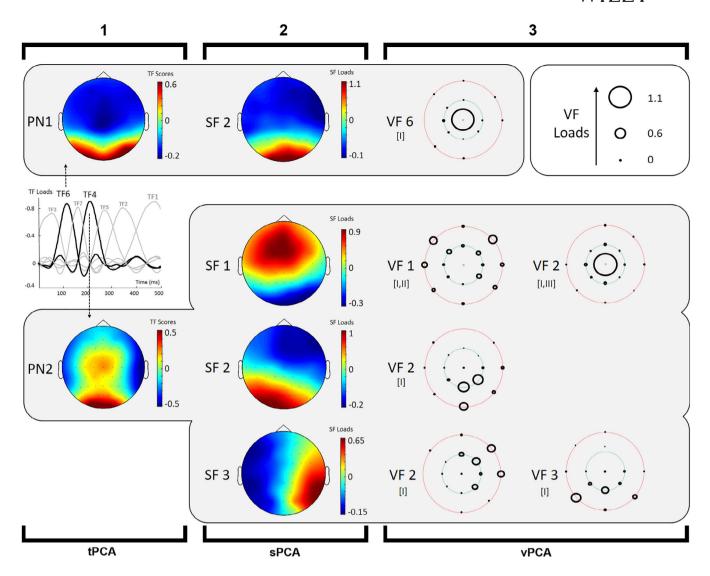


FIGURE 4 Three-step principal component analysis (PCA) analysis structure. First, the temporal PCA (tPCA) extracted temporal factors (TF) or components from original recordings, being PN1 and PN2 those relevant to our study. Second, these PN1 and PN2 TF scores were submitted to scalp PCAs (sPCA), which decomposed them into two and four scalp factors (SFs) respectively (only those finally yielding significant effects are shown). And third, visual location PCA (vPCA) grouped the 17 visual locations in a reduced set of visual location factors (VFs; only those finally yielding significant effects are shown). Significant differences in square brackets: I = Spiders > Wheels, II = Magno > Parvo, III = Parvo > Magno

region, as previously explained) were extracted per subject and condition in each SF. Finally, SF scores from these eight SFs (five corresponding to PN1 and three to PN2) were submitted to vPCAs, which reduced the 17 scalp locations to a range of 2–7 VFs, depending on the SF (Figure 4 and Table 1). VF scores were those finally submitted to ANOVAs to test experimental effects, as explained in Section 2.

3.2 | Experimental effects

Table 1 shows the mean and the standard error of means of all VF factor scores (linearly related to amplitudes, as indicated) derived from each PN1 and PN2 SFs. These factor scores were submitted to

repeated-measures ANOVAs introducing Emotion (S, W) and Visual Manipulation (M, P) as factors. In those VFs in which Emotion yielded significant effects, main effects of Visual Manipulation and the Emotion \times Visual Manipulation interaction are also relevant to test whether Emotion effects are modulated by the P/M balance of stimuli. Table 2 shows the results of all ANOVA contrasts, which will be summarized next.

3.2.1 | PN1 (120 ms)

ANOVAs yielded significant results only for a SF with bilateral occipital distribution (SF2, Figure 4 and Table 2). Concretely, this posterior PN1 (PN1p) SF showed significant main effects of Emotion in VF6,

TABLE 1 Means and standard deviations of visual location factor (VF) scores within each scalp factor (SF) of PN1 and PN2

		PN1 (120 ms)	ms)									PN2 (215 ms)	ms)				
		SF1 (anterior)	rior)	SF2 (mid-Occip)	Occip)	SF3 (post-	post-right)	SF4 (post-left)	left)	SF5 (central)	.al)	SF1 (anterior)	ior)	SF2 (post-mid left)	mid left)	SF3 (post-right)	-right)
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
VF1	SM	-0.011	0.973	-0.131	0.930	0.058	1.060	0.064	1.072	-0.012	0.822	0.302	1.068	-0.113	0.977	-0.027	1.125
	SP	0.087	0.981	0.018	0.971	0.115	0.939	-0.067	1.116	0.154	1.115	-0.036	1.019	0.020	0.933	0.054	0.937
	×	-0.186	1.107	-0.101	1.019	-0.115	1.090	0.018	0.912	-0.015	1.025	-0.099	0.849	0.072	0.971	-0.109	1.014
	WP	0.110	0.942	0.213	1.075	-0.058	0.922	-0.015	0.919	-0.128	1.033	-0.167	1.021	0.021	1.137	0.082	0.940
VF2	SM	0.156	0.924	-0.014	1.019	-0.179	0.956	-0.103	1.148	-0.041	1.058	-0.090	0.982	-0.026	0.924	0.225	0.854
	SP	-0.199	1.061	-0.085	0.931	-0.004	0.829	0.101	0.909	0.113	1.031	0.304	1.090	0.228	1.131	0.069	0.950
	ΜM	-0.058	0.782	0.063	0.870	-0.061	1.018	-0.013	0.977	-0.169	0.988	-0.268	1.057	-0.125	0.938	-0.103	1.157
	WP	0.101	1.187	0.036	1.185	0.245	1.159	0.015	0.979	0.097	0.931	0.055	0.793	-0.077	0.995	-0.191	1.002
VF3	SM	-0.136	1.047	0.029	1.024	-0.081	1.016	-0.114	1.119	-0.144	0.984			0.088	1.004	0.037	1.038
	SP	0.267	1.079	-0.022	0.973	-0.004	0.829	-0.037	1.018	-0.027	1.066			0.017	1.055	0.231	0.959
	×	-0.231	0.877	0.000	1.016	-0.061	1.018	0.050	0.991	0.000	0.982			-0.072	0.913	-0.101	0.935
	WP	0.100	0.946	-0.007	1.025	0.245	1.159	0.100	0.884	0.170	0.979			-0.032	1.054	-0.167	1.054
VF4	SM	0.000	1.000	-0.002	1.053	-0.012	0.992	0.004	0.852					0.184	1.198	-0.165	0.945
	SP	-0.004	0.513	0.086	0.981	0.077	1.094	-0.007	0.996					0.013	0.951	0.004	1.094
	×	0.008	0.508	0.056	0.915	0.037	0.986	960.0	1.031					0.119	0.770	0.135	1.035
	WP	0.007	0.491	-0.140	1.067	-0.103	0.952	-0.093	1.132					-0.316	0.997	0.025	0.933
VF5	SM	-0.014	0.982	-0.004	1.019	0.214	1.007	0.026	1.025								
	SP	0.039	0.579	0.096	0.889	-0.080	0.927	0.120	1.002								
	×	-0.004	0.496	0.069	1.036	-0.088	1.080	-0.050	0.905								
	WP	-0.010	0.462	-0.161	1.066	-0.045	0.987	-0.095	1.085								
VF6	SM	0.038	1.014	0.062	0.967	-0.089	0.978	0.126	0.915								
	SP	0.005	0.476	0.132	0.897	960.0-	1.076	0.074	0.905								
	ΜM	900'0	0.474	-0.116	1.036	0.080	0.985	-0.065	1.123								
	WP	-0.038	0.529	-0.079	1.106	0.105	0.979	-0.135	1.056								
VF7	SM	0.021	1.073	-0.108	1.070												
	SP	0.127	0.856	-0.009	1.030												
	ΜM	0.011	0.950	0.118	0.966												
	WP	-0.160	1.117	-0.001	0.955												
Note: Sig	gnificant re	Note: Significant results are shown in bold letters.	blod ni nwc	letters.													

TABLE 2 Main outputs (F, probability—f—and effect size— η_p^2) yielded by the two-way ANOVA for factor Emotion (two levels: S, W)

		PN1 (120 ms)					PN2 (215 ms)		
		SF1	SF2	SF3	SF4	SF5	SF1	SF2	SF3
		Anterior	Mid-occip	Post-right	Post-left	Central	Anterior	Post-mid left	Post-right
VF1	F	0.359	3.511	2.199	0.001	3.191	12.224 (7.996) [2.766]	2.164	0.137
	p	.553	.069	.146	.974	.082	.001 (.007) [.104]	.15	.714
	$\eta_{\rm p}^2$	0.009	0.085	0.055	<0.001	0.077	0.243 (0.174) [0.068]	0.054	0.004
VF2	F	0.102	1.14	2.176	0.001	0.507	6.694 (13.718) [0.180]	6.689 (2.917) [1.275]	5.705 (1.875) [0.455]
	р	.751	.292	.148	.982	.481	.014 (.001) [.673]	.014 (.096) [.226]	.022 (.179) [.504]
	$\eta_{\rm p}^2$	0.003	0.029	0.054	<0.001	0.013	0.150 (0.265) [0.005]	0.150 (0.071) [0.032]	0.004 (0.075) [0.012]
VF3	F	0.918	0.01	0.961	2.452	2.841		1.211	10.692 (0.376) [1.592]
	р	.344	.921	.333	.126	.1		.278	.002 (.544) [.215]
	$\eta_{\rm p}^2$	0.024	<0.001	0.025	0.061	0.07		0.031	0.220 (0.010) [0.040]
VF4	F	0.038	1.222	0.378	0.001			3.333	2.23
	р	.846	.276	.542	.982			.076	.144
	$\eta_{\rm p}^2$	<0.001	0.031	0.01	<0.001			0.081	0.055
VF5	F	0.162	0.818	1.412	2.05				
	p	.688	.371	.242	.16				
	$\eta_{\rm p}^2$	0.001	0.021	0.036	0.051				
VF6	F	0.468	4.198 (0.352) [0.042]	2.806	2.962				
	р	.495	.047 (.556) [.001]	.102	.093				
	$\eta_{\rm p}^2$	0.003	0.099 (0.009) [0.001]	0.069	0.072				
VF7	F	1.668	1.491						
	р	.204	.23						
	$\eta_{\rm p}^2$	0.042	0.038						

Note: Significant results are shown in bold letters. Where Emotion resulted significant, Visual Manipulation (M, P) results are of relevance and provided in brackets (in square brackets, results of the Emotion \times Visual Manipulation interaction). Degrees of freedom were 1 and 38 for main effects of both factors and for their interaction. SF, scalp factor; VF, visual location factor.

corresponding to responses to stimuli presented at fovea (F(1,38) = 4.198, p = .047, η_p^2 = 0.099), an S > W difference being observed (Figure 4). Main effects of Emotion did not reach significance in any peripheral VF. With respect to the main effect of Visual Manipulation and the Emotion × Visual Manipulation interaction in VF6, effects were all nonsignificant (Table 2).

3.2.2 | PN2 (215 ms)

Significant effects of Emotion were more spread in PN2 according to ANOVAs, S > W differences being observed at all the three SFs extracted for this temporal component (Figure 4b and Table 2): anterior PN2 (PN2a), at mid-left posterior (PN2p-ml), and right posterior PN2 (PN2p-r). In the case of PN2a, significant S > W differences were observed in both VFs extracted for this spatial factor: VF1, which was a "global periphery" VF with similar load in peri- and parafoveal locations (Figure 4c), and VF2, eminently foveal: F(1,38) = 12.224, p = .001, $\eta_p^2 = 0.243$ and F(1,38) = 6.694, p = .014, $\eta_p^2 = 0.150$, respectively. Main effects of Visual Manipulation reached significance in

both location factors, but in different directions: M > P in response to peripheral stimuli (VF1) and P > M in response to foveal stimuli (VF2): F(1,38) = 7.996, p = .007, $\eta_p^2 = 0.174$ and F(1,38) = 13.718, p = .001, $\eta_p^2 = 0.265$, respectively. No significant Emotion × Visual Manipulation interactions were observed in any ANOVA on these two location factors.

With respect to PN2p-ml, main effects of Emotion were significant only in response to peripheral presentations. Concretely, S > W differences were observed in VF2, a peripheral factor involving responses to the lower hemifield with maximal loads both at parand perifoveal coordinates: F(1,38) = 6.689, p = .014, $\eta_p^2 = 0.150$ (Figure 4c). Visual Manipulation and the Emotion × Visual Manipulation interaction resulted not significant in this VF.

Finally, as regards PN2p-r, Emotion factor yielded significant S > W differences in VF2 and VF3, both peripheral and showing maximal loads both at para- and perifoveal coordinates. As illustrated in Figure 4c, the former included responses to stimuli presented in the right hemifield and the latter including those presented in the lower visual hemifield: F(1,38) = 5.705, p = .022, $\eta_p^2 = 0.131$ and F(1,38) = 10.692, p = .002, $\eta_p^2 = 0.220$, respectively. Main effects of Visual

TABLE 3 Mean and standard error of means of loadings of each LoVF (locations 6–8 and14–16 in Figure 1), UVF (2–4 and 10–12), LeVF (1, 2, 8–10 and 16), RVF (4–6 and 12–14), parafoveal (9–16) and perifoveal locations (1–8)

	Mean	SEM	Т	df	р
LeVF	0.090	0.050	-4.804	5	.005
RVF	0.312	0.060			
LoVF	0.077	0.037	-3.161	5	.025
UVF	0.362	0.054			
Para	0.202	0.048	-0.363	7	.727
Peri	0.218	0.078			

Note: Student's T contrasts for the horizontal dimension (LeVF vs. RVF), the vertical dimension (LoVF vs. UVF), and the eccentricity (paravs. perifovea) are also presented (df = degrees of freedom).

Manipulation, and the Emotion × Visual Manipulation interaction, did not reach significance in any of both VFs.

In order to analyze the weight of LoVF, UVF, LeVF, and RVF on the observed effects, as well as those of parafoveal and perifoveal locations, the vPCA loads for each visual location in those PN2p factors showing Emo > Neu (S>W) effects described in previous paragraphs (PN2p-ml and PN2p-r), were quantified. Table 3 shows the average load of LoVF, UVF, LeVF, RVF, parafoveal, and perifoveal positions in these factors as well as the results of Student's T contrasts for the horizontal dimension (LeVF vs. RVF), the vertical dimension (LoVF vs. UVF), and the eccentricity (para- vs. perifovea). Significant differences were observed in the horizontal dimension (LeVF > RVF, t(5) = -4.804, p = .005), in the vertical dimension (LoVF > UVF, t(5) = -3.161, p = .025), but not in the eccentricity dimension (t(7) = 0.363, p = .727).

4 | DISCUSSION

The main scope of this study was exploring neural responses to emotional stimuli, as compared to neutral, presented at a wide range of locations within the visual field (one foveal and 16 at different peripheral peri- and parafoveal coordinates). In other words, our aim was testing a sort of emotional retinotopy, disentangling whether emotional effects are modulated by the coordinates of the visual field in which they appear. As indicated, the distribution of visual ERP components as a function of the stimulus location irrespective of emotional effects was out of our focus, and has been previously and exhaustively covered (e.g., Capilla et al., 2016; Clark et al., 1995; Di Russo et al., 2005; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). A main, initial result is that ERP perception-related temporospatial components PN1 and PN2 show an "Emo > Neu effect" (i.e., they are sensitive to the emotional load, showing greater amplitudes to emotional-spiders-than to neutral stimuli-wheels) even when stimuli are presented at the periphery of the visual field. This result is in line with previous studies showing efficient detection of emotional stimuli presented out of fixation and at different eccentricities (Bayle et al., 2009; Calvo et al., 2008; Carretié, Albert, et al., 2013; Carretié, Kessel, et al., 2013; Rigoulot et al., 2011, 2012). Next, the spatial modulation of the Emo > Neu effect is described.

First, PN1p, peaking at 120 ms, has revealed to be a "foveal component" with respect to its sensitivity to the emotional load of stimulation, showing the Emo > Neu effect only when stimuli appear at fixation. P1p has previously shown to be sensitive to affective content of negatively valenced stimulation presented at fixation (e.g., Carretié et al., 2004; Holmes, Nielsen, & Green, 2008; Luo, Feng, He, Wang, & Luo, 2010), but these studies did not present additional stimuli at peripheral locations. This study reveals that affective-related processes reflected in P1p are biased towards cone-dependent and, consequently, parvocellular-dependent visual processing. This in line with previous studies showing that P1p reflects cone-biased exogenous attention to salient events (Carretié & Ruiz-Padial, 2016). However, this bias may not occur in certain circumstances, as P1p enhanced responses to emotionally negative stimuli appearing out of fixation have also been reported in attentional tasks (Carretié et al., 2009). although these peripheral stimuli were not compared with stimuli presented at fixation since visual location was not explored. Future experiments are needed to further characterize P1p as a function of emotional and spatial location manipulations. Interestingly, the fact that P1p did not show Emo > Neu effects in response to peripheral stimuli, and that these peripheral effects are observed later, as we are about to see, suggests that foveal emotional recognition is faster than peripheral, at least as reflected by ERPs. To the best of our knowledge, latencies of emotional effects in foveally versus peripherally projected stimuli have not been previously explored, and even research on nonemotional recognition speeds for stimuli presented at fixation or at the periphery is very scarce. The main clues on this issue proceed from studies on reading speed, which indicate that peripheral processing is indeed slower than foveal vision (Chung, 2002; Latham & Whitaker, 1996). Present results suggest that this foveal temporal advantage could extend to emotion perception.

Later, PN2 (215 ms) was also sensitive to the emotional load of pictures. On the one hand, PN2a, showed the Emo > Neu effect both when stimuli were presented at fixation and at the periphery. With respect to the periphery, the most relevant to our scopes, the Emo > Neu effect was observed in all coordinates, and both at perifoveal and at parafoveal locations. Therefore, PN2a seems not to be modulated by the horizontal or vertical dimensions. On the other hand, PN2p also showed Emo > Neu significant differences, but in this case only if they were presented in the periphery, both at para- and perifoveal areas. Importantly, these effects did not show clear contralaterality, since right and left PN2p (PN2p-ml and PN2p-r, respectively) showed Emo > Neu effects mainly in response to stimuli presented in ipsilateral locations, or similar Emo > Neu effects to stimuli presented contra- and ipsilaterally. This may seem to conflict previous data on N2pc, an ERP component showing similar latency and distribution to present PN2p, but showing greater Emo > Neu effects to contralateral stimuli (e.g., Holmes, Bradley, Kragh Nielsen, & Mogg, 2009). However, these data were obtained in tasks where two different facial expressions simultaneously presented at the left and right

hemifields, conditions that are far from those employed here. According to present data, and at least in response to nonfacial emotional stimuli. the Emo > Neu effect is not contralateral.

The peripheral Emo > Neu effect observed in PN2p pointed against the LeFV bias suggested in previous literature. Rather, this effect was observed to a greater extent for stimuli presented at the RVF: responses to stimuli presented at the set of right hemifield locations loaded higher than those presented at the left in visual factors showing the Emo > Neu effects observed in PN2p. This finding apparently fails to support the "right hemisphere hypothesis" of emotional perception (Alves et al., 2009; Pizzagalli, Regard, & Lehmann, 1999), which suggests faster and more accurate recognition of emotional stimuli presented at the LeFV as compared to the RFV, a bias interpreted as an index of right hemisphere preferential involvement in emotional processing-and expression (Borod et al., 1986; Etcoff, 1986), or in negative affect (Davidson, 1984; Heller, 1993). Our results suggest that, at least in response to nonfacial stimuli (both Alves et al., 2009 and Pizzagalli et al., 1999, presented emotional expressions to their participants), this right hemisphere advantage is not evident at the ERP level. At this respect, it is important to note that significant ERP differences in early components are appreciated in response to facial vs nonfacial emotional stimuli presented to the same subjects and under the same experimental paradigm (Carretié, Kessel, et al., 2013). This finding is in line with meta-analyses failing to report a right hemisphere advantage at least in response to negative stimuli (Kober et al., 2008; Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2004). Taking into account that the scarce available data yield inconsistent results, additional research seems necessary employing different kinds of emotional stimuli and experimental paradigms in order to further define possible horizontal biases in emotional processing.

Regarding the vertical dimension, both PN2pr and PN2pml showed Emo > Neu effects mainly when stimuli appeared in the LoVF: responses to stimuli presented at this hemifield loaded to a significantly greater extent in visual factors showing the Emo > Neu effects observed in PN2p. To our knowledge, no previous studies exist comparing N2p or P2p (or any other ERP component) amplitudes to emotional stimuli presented at LoVF and UVF. However, as indicated in the Introduction, previous behavioral-oculomotor-data converge with present results in that attentional capture is biased towards emotional stimuli presented in the LoVF (Petrova & Wentura, 2012). Ultimately, this bias could reflect the evolutionary advantage of preferentially directing processing resources to the lower part of the visual scene, often linked to the peripersonal and more proximal environment (Petrova & Wentura, 2012; Previc, 1990, 1998), and to certain fearful stimuli appearing at close (and dangerous) distances such as the majority of animals potentially causing harm to humans (Isbell, 2006).

The vertical and horizontal peripheral Emo > Neu effects observed in PN2p were similar for stimuli presented at parafovea and perifovea. Indeed, responses to both para- and perifoveally presented stimuli loaded similarly in PN2p factors showing these effects. This finding is in line with studies finding a differential ERP response to

emotional stimuli (with respect to neutral) presented even 15° or more away from fixation (Carretié, Albert, et al., 2013; Rigoulot et al., 2011, 2012). Therefore, efficient perception of emotional stimuli seems not to be significantly modulated by eccentricity.

The secondary scope explored in this study was testing whether the parvocellular versus magnocellular balance of stimulation modulate the observed Emo > Neu effects. This balance yielded significant main effects in the PN2a component, where M stimuli elicited greater amplitudes than P when presented in the periphery (regardless the vertical or horizontal hemifield), and P stimuli elicited greater amplitudes than M when presented at fixation. This confirms a greater involvement of the magnocellular system in peripheral perception, and of the parvocellular pathway in foveal vision (Brown et al., 2005). However, these M/P balance effects were observed for both spiders and wheels. Therefore, present results suggest that at the perceptual levels explored here, a main effect of emotion and a main effect of M/P balance is observed in certain ERP components, but the integration of both effects in the form of interaction (i.e., enhanced processing of M-biased emotional stimuli), if produced, would be carried out in postperceptual neural mechanisms. This lack of interaction at the perceptual level, along with the observation that stimuli projected to both foveal and peripheral areas of the retina (P and M biased. respectively) elicited the Emo > Neu effects in PN1p and PN2a, lead to conclude that both M and P systems are equally efficient in perceiving emotional load in our environment. In a recent experiment using also isoluminant and heteroluminant stimulation, we observed an interaction of emotional content and M/P balance in such a way that M-biased spiders elicited the highest N2p amplitudes (significantly greater than both M-biased wheels and S-biased spiders; Carretié et al., 2017). However, this study (which did not test different locations) employed an exogenous attention task that required a response in each trial (spiders and wheels, which were presented always at the same location, were used as distractors in a digit categorization task), which was not the case in the present study. Therefore, while parvo- and magnocellular systems appear to be equally involved in the perception of peripheral static stimuli whatever their emotional content, attention processes may show enhanced involvement of magnocellular visual processing (at this respect, see a review in Carretié, 2014).

A relevant but scarcely explored question related to this study is which characteristics imbue a stimulus (even a simple representation of it, such as a silhouette), with emotional load and hence, with privileged access to perception. Morphological characteristics are probably among the most relevant (Gerdes et al., 2009). For example, a slight manipulation of a schematic flower drawing so its petals remotely resemble legs is enough for spider-phobic participants to rate them as more negative than control participants (Kolassa et al., 2007). In the present study, some wheels may resemble spiders except for the fact that leg tips (i.e., wheel radia) are "joined" by a circumference, and this is sufficient to neutralize any emotional content or perceptual advantage. In relation to this, and whereas the emotional content of spider silhouettes was clear and significant as compared to wheels, as explained in Section 2.2, the potential influence of

other factors contributing to saliency of the former in the observed effects, such as their animated (or animal) nature, absent in the latter, may not be discarded. This limitation could be overcome in future studies by further disentangling potential factors that may modulate the processing of visual stimuli as a function of their spatial location.

5 | CONCLUSIONS

In sum, several conclusions may be extracted from this study. First, our data confirm that emotional, salient stimuli presented in the periphery are efficiently perceived, and this occurs in both parafovea and perifovea, with not an evident decrease from one to another. Second, they suggest that peripheral Emo > Neu effects, which are first observed in PN2, occur later than foveal Emo > Neu effects, observed in PN1p. Third, a vertical bias consisting of greater involvement of LoVF locations than UVF locations in the Emo > Neu effect is observed. Fourth, and regarding the horizontal dimension, the perceptual Emo > Neu effect loaded to a greater extent towards stimuli presented at RVF than at LeVF, failing to support the "right hemisphere advantage" hypothesis in the processing of negative emotional stimuli, at least at the perceptual level. And fifth, the observed Emo > Neu effects were not modulated by their M/P physical condition (i.e., their figure-ground luminance or chromatic characteristics), leading to consider both magnocellular and parvocellular systems as equally efficient to perceive emotional load. This first attempt to explore how the perception of emotional stimuli is modulated by their location in the visual scene should be followed by further steps exploring more complex processes beyond perception, such as attention, memory or executive processes, and introduce other types of stimulation representing different affective loads.

ACKNOWLEDGMENTS

This research was supported by the grants PGC2018-093570-B-I00 from the Ministerio de Ciencia, Innovación y Universidades (MICINN) and S2015/HUM-3327 from the Comunidad de Madrid.

DATA AVAILABILITY STATEMENT

Data reduction preserving most part of the variance resulted necessary to further analyze our Emotion (two levels: S or W) x Visual Manipulation (two levels: M or P) x 17 Locations design, taking also into account that recordings consisted of a 59 EEG channels x 253 digitized voltages or "time points" x 4080 trials matrix (this matrix is openly available at https://osf.io/85nu3/).

ORCID

Luis Carretié https://orcid.org/0000-0001-7375-6739

REFERENCES

Alves, N., Aznar-Casanova, J., & Fukusima, S. (2009). Patterns of brain asymmetry in the perception of positive and negative facial expressions. Laterality: Asymmetries of Body, Brain and Cognition, 14, 256–272.

- Azzopardi, P., & Cowey, A. (1996). The over representation of the fovea and adjacent retina in the striate cortex and dorsal lateral geniculate nucleus of the macaque monkey. *Neuroscience*, 72, 627–639.
- Bayle, D. J., Henaff, M., & Krolak-Salmon, P. (2009). Unconsciously perceived fear in peripheral vision alerts the limbic system: A MEG study. PLoS One, 4, e8207.
- Blini, E., Desoche, C., Salemme, R., Kabil, A., Hadj-Bouziane, F., & Farnè, A. (2018). Mind the depth: Visual perception of shapes is better in peripersonal space. *Psychological Science*, *29*, 1868–1877.
- Borod, J. C., Koff, E., Lorch, M. P., & Nicholas, M. (1986). The expression and perception of facial emotion in brain-damaged patients. *Neuropsychologia*, 24, 169–180.
- Brooks, J. L., Della Sala, S., & Darling, S. (2014). Representational pseudoneglect: A review. Neuropsychology Review, 24, 148–165.
- Brown, L. E., Halpert, B. A., & Goodale, M. A. (2005). Peripheral vision for perception and action. *Experimental Brain Research*, 165, 97–106.
- Calvo, M. G., Nummenmaa, L., & Hyönä, J. (2008). Emotional scenes in peripheral vision: Selective orienting and gist processing, but not content identification. *Emotion*, 8, 68–80.
- Capilla, A., Melcón, M., Kessel, D., Calderón, R., Pazo-Álvarez, P., & Carretié, L. (2016). Retinotopic mapping of visual event-related potentials. *Biological Psychology*, 118, 114–125.
- Carretié, L. (2014). Exogenous (automatic) attention to emotional stimuli: A review. Cognitive, Affective and Behavioral Neuroscience, 14, 1228–1258.
- Carretié, L., Albert, J., López-Martín, S., Hoyos, S., Kessel, D., Tapia, M., & Capilla, A. (2013). Differential neural mechanisms underlying exogenous attention to peripheral and central distracters. *Neuropsychologia*, 51, 1838–1847.
- Carretié, L., Hinojosa, J. A., López-Martín, S., Albert, J., Tapia, M., & Pozo, M. A. (2009). Danger is worse when it moves: Neural and behavioral indices of enhanced attentional capture by dynamic threatening stimuli. Neuropsychologia, 47, 364–369.
- Carretié, L., Kessel, D., Carboni, A., López-Martín, S., Albert, J., Tapia, M., ... Hinojosa, J. A. (2013). Exogenous attention to facial vs non-facial emotional visual stimuli. Social Cognitive and Affective Neuroscience, 8, 764–773.
- Carretié, L., Kessel, D., García-Rubio, M. J., Giménez-Fernández, T., Hoyos, S., & Hernández-Lorca, M. (2017). Magnocellular bias in exogenous attention to biologically salient stimuli as revealed by manipulating their luminosity and color. *Journal of Cognitive Neuroscience*, 29, 1–14.
- Carretié, L., & Ruiz-Padial, E. (2016). Ambient light modulation of exogenous attention to threat. *Brain Topography*, 29, 847–855.
- Carretié, L., Hinojosa, J. A., Mercado, F., & Tapia, M. (2005). Cortical response to subjectively unconscious danger. *Neuroimage*, 24, 615–623.
- Carretié, L., Tapia, M., López-Martín, S., & Albert, J. (2019). EmoMadrid: An emotional pictures database for affect research. *Motivation and Emotion*, 43, 929–939.
- Carretié, L., Hinojosa, J. A., Martín-Loeches, M., Mercado, F., & Tapia, M. (2004). Automatic attention to emotional stimuli: Neural correlates. Human Brain Mapping, 22(4), 290–299.
- Chapman, C., Hoag, R., & Giaschi, D. (2004). The effect of disrupting the human magnocellular pathway on global motion perception. *Vision Research*, 44, 2551–2557.
- Chapman, R. M., & McCrary, J. W. (1995). EP component identification and measurement by principal components analysis. *Brain and Cognition*, 27, 288–310.
- Chung, S. T. (2002). The effect of letter spacing on reading speed in central and peripheral vision. *Investigative Ophthalmology & Visual Science*, 43, 1270–1276.
- Clark, V. P., Fan, S., & Hillyard, S. A. (1995). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping*, 2, 170–187.

- Cliff, N. (1987). Analyzing multivariate data. San Diego: Harcourt Brace Joyanovich.
- Davidson, R. J. (1984). Affect, cognition, and hemispheric specialization. In C. E. Izard, J. Kagan, & R. B. Zajonc (Eds.), *Emotion, cognition and behavior* (pp. 320–365). Cambridge, England: Cambridge University Press.
- De Cesarei, A., Codispoti, M., & Schupp, H. T. (2009). Peripheral vision and preferential emotion processing. *Neuroreport*, 20, 1439–1443.
- Delplanque, S., Lavoie, M. E., Hot, P., Silvert, L., & Sequeira, H. (2004). Modulation of cognitive processing by emotional valence studied through event-related potentials in humans. *Neuroscience Letters*, 356, 1–4.
- Dien, J. (2010). Evaluating two-step PCA of ERP data with geomin, infomax, oblimin, promax, and varimax rotations. *Psychophysiology*, 47, 170–183
- Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, *15*, 95–111.
- Di Russo, F., Pitzalis, S., Spitoni, G., Aprile, T., Patria, F., Spinelli, D., & Hillyard, S. A. (2005). Identification of the neural sources of the pattern-reversal VEP. *NeuroImage*, 24, 874–886.
- Etcoff, N. L. (1986). The neuropsychology of emotional expression. In G. Goldstein & R. E. Tarter (Eds.), Advances in clinical neuropsychology (Vol. 3, pp. 127–179). New York, NY: Plenum Press.
- Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *Journal of Neuroscience*, 29, 4381–4391.
- Gerdes, A. B., Uhl, G., & Alpers, G. W. (2009). Spiders are special: Fear and disgust evoked by pictures of arthropods. Evolution and Human Behavior, 30, 66–73.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15, 20–25.
- Hadjidimitrakis, K., Breveglieri, R., Placenti, G., Bosco, A., Sabatini, S. P., & Fattori, P. (2011). Fix your eyes in the space you could reach: Neurons in the macaque medial parietal cortex prefer gaze positions in peripersonal space. *PLoS One*, 6(8), e23335.
- Hatin, B., Sykes Tottenham, L., & Oriet, C. (2012). The relationship between collisions and pseudoneglect: Is it right? *Cortex*, 48, 997–1008.
- Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology*, 7, 476–489.
- Holmes, A., Bradley, B. P., Kragh Nielsen, M., & Mogg, K. (2009). Attentional selectivity for emotional faces: Evidence from human electrophysiology. *Psychophysiology*, 46, 62–68.
- Holmes, A., Nielsen, M. K., & Green, S. (2008). Effects of anxiety on the processing of fearful and happy faces: An event-related potential study. *Biological Psychology*, 77, 159–173.
- Hubel, D. H., & Wiesel, T. N. (1972). Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey. *Journal of Comparative Neurology*, 146, 421–450.
- Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*, 1–35.
- Jacobi, F., Wittchen, H. -U., Hölting, C., Höfler, M., Pfister, H., Müller, N., & Lieb, R. (2004). Prevalence, co-morbidity and correlates of mental disorders in the general population: Results from the German Health Interview and Examination Survey (GHS). Psychological Medicine, 34, 597–611.
- Jeffreys, D. A., & Axford, J. G. (1972a). Source locations of pattern-specific components of human visual evoked potentials: I. Component of striate cortical origin. Experimental Brain Research, 16, 1–21.
- Jeffreys, D. A., & Axford, J. G. (1972b). Source locations of pattern-specific components of human visual evoked potentials: II. Component of extrastriate cortical origin. Experimental Brain Research, 16, 22–40.
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and metaanalysis of performance factors in line bisection tasks. *Neuropsychologia*, 38, 93–110.

- Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., Mckeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, 37, 163–178.
- Keil, A., Müller, M. M., Gruber, T., Wienbruch, C., Stolarova, M., & Elbert, T. (2001). Effects of emotional arousal in the cerebral hemispheres: A study of oscillatory brain activity and event-related potentials. Clinical Neurophysiology, 112, 2057–2068.
- Kober, H., Barrett, L. F., Joseph, J., Bliss-Moreau, E., Lindquist, K., & Wager, T. D. (2008). Functional grouping and cortical-subcortical interactions in emotion: A meta-analysis of neuroimaging studies. NeuroImage, 42, 998–1031.
- Kolassa, I., Buchmann, A., Lauche, R., Kolassa, S., Partchev, I., Miltner, W. H., & Musial, F. (2007). Spider phobics more easily see a spider in morphed schematic pictures. *Behavioral and Brain Functions*, 3. 59.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. Gainesville, FL: University of Florida.
- Latham, K., & Whitaker, D. (1996). A comparison of word recognition and reading performance in foveal and peripheral vision. *Vision Research*, 36, 2665–2674.
- Levine, M. W., & McAnany, J. J. (2005). The relative capabilities of the upper and lower visual hemifields. *Vision Research*, 45, 2820–2830.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240, 740–749.
- Losier, B. J., & Klein, R. M. (2004). Covert orienting within peripersonal and extrapersonal space: Young adults. Cognitive Brain Research, 19, 269–274.
- Luo, W., Feng, W., He, W., Wang, N., & Luo, Y. (2010). Three stages of facial expression processing: ERP study with rapid serial visual presentation. *NeuroImage*, 49, 1857–1867.
- Milner, A., & Goodale, M. (1995). The visual brain in action. Oxford: Oxford University Press.
- Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: A meta-analysis. Cognitive, Affective, & Behavioral Neuroscience, 3, 207–233.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational Intelligence and Neuroscience, 2011, 1–9.
- Petrova, K., & Wentura, D. (2012). Upper-lower visual field asymmetries in oculomotor inhibition of emotional distractors. *Vision Research*, 62, 209-219.
- Phan, K. L., Wager, T. D., Taylor, S. F., & Liberzon, I. (2004). Functional neuroimaging studies of human emotions. CNS Spectrums, 9, 258–266.
- Pitzalis, S., Fattori, P., & Galletti, C. (2013). The functional role of the medial motion area V6. Frontiers in Behavioral Neuroscience, 6, 91.
- Pizzagalli, D., Regard, M., & Lehmann, D. (1999). Rapid emotional face processing in the human right and left brain hemispheres: An ERP study. Neuroreport, 10, 2691–2698.
- Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14, 619–633.
- Previc, F. H. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, 13, 519–542.
- Previc, F. H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, 124, 123–164.
- Rigoulot, S., D'Hondt, F., Defoort-Dhellemmes, S., Despretz, P., & Honoré, J. (2011). Fearful faces impact in peripheral vision: Behavioral and neural evidence. *Neuropsychologia*, 49, 2013–2021.
- Rigoulot, S., D'hondt, F., Honore, J., & Sequeira, H. (2012). Implicit emotional processing in peripheral vision: Behavioral and neural evidence. *Neuropsychologia*, 50, 2887–2896.

- Rossit, S., McAdam, T., Mclean, D. A., Goodale, M. A., & Culham, J. C. (2013). fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. *Cortex*, 49, 2525–2541.
- Schneider, K. A., Richter, M. C., & Kastner, S. (2004). Retinotopic organization and functional subdivisions of the human lateral geniculate nucleus: A high-resolution functional magnetic resonance imaging study. The Journal of Neuroscience, 24, 8975–8985.
- Sereno, M. I., & Tootell, R. B. (2005). From monkeys to humans: What do we now know about brain homologies? Current Opinion in Neurobiology, 15, 135–144.
- Skottun, B. (2013). On using isoluminant stimuli to separate magno-and parvocellular responses in psychophysical experiments—A few words of caution. *Behavior Research Methods*, 45, 637–645.

- Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *Journal of Vision*, 11, 1–82.
- Tootell, R. B., Hadjikhani, N. K., Mendola, J. D., Marrett, S., & Dale, A. M. (1998). From retinotopy to recognition: FMRI in human visual cortex. *Trends in Cognitive Sciences*, 2, 174–183.

How to cite this article: Carretié L, Méndez-Bértolo C, Bódalo C, et al. Retinotopy of emotion: Perception of negatively valenced stimuli presented at different spatial locations as revealed by event-related potentials. *Hum Brain Mapp.* 2020;41:1711–1724. https://doi.org/10.1002/hbm.24904