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Shedding light on emotional perception: Interaction of brightness and semantic content in extrastriate visual cortex

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ABSTRACT

The rapid extraction of affective cues from the visual environment is crucial for flexible behavior. Previous studies have reported emotion-dependent amplitude modulations of two event-related potential (ERP) components – the N1 and EPN – reflecting sensory gain control mechanisms in extrastriate visual areas. However, it is unclear whether both components are selective electrophysiological markers of attentional orienting toward emotional material or are also influenced by physical features of the visual stimuli. To address this question, electrical brain activity was recorded from seventeen male participants while viewing original and bright versions of neutral and erotic pictures. Bright neutral scenes were rated as more pleasant compared to their original counterpart, whereas erotic scenes were judged more positively when presented in their original version. Classical and mass univariate ERP analysis showed larger N1 amplitude for original relative to bright erotic pictures, with no differences for original and bright neutral scenes. Conversely, the EPN was only modulated by picture content and not by brightness, substantiating the idea that this component is a unique electrophysiological marker of attention allocation toward emotional material. Complementary topographic analysis revealed the early selective expression of a centro-parietal positivity following the presentation of original erotic scenes only, reflecting the recruitment of neural networks associated with sustained attention and facilitated memory encoding for motivationally relevant material. Overall, these results indicate that neural networks subtending the extraction of emotional information are differentially recruited depending on low-level perceptual features, which ultimately influence affective evaluations.

Introduction

In an overwhelmingly rich visual environment, attention selection mechanisms efficiently direct the organism's limited processing resources toward the most relevant information (James, 1890; Posner, 1980; Sokolov, 1963). This relevance is determined both by *bottom-up*, stimulus-driven factors that reflect changes in salient perceptual properties, and *top-down* factors, such as prior knowledge, expectations, and current goals (Corbetta and Shulman, 2002; Serences et al., 2005; Theeuwes, 1994). In addition, a large body of behavioral, electrophysiological, and neuroimaging studies have shown that the rapid and efficient selection of sensory information for further perceptual processing is also determined by the emotional or motivational significance of the stimulus for the individual (Bradley, 2009; Carretié, 2014; Dolcos et al., 2011; Lang and Bradley, 2010; Pourtois et al., 2013; Vuilleumier, 2005; Yiend, 2010).

In the laboratory, it has repeatedly been shown that viewing aversive or pleasant (compared to neutral) complex natural scenes enhances electrical brain activity in extrastriate visual areas, indicative of sensory gain control mechanisms operating early on following stimulus onset (Desimone and Duncan, 1995; Desimone, 1998; Hillyard et al., 1998). Studies recording steady-state visual evoked potentials (ssVEPs), a continuous oscillatory posterior brain response elicited by flickering visual stimuli (Norcia et al., 2015; Regan, 1977; Vialatte et al., 2010), have shown increased amplitude for emotional relative to neutral scenes (Bradley et al., 2012; Keil et al., 2003, 2008, 2009), reflecting enhanced attention allocation (Müller and Hübner, 2002; Müller et al., 1998, 2003). Furthermore, motivationally relevant distractors withdraw cognitive resources away from concurrent nonemotional tasks (Hindi Attar et al., 2010; Müller et al., 2008, 2011; Schönwald and Müller, 2014), suggesting that attentional orienting toward emotion-laden material occurs spontaneously (i.e., it does not require instruction) and may interfere with concurrent task demands (see Pessoa, 2005).

Research employing event-related potential (ERP) paradigms has also shown increased amplitude of early ERP components for emotional relative to neutral pictures (for a review, see Olofsson et al., 2008). While some studies have identified amplitude modulations as early as

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the P1 component (Carretié et al., 2004; Delplanque et al., 2004; Smith et al., 2003), the majority of findings in the literature have reported differences later on in the processing stream. In particular, the N1, an occipital negative component that is sensitive to attentional manipulations (Mangun, 1995; Vogel and Luck, 2000), has been found to be larger for emotional relative to neutral scenes (Carretié et al., 2003, 2004; Keil et al., 2002; Rozenkrants and Polich, 2008; Weinberg and Hajcak, 2010). Likewise, a more sustained early posterior negativity (EPN) is typically enhanced during the presentation of emotion-laden scenes (Junghöfer et al., 2001; Schupp et al., 2003a, 2003b, 2006a). However, it is still unclear to what extent the N1 and EPN reflect distinct cognitive processes or are both electrophysiological markers of attentional prioritization to emotional material. Numerous studies using simple visual stimuli have shown that the N1 is an indicator of stimulus discrimination that is further enhanced by attentional selection (Luck et al., 2000; Vogel and Luck, 2000). At the same time, the EPN is often considered the first reliable index of selective processing of emotionally arousing material (Schupp et al., 2006a), indicative of an orienting response to motivationally relevant visual stimuli due to their evolutionary significance (Lang and Bradley, 2010). Assuming that these two ERP components reflect comparable attention mechanisms, it is important to understand why some studies report emotion-dependent N1 modulations, whereas others identify the first marker of emotion discrimination in the EPN. One possible reason is that most of the studies cited above overlooked potential confounding effects elicited by uncontrolled low-level visual properties of the stimuli. As a matter of fact, recent work has shown that visual features such as spatial frequency (Alorda et al., 2007; Carretié et al., 2007; De Cesarei and Codispoti, 2011; Schettino et al., 2011, 2013), color (Cano et al., 2009; Miskovic et al., 2015), picture size (De Cesarei and Codispoti, 2006), complexity (Bradley et al., 2007; Schettino et al., 2012; Wiens et al., 2011), and brightness (Lakens et al., 2013) may indeed influence behavioral and electrophysiological responses to emotional scenes. Therefore, shedding light on the distinct modulation of N1 and EPN by low-level visual features and emotion would inform researchers on the time course of the extraction of physical as opposed to semantic cues from complex natural scenes, enabling to accurately pinpoint at which stage of perceptual processing emotion uniquely contributes to the electrophysiological responses recorded on the scalp.

In the present study, participants viewed neutral and erotic pictures selected from the International Affective Picture System database (IAPS; Lang et al., 2008). We selected erotic pictures in order to increase the likelihood of obtaining early emotion-dependent ERP amplitude modulations, given that previous studies have shown selective N1 and EPN enhancement for this class of stimuli (Keil et al., 2002; Schupp et al., 2003b, 2006b, 2007). Since IAPS picture ratings differ between male and female individuals (Lang et al., 2008), we decided to recruit only males to ensure that our pre-selected set of images would elicit similar emotion intensity across participants. Importantly, picture brightness was systematically manipulated while controlling for several other perceptual characteristics (see Stimuli section). Luminance variations have been found to additively influence N1 amplitude independently from attention (e.g., Hughes, 1984; Johannes et al., 1995), whereas EPN evoked by abstract stimuli (e.g., checkerboards; Junghöfer et al., 2001) does not seem to be modulated by brightness. Building on this work, the current study extends this manipulation to include complex visual scenes, systematically examining the contribution of prototypical physical features and high-level semantic content in modulating N1 and EPN amplitude.

Intriguingly, a recent behavioral study (Lakens et al., 2013) also revealed the existence of a *brightness bias*, according to which luminance variations of neutral pictures influence their affective evaluations: specifically, bright neutral scenes were rated as more pleasant compared to their darker counterpart. Therefore, our secondary aim was to explore whether this brightness bias could extend to pleasant scenes, with bright erotic pictures judged as even more pleasant than their unmodified counterpart.

From a methodological standpoint, we complemented classical parametric analysis of the amplitudes of our ERP components of interest (Keil et al., 2014; Picton et al., 2000) with non-parametric statistics (Groppe et al., 2011a, 2011b) and spatiotemporal analysis (Lehmann and Skrandies, 1980; Michel and Murray, 2012). Evidence from these three approaches would help us understand whether N1 and EPN reflect distinct or similar cognitive (i.e., attentional) mechanisms when presenting emotional material, as well as clarify the role of low-level visual properties (in this case, brightness) in the modulation of these early ERP components.

Materials and methods

Participants

Seventeen male individuals (mean age 26 years, range 19–33) were recruited from the student population of the University of Leipzig and among the general public. Five additional participants were excluded from the final sample: three of them did not comply with task instructions (i.e., they provided random picture ratings), whereas the data of two participants could not be properly saved due to technical problems. All volunteers were German speaking, right-handed, had normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders.

The study was conducted in accordance with the Declaration of Helsinki and the guidelines of the ethics committee of the University of Leipzig. All participants were required to give written informed consent and, at the end of the experiment, were fully debriefed and received either 12 € or credit points.

Stimuli

One-hundred pictures depicting various everyday scenes (e.g., people at the supermarket, at the restaurant, playing music, or doing sport), as well as nude female bodies and heterosexual interactions, were selected from the IAPS (Lang et al., 2008). Given that erotic pictures only displayed humans, we minimized the use of neutral pictures with animals, artifacts (e.g., household objects), or landscapes, in order to keep the content similar between erotic and neutral scenes and avoid animacy effects (New et al., 2007; Proverbio et al., 2007). Moreover, pictures with individual faces in the foreground were kept to a minimum due to their overall higher saliency (e.g., Kanwisher, 2000)[1]. Paired-sample *t*-tests confirmed that normative ratings for erotic scenes (arousal: $M = 6.93$, $SD = 0.40$; valence: $M = 7.41$, $SD = 0.39$) were higher, i.e., more pleasant ($t_{49} = 28.24$, $p < .001$, $r = .97$) and more arousing ($t_{49} = 37.05$, $p < .001$, $r = .98$) compared to neutral scenes (arousal: $M = 3.87$, $SD = 0.52$; valence: $M = 5.19$, $SD = 0.50$). Six additional pictures (3 neutral, 3 erotic) were selected for the practice session and were not included in the analyses.

All the stimuli were converted to grayscale and resized to 576 × 432 pixels in order to discourage eye movements. To control for picture complexity, we calculated the size (in kilobytes) of each jpeg file (Bates et al., 2003; Junghöfer et al., 2001; Marin and Leder, 2013) and verified, by means of independent-sample *t*-tests, that neutral and erotic pictures did not significantly differ (neutral: $M = 290.38$, $SD = 218.38$; erotic: $M = 249.66$, $SD = 178.48$; $t_{94.26} = -1.02$, $p = .310$, $r = .10$). We also used unpublished in-house complexity ratings collected in a sample of undergraduates at the University of Florida in the context of

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[1] IAPS image codes. *Neutral*: 2026, 2032, 2060, 2102, 2130, 2221, 2342, 2351, 2357, 2359, 2377, 2381, 2382, 2394, 2397, 2400, 2435, 2458, 2485, 2487, 2488, 2489, 2513, 2514, 2518, 2520, 2521, 2593, 2595, 2635, 2695, 2702, 2795, 2890, 4000, 4100, 4503, 4505, 4525, 4533, 4534, 4535, 4537, 4542, 4559, 4600, 4605, 5410, 8010, 8041. *Erotic*: 2300, 4001, 4002, 4006, 4007, 4008, 4071, 4085, 4090, 4130, 4141, 4142, 4180, 4210, 4220, 4225, 4232, 4235, 4240, 4255, 4275, 4300, 4302, 4310, 4311, 4325, 4607, 4608, 4611, 4647, 4649, 4651, 4652, 4656, 4658, 4659, 4660, 4666, 4668, 4669, 4687, 4690, 4692, 4693, 4694, 4695, 4697, 4698, 4770, 4800. *Practice* (*neutral*): 1908, 2211, 7506. *Practice* (*erotic*): 4005, 4320, 4604.

earlier studies (e.g., Bradley et al., 2007). Neutral and erotic scenes did not differ with respect to these subjective ratings ($t_{75.73} = -1.42$, $p = .159$, $r = .16$). Mean and standard deviation of pixel luminance values between neutral and erotic scenes were then matched using the *lumMatch* function of the SHINE toolbox (Willenbockel et al., 2010) under MATLAB v7.11.0 (The MathWorks, Inc., Natick, MA). *T*-tests with apparent contrast (i.e., standard deviation divided by mean luminance) as dependent variable confirmed no differences between picture categories ($t_{97.74} = 0.02$, $p = .982$, $r < .01$).

Two additional sets of stimuli were subsequently created. In the first one (*bright* set), luminance was enhanced for all pictures using the *bmp_contrast* MATLAB function (www.mccauslandcenter.sc.edu/CRNL/tools/bmp_contrast). A nonlinear transformation with brightness value of 0.8 and no change in contrast (parameter set at 0.5) was applied. *T*-tests confirmed higher apparent contrast in the original compared to the bright picture set for both neutral (original: $M = 0.63$, $SD = 0.03$; bright: $M = 0.46$, $SD = 0.03$; $t_{97.72} = -27.75$, $p < .001$, $r = .94$) and erotic scenes (original: $M = 0.63$, $SD = 0.03$; bright: $M = 0.45$, $SD = 0.04$; $t_{95.11} = -24.14$, $p < .001$, $r = .93$). The second stimulus set (*scrambled* set) included meaningless images created from each picture (i.e., all original and bright scenes had their scrambled counterpart). Scrambling was obtained by (i) applying a two-dimensional discrete Fourier transform and extracting the amplitude and phase components of each image; (ii) replacing the phase spectrum with random values, while keeping the original amplitude; and (ii) reconstructing the image by applying an inverse Fourier transform. This procedure resulted in images with equal luminance and spectral energy of the original scenes, but devoid of any semantic content (see also Hindi Attar and Müller, 2012; Hindi Attar et al., 2010; Müller et al., 2011). In sum, a total of 400 pictures were created, 50 for each stimulus class: (i) original neutral, (ii) original erotic, (iii) bright neutral, (iv) bright erotic, (v) scrambled original neutral, (vi) scrambled original erotic, (vii) scrambled bright neutral, and (viii) scrambled bright erotic. An example of each stimulus class is provided in Fig. 1A.

Procedure

After signing the informed consent and having sensors applied on their scalp, participants were seated in a small, dimly lit Faraday cage at approximately 60 cm from a 19″ CRT monitor (refresh rate: 100 Hz) connected to a PC (stimulus presentation: E-Prime 2.0; Schneider et al., 2002). After verbal and written instructions as well as a practice session with 6 pictures, the main experiment started. On each trial, a central fixation point (a red circle, 0.96° × 0.96° degrees of visual angle in diameter) was presented on a black background for 1500 ms. Each picture (14.48° × 10.88°) was subsequently displayed for 2000 ms, and participants were required to focus on its content. The stimuli were randomly presented across 8 blocks, with the only constraint that no more than 3 pictures with the same emotion or brightness were presented consecutively. The presentation of original and bright scenes was counterbalanced: half of the participants saw the original picture first, whereas the other half saw the bright version first. To ensure that participants were actively attending to the emotional content of the scenes, valence and arousal ratings were collected on 13% of the trials via SAM manikins (Bradley and Lang, 1994), ranging from 1 (low arousal—unpleasant valence) to 9 (high arousal—pleasant

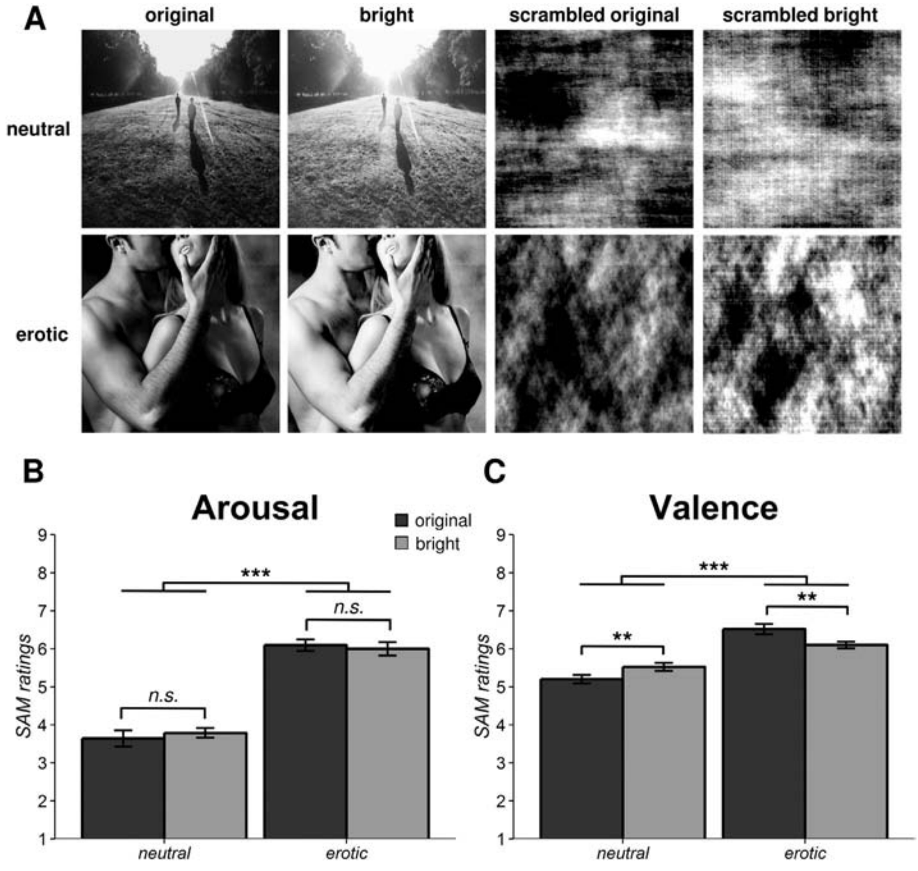

Fig. 1. Stimuli and ratings. (A) Example of the stimuli used in the experiment. Participants were required to occasionally rate valence and arousal of original and bright neutral and erotic IAPS scenes (not shown here for copyright reasons; examples are taken from public domain internet databases). Additionally, we created a set of scrambled scenes with identical low-level visual properties but no semantic content. (B, C) Average arousal (B) and valence (C) ratings of concrete scenes. Erotic scenes were judged as more arousing than neutral scenes, with no differences between original and bright picture sets. Valence ratings, on the other hand, were differentially influenced by picture brightness: neutral scenes were judged as more pleasant when they were bright, whereas erotic scenes were deemed more pleasant when shown in their original version. Vertical bars correspond to standard error of the mean. $^{**}p < .01$; $^{***}p < .001$; *n.s.*: not significant.

valence). Responses were given on the numeric pad of a standard QWERTZ keyboard connected via USB. Ratings of the remaining pictures were additionally requested at the end of the main task, in order to obtain valence and arousal ratings of all the pictures (excluding scrambled images) for each individual participant. These values were included in a 2 (*brightness*: original vs. bright) × 2 (*emotion*: neutral vs. erotic) repeated measures ANOVA (rANOVA), followed by paired-sample *t*-tests.

To assess whether valence and arousal ratings were influenced by specific personality traits, at the end of the experiment we measured levels of trait anxiety using the German version of the Spielberger's State–Trait Anxiety Inventory, trait characteristics (*STAI-T*; Laux et al., 1981). Non-parametric Spearman's rank correlations revealed no relationship between STAI-T scores ($M = 42.94$, $SD = 7.48$) and either valence or arousal ratings (all $ps > .14$). Finally, we verified that participants' mood did not change throughout the study by administering two SAM scales at the beginning and at the end of the experiment (*valence*: “Please rate how you feel right now, from very sad/angry to very happy/cheerful”; *arousal*: “Please rate how you feel right now, from very calm/relaxed to very agitated/excited). Wilcoxon signed-rank tests confirmed no change in subjective valence (pre-task: $M = 6.71$, $SD = 2.82$; post-task: $M = 6.47$, $SD = 2.63$; $Z = -0.62$, $p = .533$, $r = -.15$) or arousal (pre-task: $M = 4.00$, $SD = 1.85$; post-task: $M = 4.18$, $SD = 2.22$; $Z = -0.49$, $p = .621$, $r = -.12$).

EEG recording and preprocessing

Electroencephalographic activity (EEG) was recorded with an ActiveTwo amplifier (BioSemi, Inc., The Netherlands) at a sampling rate of 256 Hz and online band-pass filtered between 0.016 and 100 Hz. Sixty-four Ag/AgCl electrodes were fitted into an elastic cap, following the BioSemi ABCD position system (i.e., electrode positions are radially equidistant from *Cz*; www.biosemi.com/headcap.htm). Electrodes A15 and B20, i.e., T7 and T8 in the international 10/10 system (Jurcak et al., 2007), were moved in position I1 and I2 in order to increase spatial resolution at occipital sites. The common mode sense (*CMS*) active electrode and the driven right leg (*DRL*) passive electrode were used as reference and ground electrodes, respectively (www.biosemi.com/faq/cms&drl.htm). Horizontal and vertical electrooculograms (EOGs) were monitored using four facial bipolar electrodes placed on the outer canthi of each eye and in the inferior and superior areas of the left orbit.

Data preprocessing was performed offline with custom MATLAB scripts using functions included in EEGLAB v13.2.1 (Delorme and Makeig, 2004), ERPLAB v4.0.2.3 (Lopez-Calderon and Luck, 2014), and FASTER v1.2.3b (Nolan et al., 2010) toolboxes. The continuous EEG data were average-referenced and low-pass filtered (non-causal windowed-sinc finite impulse response filter, 30 Hz half-amplitude cutoff) after subtracting the mean value of the waveform (DC offset). Epochs extending from −200 ms to +2000 ms after picture onset were created, and baseline correction was applied using the pre-stimulus interval. Following the standard procedure in FASTER (Nolan et al., 2010), data exceeding a *z*-score of ±3 standard deviations were labeled as contaminated by artifacts. Noisy channels were interpolated via a spherical spline procedure (Perrin et al., 1989). Epochs containing artifacts and/or more than 12 interpolated channels were discarded. After preprocessing, the average number of interpolated channels was 2.29 ($SD = 1.31$, range 1–4) and the percentage of rejected epochs was 7.15% ($SD = 1.69$, range 4.44–10.50), with no differences across conditions. Finally, a total of 8 grand averages were computed: (i) original neutral, (ii) original erotic, (iii) bright neutral, (iv) bright erotic, (v) scrambled original neutral, (vi) scrambled original erotic, (vii) scrambled bright neutral, and (viii) scrambled bright erotic.

Analysis of ERP data

In a first step, ERP analysis using peak and mean amplitude scoring (Keil et al., 2014) was conducted to assess modulations of early brain activity as a function of stimulus type, brightness, and emotion. Following visual inspection of grand average ERPs, we identified the N1 at 200–280 ms post-stimulus onset and the EPN at 280–400 ms after picture onset at a cluster of bilateral posterior sensors: I1, O1, PO7, P9, I2, O2, PO8, and P10 (see Fig. 2B). Peak amplitude values[2] of the N1 (maximal negative local peak over ~16 ms) and mean amplitude values of the EPN (amplitude average within 280–400 ms) for each individual participant were extracted in the respective time windows. Amplitude differences across conditions were analyzed by means of 2 × 2 × 2 rANOVAs, with *stimulus type* (concrete vs. scrambled), *brightness* (original vs. bright), and *emotion* (neutral vs. erotic) as within-subject factors, followed by paired-sample two-tailed *t*-tests.

Mass univariate ERP analysis

To further explore ERP differences between original and bright (neutral and erotic) scenes, we conducted repeated measures, two-tailed permutation tests based on the $t_{\max}$ statistic (Blair and Karniski, 1993). This non-parametric technique allows to detect the precise onset and offset time of the differences of interest across all channels and time points, while simultaneously maintaining a desired family-wise $\alpha = .05$ (i.e., inherently correcting for multiple comparisons). All time points between 0 and 2000 ms (i.e., 512 time points at 256 Hz sampling rate) at all 64 scalp channels were included in our analysis, resulting in 32,768 total comparisons. The distribution of the null hypothesis was estimated using 5000 random within-participant permutations of the data. Any differences in the original data were deemed reliable if they exceeded the most extreme t-score of each set of tests (i.e., $t_{\max}$), in our case $+/-5.95$ for the comparison between original and bright neutral scenes and $+/-5.98$ for the comparison between original and bright erotic scenes (corresponding to a test-wise $\alpha = .00002$). These analyses were carried out using the Mass Univariate ERP toolbox (Groppe et al., 2011a, 2011b).

Spatiotemporal analysis

Spatiotemporal (or topographic) analysis is a data-driven approach that allows identifying and summarizing the dominant spatial configurations (i.e., topographic maps) of the global electric field time-locked to the onset of the stimulus, thereby avoiding experimenters' biases that may inflate type I errors (e.g., a priori selection of channels or time frames; see Murray et al., 2008; Pourtois et al., 2008). Topographic analysis was performed using CARTOOL v3.55 (Brunet et al., 2011). A spatiotemporal clustering algorithm (Atomize and Agglomerate Hierarchical Clustering, AAHC; Tibshirani and Walther, 2005) identified the dominant scalp maps in the grand average ERP data for each condition over a time window from 0 to 2000 ms after picture onset. Cluster maps that correlated more than 80% were merged. The selection of the optimal number of maps was based on a cross-validation criterion (Pascual-Marqui et al., 1995). The final maps were subsequently projected back to the single-subject data (i.e., *fitting*; Brandeis et al., 1995) in time windows where the clustering algorithm found reliable topographic differences, indicating changes in the underlying neural generators (Lehmann and Skrandies, 1980). The dependent variable was the global explained variance (GEV), which represents a quantitative estimate of the relative expression of each map across subjects and conditions (Murray et al., 2008). These values were entered in rANOVAs with *map*, *emotion*, and *brightness* as within-subject factors, followed by paired-sample *t*-tests when appropriate.

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[2] We opted for the extraction of peak amplitude values in order to take into account latency differences between scrambled and concrete pictures. Similar results were obtained with mean amplitude values.

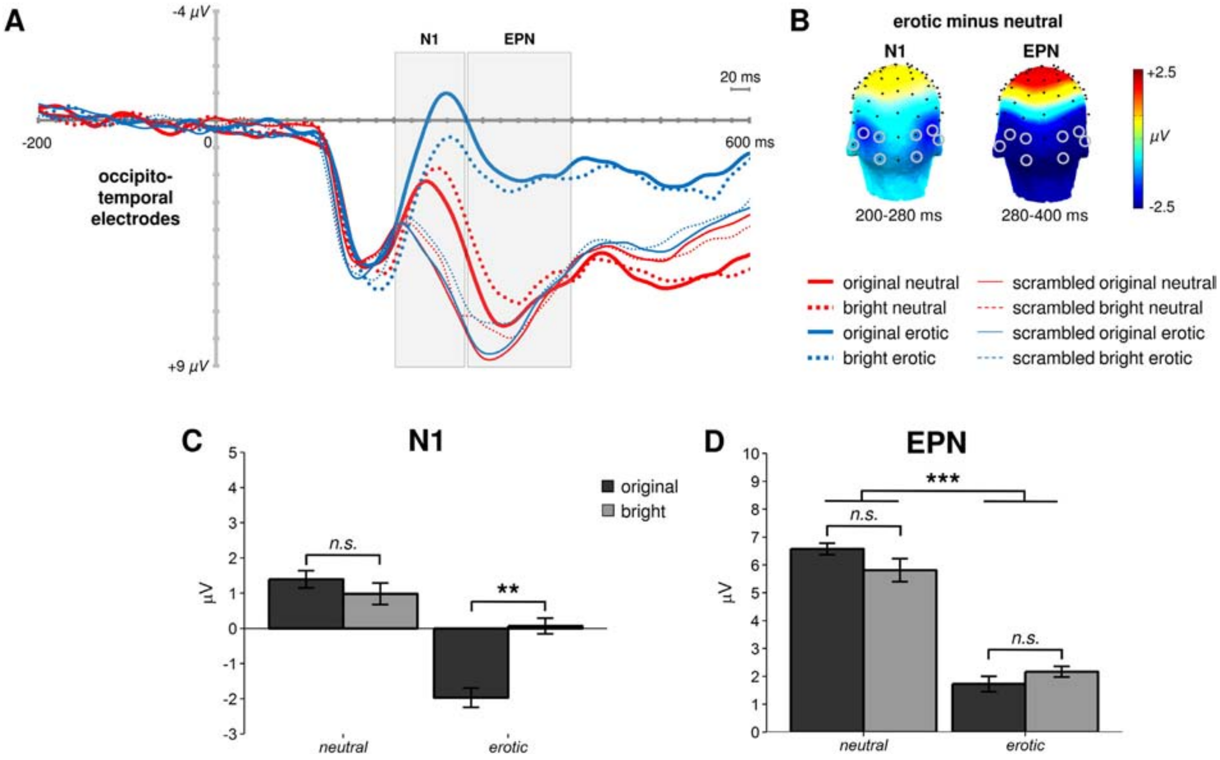

Fig. 2. Results of the classical ERP analysis. (A) Grand average ERPs ($N = 17$) recorded from an array of occipito-temporal electrodes for original (solid), bright (dotted), neutral (red), and erotic (blue) scenes, separately for concrete and scrambled images (thick vs. thin lines, respectively). Gray areas indicate the selected time windows in which amplitude values were extracted for the N1 and EPN components (200–280 and 280–400 ms, respectively). Negative is plotted upward. (B) Topographies of concrete erotic minus neutral scenes (averaged across brightness conditions) are shown to highlight the expected occipital negativity in the N1-EPN time range. The occipito-temporal electrodes selected for the statistical analyses are circled in gray (see *Analysis of ERP data* section for details). (C) Amplitude values of the N1 elicited by concrete neutral and erotic pictures, separately for original (dark gray) and bright (light gray) versions. Erotic scenes elicited larger (i.e., more negative) N1 in the original compared to bright picture set, whereas no differences were observed for neutral scenes. (D) With regards to the EPN, activity was more negative for erotic relative to neutral scenes, with no modulation by brightness. Vertical bars correspond to standard error of the mean. $^{**}p < .01$; $^{***}p < .001$; *n.s.*: not significant.

General statistical procedure

Statistical analyses were performed using *R* v3.1.3 (R Core Team, 2015) and packages *bear* v2.6.4 (Lee and Lee, 2014), *plyr* v1.8.1 (Wickham, 2011), *ez* v4.2–2 (Lawrence, 2013), *schoRsch* v1.1 (Pfister and Janczyk, 2014), and *ggplot2* v1.0.1 (Wickham, 2009). The significance level for all tests was set at $p = .05$. With rANOVAs, Greenhouse–Geisser correction was employed whenever Mauchly's test revealed violation of the assumption of sphericity, and partial eta squared (η_p^2) was used as a measure of effect size. Welch's two-tailed independent-sample *t*-tests were used when Levene's test revealed violation of the assumption of homoscedasticity, and Pearson's *r* was calculated as a measure of effect size (Cohen, 1992; Field et al., 2012).

Results

Self-reported affect

Mean ratings of emotional arousal and hedonic valence (pleasure) for the pictures presented during the experiment are reported in Table 1. A 2 (*emotion*) × 2 (*brightness*) rANOVA on arousal ratings showed a significant main effect of *emotion* ($F_{1,\,16} = 58.32$, $p < .001$, $\eta_p^2 = .78$), with higher values for erotic compared to neutral pictures ($t_{33} = 10.68$, $p < .001$, $r = .88$) (Fig. 1B). A 2 × 2 rANOVA on valence ratings also showed a significant main effect of *emotion* ($F_{1,\,16} = 27.05$, $p < .001$, $\eta_p^2 = .63$), together with a significant *emotion* × *brightness* interaction ($F_{1,\,16} = 34.40$, $p < .001$, $\eta_p^2 = .68$). Follow-up pairwise comparisons showed higher pleasure ratings for bright compared to original neutral scenes ($t_{16} = -3.02$, $p = .008$, $r = .60$). Conversely, original erotic pictures were rated higher in pleasure compared to their bright counterpart ($t_{16} = 3.16$, $p = .006$, $r = .62$) (see Fig. 1C). These results show that brightness manipulation has an opposite effect on valence ratings of neutral and erotic scenes.

Table 1
Means and standard deviations (in parenthesis) of participants' arousal and valence ratings of the pictures presented during the experiment.

Emotion	Brightness	Arousal	Valence
Neutral	Original	3.64 (0.98)	5.20 (0.52)
	Bright	3.79 (0.59)	5.53 (0.49)
Erotic	Original	6.10 (0.70)	6.52 (0.63)
	Bright	6.00 (0.81)	6.10 (0.41)

Note. Arousal and valence ratings range from 1 to 9, with 9 being highest arousal and most positive valence.

ERP results

Grand average ERPs recorded from an array of occipito-temporal electrodes are displayed in Fig. 2A[3]. Topographies of erotic minus neutral difference waves are presented in Fig. 2B to illustrate the scalp distribution of the components. Amplitude values of N1 and EPN for each experimental condition are reported in Table 2, and all relevant comparisons are visualized in Fig. 2C and 2D.

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[3] The grand average ERPs also showed a positive peak between 140 and 200 ms after picture onset, corresponding to the *P1* (Luck et al., 1990; Mangun, 1995). Although not part of our initial hypothesis, we nonetheless explored amplitude modulations of this early visual component by means of a 2 (*stimulus type*) × 2 (*brightness*) × 2 (*emotion*) rANOVA. No significant main effects or interactions were observed (all *ps* > .07).

Table 2
Means and standard deviations (in parenthesis) of amplitude values (in μV) of the N1 and EPN components.

Stimulus type	Emotion	Brightness	N1	EPN
Concrete	Neutral	Original	1.40 (2.70)	6.58 (3.23)
		Bright	0.98 (2.61)	5.81 (3.17)
	Erotic	Original	−1.97 (3.06)	1.73 (4.11)
		Bright	0.07 (2.31)	2.17 (3.26)
Scrambled	Neutral	Original	3.40 (2.71)	7.53 (2.75)
		Bright	2.91 (1.40)	7.13 (2.31)
	Erotic	Original	3.17 (2.58)	7.34 (2.76)
		Bright	2.93 (2.32)	6.77 (3.07)

N1

An omnibus rANOVA on peak amplitude values showed significant effects of *stimulus type* ($F_{1,\,16} = 21.08$, $p < .001$, $\eta_p^2 = .57$), *emotion* ($F_{1,\,16} = 18.37$, $p = .001$, $\eta_p^2 = .53$), *stimulus type* × *emotion* ($F_{1,\,16} = 24.73$, $p < .001$, $\eta_p^2 = .61$), *brightness* × *emotion* ($F_{1,\,16} = 23.42$, $p < .001$, $\eta_p^2 = .59$), and, importantly, a significant *stimulus type* × *brightness* × *emotion* interaction ($F_{1,\,16} = 6.41$, $p = .022$, $\eta_p^2 = .29$). We then considered scrambled and concrete pictures separately. While a follow-up 2 × 2 rANOVA on scrambled pictures showed no significant differences (all $ps > .46$), the same analysis on concrete scenes revealed significant main effects of *brightness* ($F_{1,\,16} = 7.29$, $p = .016$, $\eta_p^2 = .31$) and *emotion* ($F_{1,\,16} = 41.40$, $p < .001$, $\eta_p^2 = .72$), as well as a significant *brightness* × *emotion* interaction ($F_{1,\,16} = 22.32$, $p < .001$, $\eta_p^2 = .58$). Pairwise comparisons showed that the N1 was reliably larger (i.e., more negative) for original relative to bright erotic scenes ($t_{16} = -5.68$, $p < .001$, $r = .82$), whereas no amplitude differences were observed between original and bright neutral scenes ($t_{16} = 0.95$, $p = .354$, $r = .23$) (Fig. 2C). These results indicate interactive effects of low-level (i.e., brightness) and high-level features (i.e., emotional content) in this time window.

EPN

A 2 × 2 × 2 rANOVA on mean amplitude values revealed significant effects of *stimulus type* ($F_{1,\,16} = 22.41$, $p < .001$, $\eta_p^2 = .58$) and *emotion* ($F_{1,\,16} = 77.32$, $p < .001$, $\eta_p^2 = .83$), accompanied by a significant *stimulus type* × *emotion* interaction ($F_{1,\,16} = 127.86$, $p < .001$, $\eta_p^2 = .89$). A follow-up 2 × 2 rANOVA on scrambled pictures only showed a main effect of *brightness* ($F_{1,\,16} = 4.57$, $p = .048$, $\eta_p^2 = .22$), with slightly more negative amplitude for bright compared to original images (6.95 vs. 7.43 μV; $t_{33} = -2.10$, $p = .043$, $r = .34$). The same analysis on concrete pictures showed a significant main effect of *emotion* ($F_{1,\,16} = 151.16$, $p < .001$, $\eta_p^2 = .91$), indicating more negative EPN for erotic compared to neutral scenes ($t_{33} = -12.65$, $p < .001$, $r = .91$), but neither a main effect of *brightness* ($F_{1,16} = 0.25$, $p = .623$, $\eta_p^2 = .02$) nor a *brightness* × *emotion* interaction ($F_{1,\,16} = 3.98$, $p = .063$, $\eta_p^2 = .20$) (see Fig. 2D). Pairwise comparisons confirmed no statistically significant differences between original and bright neutral ($t_{16} = 1.40$, $p = .180$, $r = .33$) or erotic scenes ($t_{16} = -1.38$, $p = .186$, $r = .33$).

Given that the *p*-value of the *brightness* × *emotion* interaction was close to the conventionally accepted threshold of significance of $p = .05$, we turned to Bayesian inference testing (Jeffreys, 1961; Kass and Raftery, 1995) to quantify the degree of evidence in favor of our hypothesis, i.e., emotion explains variations in EPN amplitude more reliably than brightness. Using the function *anovaBF* from the *R* package *BayesFactor* v0.9.12–2 (Morey et al., 2015), we estimated the Bayes factor – using Monte-Carlo sampling (10,000 iterations) – for each model of interest: main effect of *emotion*, main effect of *brightness*, both main effects, and both main effects plus the *emotion* × *brightness* interaction, i.e., the full model (Rouder et al., 2012, 2016). We used Jeffrey–Zellner–Siow priors (*JZS*) with scaling factors of $r = 1$, $r = .707$, and $r = .5$, to verify the robustness of the results regardless of the selected prior (Schönbrodt et al., 2015). Participants were included in all models as random factor, and their variance considered as nuisance.

The results are reported in Table 3. When comparing the full model and the model with the main effect of emotion alone, the Bayes factor BF_{24} indicated that the observed EPN amplitudes were at least 3.29 times more probable when emotion is the only factor compared to when it interacts with brightness. This result can be descriptively qualified as *positive* evidence in favor of the model with only the main effect of emotion (Kass and Raftery, 1995). Moreover, the comparison between the models with the main effect of *emotion* vs. *brightness* (BF_{21}) revealed that EPN amplitudes were at least 4.35×10^{14} times more probable when emotion is the only factor compared to brightness alone. This qualifies as *very strong evidence* to support the model with only the main effect of emotion.

In sum, both null hypothesis statistical testing and Bayesian analyses confirmed that, during the presentation of meaningful scenes, the EPN was more sensitive to stimulus variations due to emotion rather than brightness.

Results of the mass univariate ERP analysis

The results of the point-by-point permutation test confirmed no differences between original and bright neutral scenes: none of the comparisons across electrodes and time points exceeded the $t_{\max}$ value. Conversely, activity elicited by original erotic scenes was reliably more negative than activity in response to bright scenes. This difference started at approximately 191 ms and lasted until 250 ms and was mainly localized at a cluster of occipito-temporal electrodes (Oz, P10, PO8, PO4, and O2) and one frontal electrode (F4) on the right hemisphere (Fig. 3). This non-parametric analysis corroborated the results of the classical parametric ERP analysis (see above) and more accurately pinpointed the precise onset and offset of the effect.

Results of the spatiotemporal cluster analysis

Complementary spatiotemporal cluster analysis carried out in a time window from 0 to 2000 ms after stimulus onset (Fig. 4A) revealed six distinct dominant field topographies explaining 92.04% of the total variance (Fig. 4B). Based on the topographic distribution and onset time, maps 1, 3, and 6 likely indicated baseline activity or late cognitive processes (e.g., memory), which were not the focus of the present investigation; therefore, they will not be discussed further. Scrambled pictures were predominantly explained by map 2, which resembled the characteristic occipital distribution of the P1 component reflecting low-level visual processing (Luck et al., 1990; Mangun, 1995; Taylor, 2002). No topographic changes were observed for scrambled images across emotion and brightness conditions; therefore, activity elicited by these images was not further analyzed. With regards to concrete scenes, the other two dominant maps (besides map 2) were an occipito-parietal positivity (map 4) and a centro-parietal positivity with a concurrent occipital negativity (map 5). Topographic changes, indicating shifts in the neural generators, were identified in *early*

Table 3
Bayes factors (*BF*) and percentage of proportional errors (% pe) for each model of interest, obtained by using JZS priors with different scaling factors (see *ERP results* section for details).

Model	$r = 1$		$r = .707$		$r = .5$	
	BF	% pe	BF	% pe	BF	% pe
[1] Br	0.25	±3.11	0.19	±1.05	0.26	±2.56
[2] Emo	1.16×10^{14}	±1.36	1.56×10^{14}	±2.52	1.13×10^{14}	±2.12
[3] Br + Emo	2.99×10^{13}	±2.83	3.06×10^{13}	±1.64	3.06×10^{13}	±1.70
[4] Br + Emo + Br*Emo	3.52×10^{13}	±2.42	3.07×10^{13}	±2.71	3.44×10^{13}	±2.23
BF_{24}	3.29	±2.48	5.07	±3.70	3.29	±3.08
BF_{21}	4.35×10^{14}	±3.40	8.24×10^{14}	±2.30	4.44×10^{14}	±1.91

Note. Br: brightness; Emo: emotion; $BF_{24} = BF[2]/BF[4]$; $BF_{21} = BF[2]/BF[1]$.

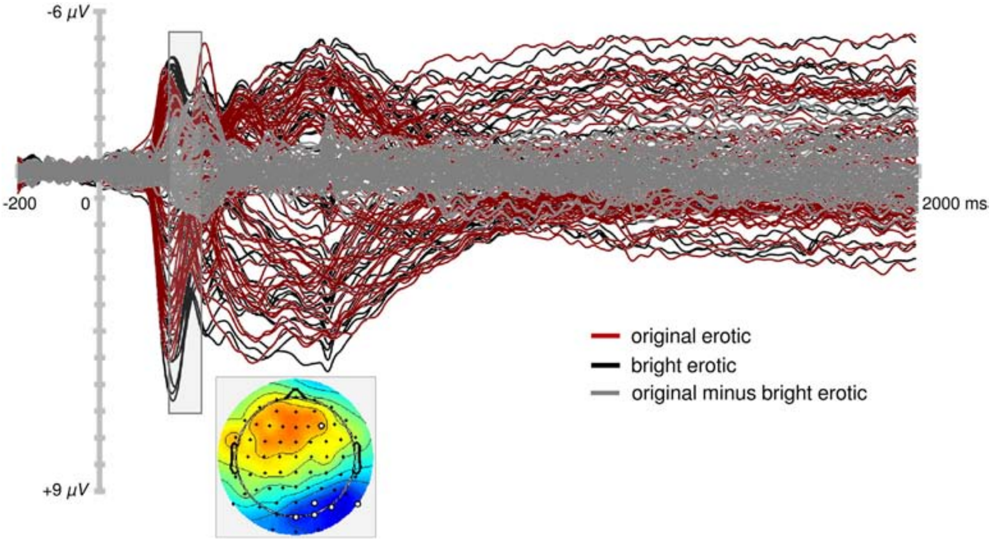

Fig. 3. Results of the mass univariate ERP analysis. Grand average ERP waveforms of activity elicited by erotic original (red) and bright (black) pictures, as well as their difference (in gray). The light gray area indicates the time window – from 191 to 250 ms – in which the point-by-point permutation test identified robust differences between conditions, which were mainly localized at occipito-temporal electrodes on the right hemisphere (in white).

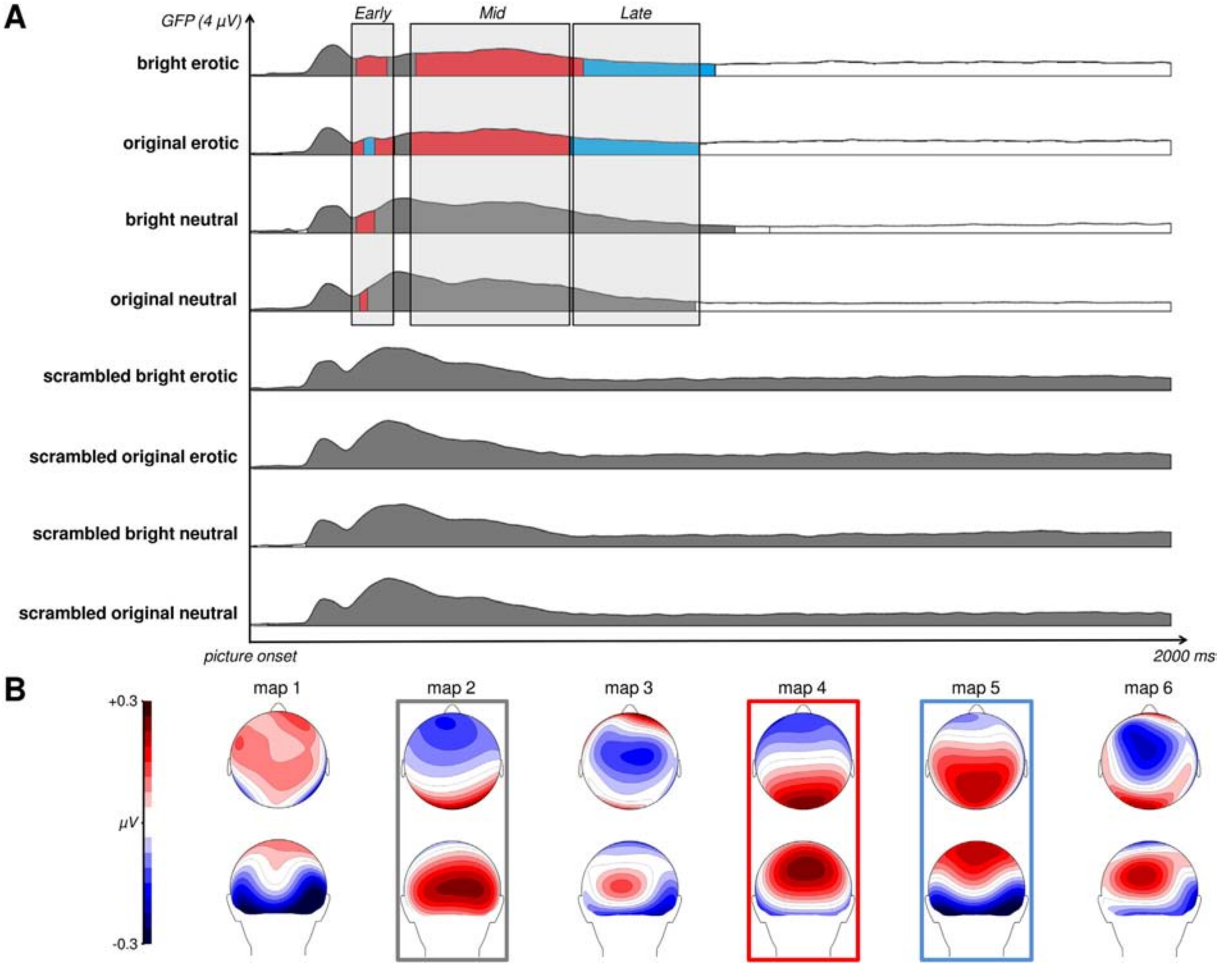

Fig. 4. Results of the spatiotemporal analysis. (A) Results of the spatiotemporal cluster analysis (0–2000 ms post-stimulus onset) across all experimental conditions. Six maps were found to explain 92.04% of the variance. The light gray areas indicate three time windows in which reliable topographic changes occurred: (1) *early* (214–304 ms), maps 2, 4, and 5; (2) *mid* (343–683 ms), maps 2 and 4; (3) *late* (683–967 ms), maps 2 and 5. Same colors under the global field power (GFP) trace indicate same maps across conditions: map 2 in gray, map 4 in red, map 5 in blue. (B) Horizontal and coronal views of the six dominant maps extracted by the spatial cluster analysis. These topographies were created with BrainVision Analyzer 2.0 (Brain Products™ GmbH, Munich, Germany; www.brainproducts.com).

(214–304 ms), *mid* (343–683 ms), and *late* (683–967 ms) time windows (Fig. 4A).

Early time window (214–304 ms)

The contribution of maps 2, 4, and 5 across all concrete conditions was quantified by fitting them to the individual ERP data and extracting the GEV (see *Spatiotemporal analysis* section for details). A 3 (*map*) × 2 (*brightness*) × 2 (*emotion*) rANOVA showed significant effects of *map* ($F_{2,\ 32} = 5.04$, $p = .012$, $\eta_p^2 = .24$), *emotion* ($F_{1,\ 16} = 6.58$, $p = .021$, $\eta_p^2 = .29$), map × emotion ($F_{1.23,\ 19.71} = 10.15$, $p = .003$, $\eta_p^2 = .39$) and, importantly, *map* × *brightness* × *emotion* ($F_{2,\ 32} = 5.11$, $p = .012$, $\eta_p^2 = .24$). A follow-up 3 × 2 rANOVA on neutral scenes showed only a main effect of *map* ($F_{1.26,\ 20.10} = 11.80$, $p = .002$, $\eta_p^2 = .42$): map 2 generally explained most of the variance, followed by map 4 and map 5 (all *ps* < .003), with no influence of brightness (Fig. 5A). Conversely, the same analysis on erotic scenes revealed a significant *map* × *brightness* interaction ($F_{2,\ 32} = 4.65$, $p = .017$, $\eta_p^2 = .23$). Pairwise comparisons showed that map 2 explained more variance for bright compared to original erotic scenes ($t_{16} = 2.81$, $p = .013$ $r = .57$), whereas the opposite was true for map 5 ($t_{16} = -2.82$, $p = .012$ $r = .58$), and no differences for map 4 ($t_{16} = 0.73$, $p = .476$, $r = .18$) (Fig. 5B). These results suggest that, in this time window, map 5 appears to be the dominant topography in situations of maximal emotional reactions, i.e., in response to original erotic scenes.

Mid time window (343–683 ms)

Here, regardless of brightness, concrete erotic scenes were mostly explained by map 4, whereas map 2 was the dominant topography for neutral scenes. A 2 (*map*) × 2 (*brightness*) × 2 (*emotion*) rANOVA showed a marginally significant effect of *map* ($F_{1,\ 16} = 4.24$, $p = .056$, $\eta_p^2 = .21$) and a significant *map* × *emotion* interaction ($F_{1,\ 16} = 46.46$, $p < .001$, $\eta_p^2 = .74$). Follow-up comparisons revealed that map 2 explained more variance for neutral compared to erotic scenes ($t_{33} = -8.65$, $p < .001$, $r = .83$), whereas the opposite was true for map 4 ($t_{33} = 7.14$, $p < .001$, $r = .78$) (Fig. 5C). Brightness did not have any impact on the GEV in this time window.

Late time window (683–967 ms)

In this time window, neutral and erotic scenes were best explained by maps 2 and 5, respectively. A 2 (*map*) × 2 (*brightness*) × 2 (*emotion*) rANOVA showed a significant main effect of *map* ($F_{1,\ 16} = 5.34$, $p = .034$, $\eta_p^2 = .25$) and a significant *map* × *emotion* interaction ($F_{1,\ 16} = 50.00$, $p < .001$, $\eta_p^2 = .76$). Paired *t*-tests confirmed that map 2 explained most of the variance for neutral scenes ($t_{33} = -7.88$,

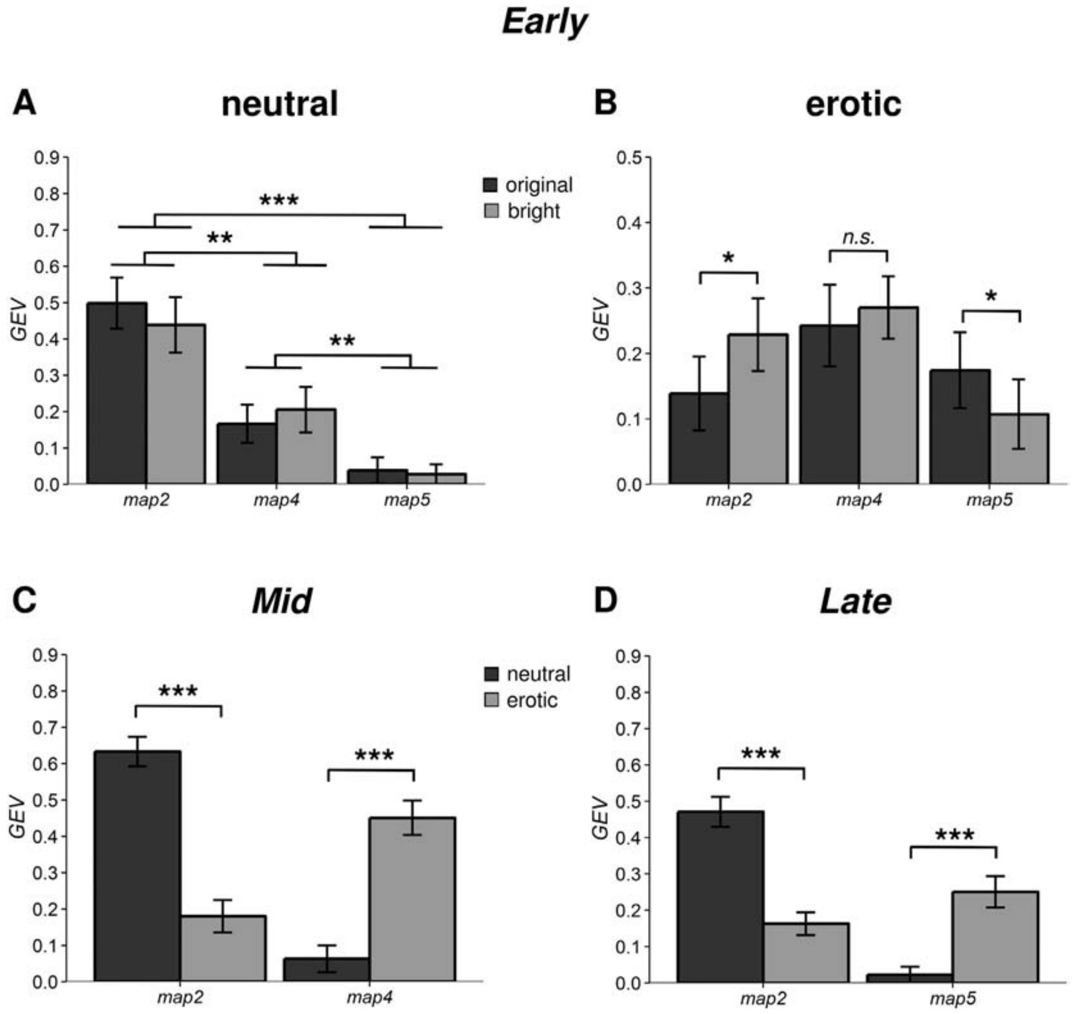

Fig. 5. Results of the fitting procedure. (A, B) Statistical results of the global explained variance (GEV) of maps 2, 4, and 5 in the *early* time window (214–304 ms following stimulus onset), separately for original (dark gray) and bright (light gray) pictures. (A) Neutral pictures were best explained by map 2, followed by map 4 and map 5, with no differences between bright and original scenes. (B) Conversely, brightness modulated the expression of these three maps during the presentation of erotic scenes. While map 4 was not influenced by brightness, map 2 was found to better explain bright scenes, and map 5 explained more variance during the presentation of original scenes. (C) In the *mid* time window (343–683 ms after picture onset), neutral scenes (dark gray) were better explained by map 2, whereas map 4 better explained erotic scenes (light gray), with no influence of brightness (factor collapsed). (D) Similarly, in the *late* time window (683–967 ms post-stimulus onset), map 2 explained more variance during the presentation of neutral scenes, while erotic scenes were better explained by map 5. GEV is expressed in arbitrary units. Vertical bars correspond to standard error of the mean. *$p < .05$; **$p < .01$; ***$p < .001$; *n.s.*: not significant.

$p < .001$, $r = .81$), while map 5 was the dominant topography for erotic scenes ($t_{33} = 7.19$, $p < .001$, $r = .78$) (Fig. 5D). Again, brightness did not influence GEV.

Auxiliary analysis: association of N1 and EPN amplitude with spatial frequency content

To assess the extent to which amplitude measures extracted for the N1 and EPN windows varied as a function of spatial frequency, we used *F*-trend analyses (also known as contrast analyses), quantifying the fit of the respective picture property to the data matrices containing the N1 and EPN voltages for each participants as rows and the experimental conditions as columns. To this end, the spatial frequency energy in two bands was determined for each picture category (erotic original, erotic bright, neutral original, neutral bright; concrete scenes only). The spatial spectrum was calculated using two-dimensional FFT implemented in MATLAB, and the resulting spectrum of energy values was binned into two frequency bands: (1) *SF1*, 0 to 1 cycles per degree (cpd); (2) *SF2*, 1 to 3.5 cpd (the selection of these frequency bands follows Loftus and Harley, 2004; Schor et al., 1998). To statistically quantify the correspondence of the condition means obtained from the ERPs with the spatial frequency values, one planned *F*-trend analysis was calculated for each dependent variable (N1 and EPN amplitude values) and each spatial frequency band. As recommended by Rosnow and Rosenthal (1996), the weights for the *F*-trend analyses were determined by *z*-scoring the manipulation of interest, i.e., the respective spatial frequency power values across the 4 experimental conditions, thus leading to a vector of 4 numbers with a mean of zero. These numbers were then used as weights for the *F*-trend models, leading to an *F*-value and effect size (expressed as R^2) for each dependent variable and picture property. Results showed that N1 amplitude across our experimental conditions significantly varied as a function of spatial frequency content, both for SF1 ($F_{1,\ 51} = 14.51$, $p < .01$, $R^2 = .46$) and SF2 ($F_{1,\ 51} = 3.39$, $p < .05$, $R^2 = .16$). The EPN, on the other hand, was not modulated by spatial frequency content, either for SF1 ($F_{1,\ 51} = 1.93$, $p > .05$, $R^2 = .10$) or SF2 ($F_{1,\ 51} = 0.59$, $p > .05$, $R^2 = .03$).

Auxiliary analysis: LPP

The so-called late positive potential (LPP) is widely used as an ERP-derived index of emotional picture processing. This positive ERP component is typically enhanced following the presentation of emotional compared to neutral pictures and is thought to reflect sustained attention toward motivationally relevant stimuli (Cuthbert et al., 2000; Hajcak et al., 2010; Schupp et al., 2000) as well as their preferential encoding and storage in memory (Dolcos and Cabeza, 2002; Koenig and Mecklinger, 2008). Although outside the scope of the present analysis, it was considered here to facilitate comparison with other studies and allow validation of the stimulus material and procedures. Mean amplitude values were extracted from an array of centro-parietal electrodes (Pz, CPz, Cz, P1, CP1, C1, P2, CP2, C2) in a time window 400–1000 ms after picture onset (see Fig. 6A–B). A 2 (*stimulus type*) × 2 (*brightness*) × 2 (*emotion*) rANOVA revealed significant effects of *stimulus type* ($F_{1,\ 16} = 19.20$, $p < .001$, $\eta_p^2 = .55$) and *emotion* ($F_{1,\ 16} = 59.33$, $p < .001$, $\eta_p^2 = .79$), accompanied by significant *stimulus type* × *emotion* ($F_{1,\ 16} = 37.86$, $p < .001$, $\eta_p^2 = .70$) and *brightness* × *emotion* interactions ($F_{1,\ 16} = 7.17$, $p = .016$, $\eta_p^2 = .31$). A follow-up 2 × 2 rANOVA on scrambled scenes showed a significant *brightness* × *emotion* interaction ($F_{1,\ 16} = 7.59$, $p = .014$, $\eta_p^2 = .32$), which we consider to be spurious for three reasons: (1) no semantic content could be extracted from these images, therefore participants could not have possibly responded to their emotional content; (2) amplitude values were very low, ranging from -0.21 to 0.66 μV, as opposed to larger LPP amplitudes in response to concrete scenes, ranging between 0.12 and 2.98 μV; (3) mass univariate ERP analysis comparing activity in response to scrambled original vs. bright erotic images revealed no significant results at any time point or electrode.

Importantly, the same 2 × 2 × 2 rANOVA on concrete pictures only showed a significant main effect of *emotion* ($F_{1,\ 16} = 80.53$, $p < .001$, $\eta_p^2 = .83$), with more positive amplitude for erotic relative to neutral scenes ($t_{33} = 10.42$, $p < .001$, $r = .88$) (Fig. 6C). Therefore, when meaningful scenes were presented, the LPP was exclusively modulated by emotional content and not by brightness.

Control for possible order effects

In the present study, each participant saw the same picture twice, once in its original and once in its bright version. In order to avoid order effects, half of the participants were presented first with the original version and the other half with the bright version (see *Procedure* section). Nonetheless, we formally examined the extent to which order influenced the behavioral and/or electrophysiological measures. Split-plot rANOVAs with *order* (original first vs. bright first) as between-subject factor and *stimulus type*, *brightness*, and *emotion* as within-subject factors were conducted on amplitude values of N1, EPN, and LPP. Neither a main effect of *order* nor an interaction of *order* with other factors was found (all *ps* > .10). Split-plot rANOVAs with *order* as between-subject factor and *brightness* and *emotion* as within-subject factors on arousal ratings also showed no significant effect of *order* (all *ps* > .08). The same analysis on valence ratings showed a significant *brightness* × *order* interaction ($F_{1,\ 15} = 30.97$, $p < .001$, $\eta_p^2 = .67$), driven by higher ratings for original pictures when participants were presented with their bright version first ($t_{22.82} = -2.91$, $p = .008$, $r = .52$). However, no significant *order* × *emotion* interaction was observed ($F_{1,\ 15} = 0.31$, $p = .583$, $\eta_p^2 = .02$). These results suggest that the order of presentation did not systematically influence the processing of the emotional content of original and bright scenes.

Discussion

The purpose of this study was to accurately pinpoint the first electrophysiological markers of attention allocation toward emotional cues in complex natural pictures, as well as their interaction with basic perceptual features. EEG was recorded from seventeen male participants who were asked to rate original and bright versions of grayscale neutral and erotic IAPS scenes. The amplitude of the N1 ERP component was not influenced by brightness when viewing *neutral* scenes[4] but was larger for original compared to bright *erotic* scenes, suggesting early interactive effects, in extrastriate visual areas, of low-level visual features and attentional allocation toward salient emotional content. Complementary non-parametric analyses further revealed that these amplitude differences between original and bright erotic scenes could reliably be observed between 191 and 250 ms post-stimulus onset at right posterior electrodes, consistent with the well-known hemispheric lateralization of attentional networks specialized for the detection of behaviorally relevant stimuli (Corbetta and Shulman, 2002; see also Gainotti, 2012). Additional analyses showed that the N1 was also sensitive to spectral energy in low (<1 cpd) and high (1–3.5 cpd) spatial frequency bands. This result is not surprising, for at least two reasons: (i) our experimental manipulation (i.e., brightness) necessarily changed picture contrast, which is tightly linked to spatial frequency content (Field, 1987; Hansen et al., 2011; Simoncelli and Olshausen, 2001; Torralba and Oliva, 2003); (ii) several studies have already reported N1 modulations as a function of spatial frequency (e.g., Craddock et al., 2015; Ellemberg et al., 2001; Hansen et al., 2011, 2012). It is unlikely that, in our study, N1 amplitude was exclusively

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[4] While original and bright neutral scenes differed with respect to behavioral ratings, N1 amplitudes were similar. We correlated N1 amplitude values with valence and arousal ratings, in order to verify whether affective evaluations were really dissociated from early brain responses. Non-parametric Spearman's rank correlations revealed no relationship between behavior and brain measures (all *ps* > .19).

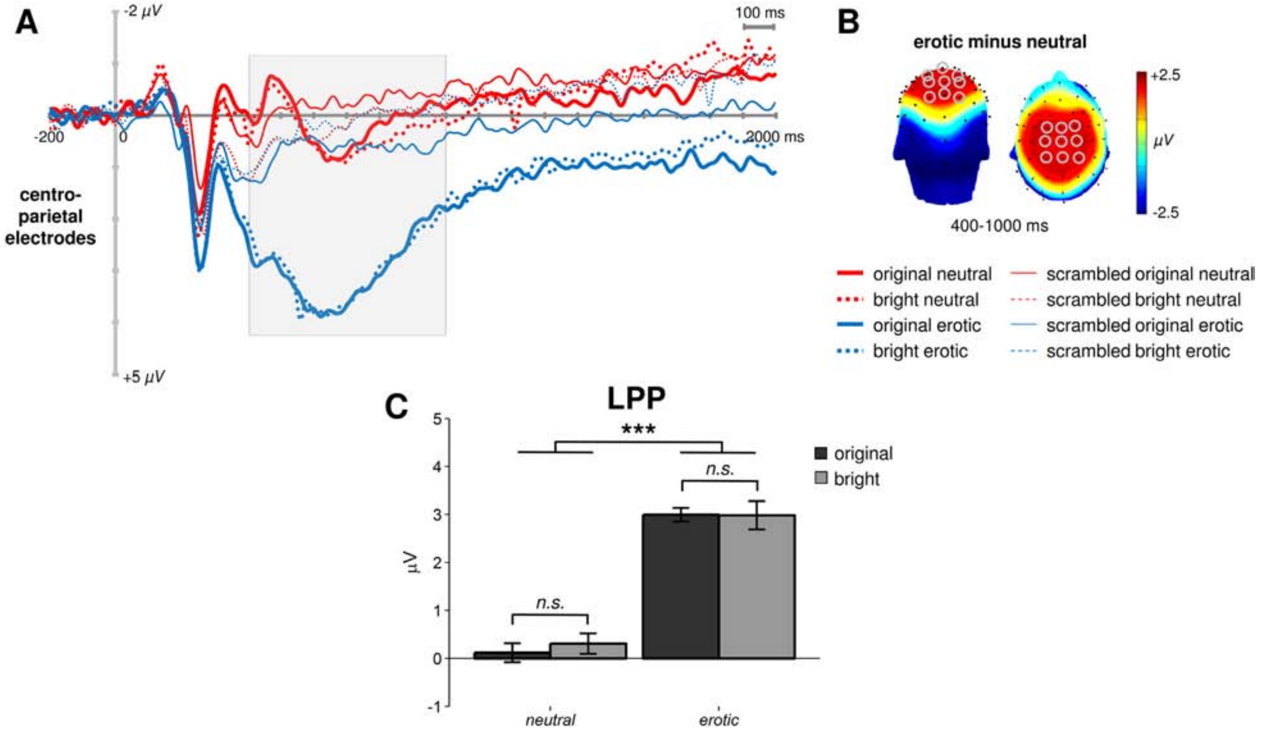

Fig. 6. Auxiliary analysis of the LPP. (A) Grand average ERPs recorded from an array of centro-parietal electrodes for original (solid), bright (dotted), neutral (red), and erotic (blue) scenes, separately for concrete and scrambled images (thick vs. thin lines, respectively). Gray areas indicate the selected time window in which mean amplitude values were extracted (400–1000 ms after picture onset). Negative is plotted upward. (B) Back and top view of topography of concrete erotic minus neutral scenes (averaged across brightness conditions) confirmed the centro-parietal distribution of the LPP. The electrodes selected for the statistical analyses are circled in gray (see *Auxiliary analysis: LPP* section for details). (C) Amplitude values of the LPP elicited by concrete neutral and erotic pictures, separately for original (dark gray) and bright (light gray) versions. Erotic scenes elicited larger LPP compared to neutral scenes, with no differences as a function of brightness. Vertical bars correspond to standard error of the mean. ***$p < .001$; *n.s.*: not significant.

dependent on spatial frequency: if that were the case, we would have found similar modulations in response to scrambled scenes, which contained similar spectral energy as their concrete counterpart but were devoid of any semantic content. Instead, it is more plausible that the N1 reflects an integration of perceptual (e.g., Craddock et al., 2015; Johannes et al., 1995) and attentional mechanisms (e.g., Luck et al., 2000). However, variations in physical properties indeed have a remarkable influence on N1 amplitude, and thus its modulation cannot unequivocally be ascribed to attentional prioritization of emotionally relevant visual stimuli. On the contrary, the EPN was unaffected by luminance or spectral energy variations[5] and was only influenced by semantic content. Since we controlled for picture complexity, which is known to affect EPN amplitude (Bradley et al., 2007; Wiens et al., 2011), these results support the notion that this component is a robust electrophysiological marker of attention allocation toward emotion-laden stimuli, regardless of their nature (symbolic gestures, e.g., Flaisch et al., 2010; pictures, e.g., Junghöfer et al., 2001; words, e.g., Kissler et al., 2007; faces, e.g., Schupp et al., 2003b) or even their presence in the visual field (see recent results on EPN and mental imagery, e.g., Süß and Abdel Rahman, 2015)[6].

Intriguingly, the results of the spatiotemporal analysis revealed that the interaction of low-level (i.e., brightness) and high-level (i.e., emotion) processes was not just reflected in amplitude changes of specific ERP components but was linked to switches between large-scale distributed neural networks. Topographic changes 214–304 ms after stimulus onset revealed that, while the expression of an occipital positivity (map 2) in response to neutral scenes was not influenced by brightness, the centro-parietal positivity with a concurrent occipital negativity (map 5) in response to erotic scenes explained even more interindividual variance when *original* erotic scenes were displayed (see Fig. 5B). Interestingly, map 5 bears resemblance with the topography of the LPP (Fig. 6B). Thus, not only these findings converge with the results of the N1 amplitude described above, but additionally suggest that original erotic scenes were "tagged" as more salient compared to their bright counterpart (as confirmed by self-reported affective evaluations), and this prompted an increased activation of specialized neural networks responsible for an in-depth analysis and storage of such stimuli. On the other hand, the expression of maps 2, 4, and 5 at mid (343–683 ms) and late (683–967 ms) time windows was solely influenced by picture content, with map 2 mostly explaining neutral scenes and maps 4 and 5 erotic scenes. Notably, map 4 seemed to act as a sort of "transition" between the topography expressing the processing of physical features (map 2) and the one reflecting sustained attention toward emotional stimuli (map 5). However, caution must be exercised when claiming that the map 5 in the late time window originates from the same neural generators as the map 5 in the early time window, since identical scalp topographies can be the result of different combinations of dipoles (Grech et al., 2008; Pascual-Marqui, 1999). Nonetheless, from a functional perspective, it seems plausible that the brain would initially "tag" motivationally relevant stimuli and, by means of recurrent processing, reinforce their perceptual representation in order to prepare the organism for action (Lang and Bradley, 2010).

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[5] In an auxiliary analysis, Bradley et al. (2007, p. 368) found that spatial frequency content had no effect on EPN amplitude when viewing simple figure-ground pictures, whereas more complex scenes elicited larger (i.e., less positive) EPN when low in spatial frequency. In our study, no influence of spatial frequency on EPN amplitude was observed because figure and background were easy to distinguish in our pre-selected pictures, as confirmed by subjective complexity ratings around 3 (on a scale from 1 to 9) for both neutral and erotic scenes.

[6] When using simple and/or overlearned stimuli, the extraction of affective cues may occur at earlier stages of visual processing. For example, several studies have shown that neutral and emotional *facial expressions* can be dissociated as early as the P1 component (Batty and Taylor, 2003; Eger et al., 2003; Pourtois et al., 2004, 2005; Rotshtein et al., 2010). However, our results highlight the unique contribution of emotional information in modulating electrical brain activity in response to *complex natural scenes*, once the confounding role of physical properties is taken into account.

As a secondary aim, we sought to better characterize the so-called *brightness bias*, i.e., the tendency to attribute a more positive connotation to bright neutral stimuli as opposed to their darker counterparts. In our experiment, participants systematically judged neutral bright scenes as more pleasant, replicating one previous study (Lakens et al., 2013). These findings are also consistent with work showing impaired word categorization when stimulus brightness (i.e., the luminance of the letters composing the word) and valence (i.e., the affectively charged meaning of the word) are incongruent (Meier et al., 2004; Okubo and Ishikawa, 2011; Sherman and Clore, 2009). More generally, this preference for bright as opposed to dark stimuli might be an evolutionary trait common to all diurnal animals, for which darkness is often associated with uneasiness and increased anxiety (Grillon et al., 1997). Whether this association between brightness and valence is automatic or elicited by contextual factors is still subject to debate (e.g., Lakens et al., 2012) and could be explored in future studies.

If brightness “magnifies” the positive judgment of neutral scenes, one would expect an even larger effect when evaluating intrinsically pleasant stimuli, such as erotica; alternatively, changes in luminance might not be salient enough to modify the strongly polarized affective content of these scenes and, consequently, no differences in ratings should be observed. Instead, and somewhat surprisingly, erotic pictures were rated as more pleasant when presented in their *original* version. A plausible explanation for this result could be that the emotion evaluation of bright erotic scenes was somehow dampened because of a slight overexposure that impoverished the perception of contours, ultimately rendering bright erotic pictures less intelligible (see Lakens et al., 2013, p. 15). Conversely, it is possible that original erotic scenes were rated as more pleasant because of their higher contrast, in line with the assumption that people typically prefer high-contrast objects over low-contrast ones (e.g., Reber et al., 1998). This explanation is also compatible with the idea that affective evaluations are directly influenced by the ease with which humans process visual stimuli, also termed *perceptual fluency* (for a review, see Winkielman et al., 2003). Under this hypothesis, pleasant information may have been extracted more readily from higher contrast pictures such as original erotic scenes, and this facilitated processing may have in turn influenced their valence ratings.

For the sake of clarity, three limitations of the present study are discussed. First, the exclusive use of erotic pictures as emotional material prevents us to draw definitive conclusions with regards to the distinct role of arousal and valence in modulating electrophysiological activity of our original and bright scenes. As specified in the Introduction, this choice was made to increase the likelihood of detecting N1 and EPN amplitude differences, given that these components have been shown to be particularly sensitive to erotic content (Keil et al., 2002; Schupp et al., 2003b, 2006b, 2007). Future studies will address the separate contribution of arousal and valence by including unpleasant pictures in the experimental design. According to the brightness bias hypothesis, bright unpleasant scenes would probably be rated less negatively compared to their original version. Based on the electrophysiological results reported here, we could also expect lower N1 for bright as opposed to original unpleasant scenes (similarly to what has been observed in response to erotic pictures) because lower ratings might be linked to lower N1 amplitude. Second, a dark version of the stimuli was not presented here but could be included in a follow-up experiment. Darker pictures could be evaluated as generally more negative, with a concurrent linear modulation of N1 amplitude. The third limitation pertains to the recruitment of male participants only, which may raise questions regarding the generalizability of our results. Given that male and female individuals differ with respect to valence and arousal ratings (particularly when presented with erotic scenes; see Lang et al., 2008), the inclusion of participants of both genders would have required the use of separate stimulus sets, ultimately making the careful control of visual properties unfeasible. Follow-up studies will investigate whether physical picture properties might interact with previously reported gender differences in the activation of defensive and appetitive systems when viewing emotion-laden scenes (Bradley et al., 2001; Kemp et al., 2004; Lithari et al., 2010).

Conclusions

The present study offers electrophysiological evidence of the tight interaction between the perceptual processing of low-level visual features and the attentional prioritization of emotional scenes in extrastriate visual cortex. A pronounced dissociation was observed between the N1 and EPN components. N1 amplitude was relatively heightened for high-contrast, low-luminance erotic stimuli, whereas neutral control scenes did not show such a pattern. The EPN, on the other hand, was not affected by physical properties but was reliably modulated by picture content, making it a stable and reliable electrophysiological marker of attentional prioritization of emotional material. The results of the spatiotemporal analysis additionally revealed, within 300 ms after the presentation of emotional scenes whose semantic content could easily be extracted (i.e., original erotic scenes), the selective expression of a centro-parietal positivity reflecting the recruitment of neural networks typically linked to sustained attention and facilitated memory encoding for motivationally salient material.

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