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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

[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.