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Electrocortical amplification for emotionally arousing natural scenes: The contribution of luminance and chromatic visual channels

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Abstract

Emotionally arousing scenes readily capture visual attention, prompting amplified neural activity in sensory regions of the brain. The physical stimulus features and related information channels in the human visual system that contribute to this modulation, however, are not known. Here, we manipulated low-level physical parameters of complex scenes varying in hedonic valence and emotional arousal in order to target the relative contributions of luminance based versus chromatic visual channels to emotional perception. Stimulus-evoked brain electrical activity was measured during picture viewing and used to quantify neural responses sensitive to lower-tier visual cortical involvement (steady-state visual evoked potentials) as well as the late positive potential, reflecting a more distributed cortical event. Results showed that the enhancement for emotional content was stimulus-selective when examining the steady-state segments of the evoked visual potentials. Response amplification was present only for low spatial frequency, grayscale stimuli, and not for high spatial frequency, red/green stimuli. In contrast, the late positive potential was modulated by emotion regardless of the scene's physical properties. Our findings are discussed in relation to neurophysiologically plausible constraints operating at distinct stages of the cortical processing stream.

Since pictorial cues share many of the same perceptual and sensory features as the real-world objects that they depict, affective picture viewing reliably activates ancient motivational circuits in the brain that have evolved to facilitate survival in natural

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environments (Lang & Bradley, 2010). The activation of motivational circuits by pictures of emotionally arousing natural scenes (e.g., depictions of mutilation, injury or nude bodies) produces a cascade of effects that promote increased information gathering in the service of guiding adaptive action. Perceptual and sensory processing is enhanced for motivationally relevant objects in a process that has been referred to as ‘natural selective attention’ (Bradley, 2009; Bradley, Keil, & Lang, 2012). For example, even in the absence of an explicit cognitive task, aversive and pleasant, compared to emotionally neutral, pictures evoke enhanced activity within the visual cortex, regardless of whether brain activity is quantified using electro-magnetic or hemodynamic measures (see e.g., Lang & Bradley, 2010, Vuilleumier, 2005 for reviews).

Scene processing in the primate visual system is massively parallel and involves the extraction of specific compositional features that constitute the image (Nassi & Callaway, 2009). A typical natural scene provides a wealth of visual information, which is processed through several channels that differ in their sensitivity to luminance and chromatic (“color”) signals (Prenger, Wu, David, & Gallant, 2004), with changes in luminance and spectral content transmitted from the retina to the visual cortex through dedicated sub-cortical channels (e.g., Johnson, Hawken, & Shapley, 2004). In this study, we focused on two channels: (i) the luminance channel, which responds to a sum of weighted long-wave (L), middle-wave (M) and, under certain conditions (Ripamonti, Woo, Crowther, & Stockman, 2009), short-wave (S) differential cone excitations (L+M+S) and (ii) a chromatic channel that is sensitive to reddish-greenish hue variations through coding the weighted difference of L and M differential cone excitations (L-M) as well as bluish-yellowish hue variations through coding the weighted difference between the differential S-cone and the summed differential L and M cone excitations (S-(L+M); for review, see Stockman & Brainard, 2010).

Recently, several popular hypotheses have been advanced about the putatively unique contributions of these visual channels as conduits for sensory impressions related to motivational salience. For instance, spatially coarse information conveyed through luminance channels has been suggested to be particularly important for the elicitation of emotional responses (Liddel et al., 2004; Vuilleumier, Armony, Driver, & Dolan, 2003). Several authors have discussed the putative overlap of luminance and chromatic channels with neuro-anatomically defined pathways, which also have been differentially related to emotional processing, such as the magnocellular or parvocellular pathways that lead from the retina to V1 (Bocanegra & Zeelenberg, 2009). One idea is that the magnocellular visual pathway, which is activated primarily by low spatial frequency, low contrast, achromatic stimuli (e.g., blurred grayscale pictures), is preferentially engaged when viewing emotional stimuli, due to more extensive connectivity with motivational brain circuitry, most notably the amygdaloid bodies (Zeelenberg, Wagenmakers, & Rotteveel, 2006). According to this hypothesis, the sensory amplification typically observed for emotionally engaging information is mediated to a large extent by reentrant connections rooted in magnocellular pathways. Such theorizing has intuitive appeal, in light of tracer studies demonstrating that large cells in the basal nucleus of the amygdala (i.e. neurons located in its magnocellular division) send widespread projections to occipital and temporal visual areas of the primate brain (Amaral, Behnia, & Kelly, 2003). In contrast, parvocellular pathways are thought to

convey fine-grained, chromatic information, sharing limited direct connectivity with the brain's motivational circuits, and thus hypothesized to be less important for influencing sensory responses to emotionally relevant signals (Zeelenberg et al., 2006).

Considerable research has manipulated specific physical dimensions of emotional images (e.g. spatial frequency, color content, or contrast) as a way of exploring the contribution of distinct visual pathways to affective viewing (De Cesarei & Codispoti, 2013). Initial studies with pictures of scenes or faces have suggested that early sensory amplification for emotional stimuli largely depends on the brain's ability to extract coarse information from low spatial frequency and luminance channels (Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005). However, other studies examining late neuroelectrical correlates of higher-order emotion processing have failed to find evidence that emotional modulation of cortical activity is preferentially affected by low spatial frequencies (Bradley, Hamby, Low, & Lang, 2007; De Cesarei & Codispoti, 2011). In contrast, selective engagement of chromatic mechanisms, which under ideal conditions (e.g., using high spatial frequencies) may bias the processing towards parvocellular pathways, has been less consistently implicated in emotional facilitation of sensory processing (e.g., Pourtois et al., 2005). Several authors have interpreted this finding to reflect the more limited connectivity of the parvocellular pathway with structures such as the amygdaloid complex, which is sensitive to emotional content and involved in modulating up- and downstream processing (Bocanegra & Zeelenberg, 2009). It is notable however that color manipulations in complex scenes consistently have resulted in no or very limited impact on indices of higher-order cortical processing (Bradley et al., 2003). Thus, an important methodological factor that may influence the extent to which physical parameters of emotional visual stimuli impact upon cortical response amplification concerns the stage of the visual processing hierarchy that is being assayed.

A reliable method for non-invasively isolating population-level neuronal responses at low levels of the traditional visual hierarchy is the steady-state visual evoked potential (ssVEP) technique. Steady-state evoked potentials are large-scale cortical electric fields that are entrained to the frequency of an external pacemaker (Regan, 1989; Spekreijse, Dagnelie, Maier, & Regan, 1985). In humans, generators of the ssVEP have been localized to the extended visual cortex (Müller, Teder, & Hillyard, 1997), with strong contributions from V1, but also higher-order cortices (Di Russo et al., 2007). There is evidence that fundamental ssVEP responses evoked by modulation frequencies in excess of ~15 Hz localize primarily within early visual cortex (Wieser & Keil, 2011). At such frequencies, new volleys of excitation arrive at rates exceeding ~66 milliseconds and this is likely insufficient time for the signal to propagate extensively outside of the lower tiers of the visual cortex.

Using ssVEPs, sensory circuit function was isolated in a recent study in which visual (grating) stimuli acquired emotional relevance through classical fear conditioning (Keil, Miskovic, Gray, & Martinovic, 2013). These stimuli were manipulated to predominantly challenge either luminance or chromatic channels, by (a) rapidly phase-reversing two spatially anti-phasic grayscale gratings (the luminance stimulus) or (b) alternating isoluminant red and green versions of the gratings at the same rapid temporal rate (14 or 15

Hz). Additionally, the gratings were filtered to predominantly contain either low or high spatial frequencies. These manipulations introduced a degree of bias towards magnocellular or parvocellular pathways. Robust amplification of ssVEPs following aversive conditioning was observed only for the luminance but not for the chromatic visual cues. This difference was interpreted to reflect differential connectivity profiles between lower-tier visual cortex and structures sensitive to the learned motivational relevance of stimuli, for achromatic, blurry information, versus chromatic, spatially fine-grained information.

In contrast to the ssVEP, the effects of low-level image properties seem to have a relatively negligible effect on late evoked potentials which reflect contributions from neural generators that are not confined to circumscribed, lower-tier visual cortex. For example, the late positive potential (LPP), a centro-parietal evoked component that is most consistently modulated by hedonic content (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Schupp et al., 2000), appears to be immune to the image's physical properties, provided that individuals are able to categorize the stimuli (De Cesare & Codispoti, 2011, 2013). Although the neurobiological mechanisms that give rise to the LPP remain to be explored more extensively, the existing evidence suggests that this component is generated and sustained by a very broadly distributed network of cortical and subcortical structures including many that lie outside of traditional sensory areas (Liu, Huang, McGinnis-Deweese, Keil, & Ding, 2012; Sabatinelli, Keil, Frank, & Lang, 2013; Sabatinelli, Lang, Keil, & Bradley, 2007). A recent study that simultaneously measured the ssVEP and LPP in the context of emotional picture viewing found that these two evoked potentials provided non-redundant information about emotional influences on visual attention (Hajcak, Macnamara, Foti, Ferri, & Keil, 2013). Such dissociations are to be expected to the extent that at fast temporal frequencies the ssVEP largely reflects circumscribed activity of neuronal populations low (early) in the visual hierarchy and the LPP indexes the integration of multiple neural systems mediating the cerebral response to an emotional stimulus.

The present research addressed two specific experimental questions. First, is sensory amplification by emotionally engaging content in lower-tier visual cortex specific to low-spatial frequency luminant stimuli as opposed to high-frequency chromatic stimuli, paralleling earlier work with conditioned Gabor gratings? Second, do late indices of emotion processing in widespread cortical regions also show differential sensitivity to emotional content conveyed via chromatic versus luminance channels? To address these questions, participants viewed flickering natural scenes that varied in hedonic valence and arousal while high-density brain electrical activity was recorded. Crucially, the images were physically manipulated to contain either (i) luminance information at coarse spatial frequencies (i.e., fuzzy grayscale images) or (ii) chromatic information at high spatial resolution (red/green sharpened images). Analyses were focused on two distinct features of the evoked brain electrical response, the ssVEP and LPP, to quantify lower-tier and higher-order aspects of cortical processing respectively.

If luminance-driven processes in early visual cortex possess a larger number or denser bidirectional connections with brain circuits that are sensitive to affective content, greater ssVEP enhancement should be observed for achromatic (grayscale) emotionally arousing pictures which engage these luminance channels, compared to stimuli that engage chromatic

(here: reddish/greenish hue) channels. On the other hand, since the LPP has been demonstrated to reflect a more general response with contributions from an aggregate conglomerate of brain regions, the amplitude of this cortical process should be relatively unaffected by low-level physical manipulations of emotional images.

Method

Participants

Fifteen (9 female; mean age 19.1 years) students from University of Florida undergraduate psychology courses participated for course credit¹. All participants reported normal or corrected to normal vision and a negative personal and family history of seizure disorder and photic epilepsy. Written informed consent was obtained prior to the study. Procedures were in accordance with the Declaration of Helsinki, and the study was approved by the Institutional Review Board of the University of Florida.

Stimuli and Design

Participants viewed 75 pictures selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005) based on normative ratings of hedonic valence and emotional arousal to be pleasant, neutral, or unpleasant in content². IAPS numbers are given in the appendix.

To engage luminance (see Figure 1C) or chromatic (see Figure 1D) channels, IAPS pictures were manipulated using functions implemented in the Matlab (Mathworks, USA) Image Processing Toolbox. First, a blurred grayscale version of each picture was created and filtered with a 2-dimensional low-pass average filter, set to increasingly attenuate spatial frequencies above 1 cycles per degree (cpd) using a square average kernel of 12 pixels. As illustrated in the spatial spectrum in Figure 1B, this leads to substantial reduction of contrast energy at frequencies above 3–4 cpd, which allows accurate identification of picture content (De Cesare & Codispoti, 2011), while still primarily yielding low spatial frequency signals (Loftus & Harley, 2005). A negative image was then created from this picture by subtracting the mean gray value, multiplying by -1 and then rescaling to the original gray value range. Manipulations of image spatial frequency were independent from the presentation of visual stimuli at a fixed temporal frequency, described below.

Pairs (a reddish and a greenish exemplar) of chromatic stimuli were created in a second step. Each original picture was submitted to a 2-D Laplacian of Gaussians high-pass filter kernel of size 5 by 5 pixels, with a standard deviation of .2, attenuating low frequencies. Then, pixels with the top 10% red and green values, respectively, were identified and these values

¹A concern with our female-dominant sample might be related to the menstrual variability in low- and mid-level perception as recently discussed in the literature (Eisner, Burke, & Toomey, 2004). However, this should have diminished rather than enhanced the pattern of findings being reported below.

²IAPS numbers were as follows: pleasant

(2071,4574,4071,2152,4575,8161,2314,8470,8260,7325,8032,8021,4597,8380,4626,4599,4619,4612,2530,5831,4141,4006,4085,4604,4142), neutral (2500,2302,2374,2358,2320,2200,2512,2101,2107,2190,4505,2394,2104,2102,2489,2359,2488,8312,2411,2377,2487,2485,2034,2850,2026), unpleasant (3266,2457,6200,3168,6570,9326,6314,9325,6010,9582,9421,3220,9584,6242,9440,3350,6220,6560,6313,9413,6315,6312,6213,6821,9433).

were set to 100% red in one version of the picture and to green of varying levels in the other, depending on the red-green isoluminance level determined by flicker photometry in a given observer (see below). All remaining pixels were set to 0, thus appearing in black when shown on the screen. This procedure (i.e., selecting the top 10 % from the distribution of red and green values for inclusion and setting the remaining pixels to zero) was demonstrated to maximize recognizability and similarity of affective ratings with the original versions in a series of small pilot studies. Examples of both picture types are provided in Figure 1, along with the normalized spatial frequency spectrum for each picture category.

Steady-state VEPs were elicited by pattern reversal implemented by alternating between the two versions of the grayscale and the chromatic pictures, respectively. Presentation alternated between a given picture and its counterpart at a rate of 17.5 Hz (8.75 Hz for a full cycle of both pictures) on a CRT monitor set to a 70 Hz refresh rate. This procedure produced pattern-reversal ssVEPs at the first harmonic of the full cycle frequency, i.e., at 17.5 Hz. This same frequency was also used in a session preceding the experiment proper, in which isoluminance was determined by means of flicker photometry: using monochromatic green circles embedded in a monochromatic red field, observers adjusted the intensity of the green gun such that no flicker was perceived when alternating between red and green. Color trivalues were stored and used for a given participant.

Procedure and design

The experiment consisted of 150 trials in total: Each of the 75 picture pairs was shown twice, once in grayscale and once in a chromatic (red/green) version. There were 25 pictures within each of the unpleasant, neutral and pleasant categories. Stimulus presentation was randomized. All trials had a duration of 52 full cycles at 8.75 Hz, resulting in a trial length of 2971 ms during which the pattern reversing pictures were viewed on a CRT monitor at 100 cm distance, spanning a horizontal visual angle of 10° and a vertical angle of 7°.

Participants were seated in a sound-attenuated, electrically shielded chamber with very dim lighting. An IBM-compatible computer was used for stimulus presentation, running Matlab in conjunction with functions from the Psychtoolbox stimulus control suite (Brainard, 1997). The EEG sensor net was applied and participants were instructed to fixate, avoid eye movements and blinks, and view the pictures attentively. Following the EEG recording the sensor net was removed and participants rated 8 exemplars of each of the six representative image categories (corresponding to three categories of picture content depicted as grayscale or with color) using the Self-Assessment Manikin (SAM), a nine-level pictorial scale of affective evaluation that involves separate measures of hedonic valence and emotional arousal (Lang, 1980). This approach aimed to reduce the duration of the session and thereby heighten compliance while reducing fatigue.

EEG Recording and Data Collection

The electroencephalogram (EEG) was continuously recorded from 129 electrodes by means of an Electrical Geodesics (EGI) high-density sensor net, using Cz as the recording reference and keeping impedances below 60 kΩ. This sensor net provides extensive coverage over occipital regions, including dense coverage around and inferior to the

occipital pole, which is helpful for capturing activity in retinotopic areas of the visual system (Foxe & Simpson, 2002). Data were sampled at a rate of 250 Hz with an online bandpass filter with 3dB points set at 0.1 Hz (high-pass) and 100 Hz (low-pass). Additional data processing occurred offline by means of *EMEGS* toolbox for Matlab (Peyk, DeCesarei, & Junghöfer, 2011). Data were filtered using a 25 Hz low-pass (cut-off at 3 dB point; 45 dB/octave, 10th order Butterworth) and a 1 Hz high-pass (cut-off at 3 dB point; 18 dB/octave, 4th order Butterworth). Filter order for the low-pass was chosen so as to preserve maximal power at the driving frequency of 17.5 Hz. Relative to stimulus onset, epochs were extracted from the raw EEG that included 1000 ms pre- and 4000 ms post-onset for all conditions. Then, statistical parameters were used to find and remove artifact-contaminated channels and trials (Junghöfer, Elbert, Tucker, & Rockstroh, 2000): the original recording reference (Cz) was first used to detect recording artifacts, and then the data was average referenced to detect global artifacts. Subsequently, bad sensors within individual trials were identified and interpolated based on rejection criteria for amplitude, standard deviation, and gradient. Trials in which more than 20 out of the 129 sensors were outliers were rejected from further analysis. After artifact rejection, an average of 19.1 trials per condition (range: 14 to 25) were retained for analysis.

Data reduction and statistical analysis

Artifact free segments were averaged in the time domain, following the factorial design of the present study. These averages were then transformed into the time-frequency domain using complex demodulation analysis (Regan, 1989). This procedure used sine and cosine functions at the stimulation frequency, multiplied with the empirical signal. The products were then low-pass filtered (3rd order 1-Hz low-pass Butterworth filter, 12 dB/Octave) and their absolute value was obtained as the modulus of the sine and cosine products (Müller, Keil, Kissler, & Gruber, 2001). This resulted in time-varying amplitude (in microVolts) of the signal at the stimulation frequency, with a time resolution (full width at half maximum of the impulse response) of 531 ms. The mean of the segment between -800 and -200 ms prior to picture onset was subtracted as baseline.

For statistical analyses, the resulting time varying amplitude estimates were averaged across seven occipital sensors, including the EGI sensor corresponding to Oz in the 10/20 International System and its neighbors (sensors 70, 71, 74, 75, 76, 82 and 83, see Figure 2 inset for illustration purposes). The resulting ssVEP amplitude values were entered as the dependent variables into an omnibus repeated measures ANOVA with the within-subject factors of VISUAL CHANNEL (2: Luminance/Chromatic), PICTURE CONTENT (3: pleasant/neutral/unpleasant) and TIME SEGMENT (7: 0–500ms to 2500–3000ms). Similar to previous studies, the LPP was scored as the mean amplitude within a centro-parietal cluster of sensors (averaged across EGI sensors 54, 55 and 79; see Figure 3) occurring between 500 to 900 ms. The hedonic valence and arousal scales of the SAM were each submitted to a repeated-measures ANOVA analysis with two within-factors (PICTURE CONTENT and VISUAL CHANNEL).

To further explore the extent to which the ssVEP and LPP measures provided complimentary versus redundant information, we computed pleasant vs. neutral and

unpleasant vs. neutral residual scores, separately for the luminance and chromatic images, and examined Spearman rank-order correlation coefficients between the two neural indices. Since these analyses were considered exploratory, no corrections for false-positives were applied and results are used descriptively, to guide future research.

An alpha level of 0.05 (two-tailed) was employed for all other analyses. Greenhouse-Geisser adjusted degrees of freedom and p -values are reported where the assumption of sphericity was violated as determined by Mauchly's test.

Results

ssVEPs

A main effect of TIME SEGMENT [$F(1.91,26.85) = 6.38, p < 0.01, \eta_p^2 = 0.31$] reflected the initial rise, steady-state period, and final decrease of the oscillatory response, confirmed by a quadratic contrast ($p < 0.01, \eta_p^2 = 0.31$). A main effect of VISUAL CHANNEL [$F(1,14) = 10.28, p < 0.01, \eta_p^2 = 0.42$] was also observed, such that luminance stimuli elicited larger ($M = 0.31, S.E.M. = 0.06$) ssVEP amplitudes overall compared to the chromatic stimuli ($M = 0.14, S.E.M. = 0.03$). More importantly, there was a significant VISUAL CHANNEL x PICTURE CONTENT [$F(2,28) = 3.37, p < 0.05, \eta_p^2 = 0.19$] interaction. To follow up, repeated measures ANOVAs were conducted separately for each of the visual channels. The visual impression conveyed by Figure 2 was statistically supported: emotionally engaging pictures elicited heightened ssVEP amplitude compared to neutral pictures [$F(2,28) = 3.77, p < 0.05, \eta_p^2 = 0.21; F_{quad} = 8.68, p = 0.01, \eta_p^2 = 0.38$] only for the luminance images. There was no effect of PICTURE CONTENT on ssVEP amplitude when viewing chromatic images ($F < 1, p > 0.7$).

In the luminance condition, pleasant images elicited a stronger ssVEP (Pleasant $M = 0.35, SEM = 0.07$ vs. Neutral $M = 0.27, SEM = 0.06$) than neutral images [$F(1,14) = 10.20, p < 0.01, \eta_p^2 = 0.42$] but unpleasant images ($M = 0.32, SEM = 0.06$) did not [$F(1,14) = 2.66, p = 0.13, \eta_p^2 = 0.16$]. On the other hand, ssVEP amplitude was not different when pleasant and unpleasant picture contents were directly compared ($F < 1$).

LPP

As illustrated in Figure 3, picture content affected LPP amplitude [$F(2,28) = 7.52, p < 0.01, \eta_p^2 = 0.35$], prompting a significant quadratic trend [$F(1,14) = 14.47, p < 0.01, \eta_p^2 = 0.51$]. Compared to neutral pictures, both pleasant [$F(1,14) = 10.60, p < 0.01, \eta_p^2 = 0.43$] and unpleasant pictures [$F(1,14) = 11.53, p < 0.01, \eta_p^2 = 0.45$] elicited a larger LPP. There was no difference in LPP magnitude elicited by pleasant compared to unpleasant images ($F < 1$).

Effects of visual channel were not significant. A trend for an interaction between PICTURE CONTENT and VISUAL CHANNEL [$F(2,28) = 3.20, p = 0.06$] emerged, but, contrast analyses indicated that the quadratic contrast for hedonic valence was significant in both the luminance [$F_{quad} = 6.61, p = 0.02, \eta_p^2 = 0.32$] and chromatic [$F_{quad} = 13.71, p = 0.002, \eta_p^2 = 0.50$] channel conditions, consistent with the visual impression conveyed by the condition-specific bar plots depicted in the Figure 3 inset.

Correlation analyses

Correlation analyses yielded no significant correlations between the ssVEP and LPP residual scores (r range: -0.49 to 0.38 , $ps = 0.06$ to 0.99). The relatively low p value of 0.06 ($r = -0.49$, $p = 0.06$) emerged for the correlation between the chromatic unpleasant LPP and ssVEP residuals. However, this effect was driven by a single outlier, as removal of this participant eliminated the trend ($p > 0.12$).

Ratings

A main effect of PICTURE CONTENT [$F(2,28) = 148.63$, $p < 0.0001$, $\eta_p^2 = 0.91$] was qualified by an interaction between PICTURE CONTENT and VISUAL CHANNEL [$F(2,28) = 5.70$, $p < 0.01$, $\eta_p^2 = 0.29$]. Ratings varied linearly as a function PICTURE CONTENT for both luminance [$F(1,14) = 193.18$, $p < 0.001$, $\eta_p^2 = 0.93$] and chromatic stimuli [$F(1,14) = 247.65$, $p < 0.001$, $\eta_p^2 = 0.95$, with pleasant luminance stimuli rated more pleasant than neutral [$t(14) = 7.54$, $p < 0.0001$] or unpleasant [$t(14) = 13.90$, $p < 0.0001$] exemplars. Unpleasant luminance stimuli were rated less pleasant than neutral images [$t(14) = 10.15$, $p < 0.001$]. Similar patterns were observed for the chromatic stimuli (all paired contrast $ps < 0.001$). The interaction indicated that neutral luminance stimuli were rated as somewhat more pleasant [$t(14) = 3.99$, $p < 0.001$] than chromatic stimuli, and aversive luminance stimuli were rated as somewhat more aversive compared to chromatic versions [$t(14) = 2.75$, $p < 0.05$].

In terms of arousal, there was an overall quadratic effect of PICTURE CONTENT, [$F(1,14) = 175.48$, $p < 0.0001$, $\eta_p^2 = 0.93$]. As expected, both pleasant [$F(1,14) = 100.59$, $p < 0.0001$, $\eta_p^2 = 0.88$] and unpleasant [$F(1,14) = 173.13$, $p < 0.0001$, $\eta_p^2 = 0.93$] pictures were rated as more arousing than neutral pictures. Unpleasant pictures were also rated slightly more arousing [$F(1,14) = 18.10$, $p = 0.001$, $\eta_p^2 = 0.56$] than pleasant pictures. Neither the main effect of VISUAL CHANNEL nor the interaction was significant ($F_s < 1$, $ps > 0.83$).

Discussion

This study used large-scale evoked neural responses to explore the distinctive contributions of luminance and chromatic biased channels to the processing of emotional images at different stages of the cortical processing stream. Based on our results, only luminance-defined stimuli led to amplification of ssVEP activity when viewing emotionally engaging picture content, whereas viewing chromatic stimuli did not prompt differential modulation as a function of hedonic content. Importantly, the LPP, an electrophysiological component that reflects contributions from multiple neural processes related to higher stages of scene analysis resulted in heightened response amplitudes for emotionally arousing content, independent of variation in the physical parameters of the images, confirming affective engagement.

These findings converge with data from a recent aversive conditioning experiment (Keil et al., 2013), in which flicker-evoked visual amplification for a conditioned aversive stimulus was observed only for a grayscale stimulus biased towards engaging the luminance channel. The present study extends these findings by further demonstrating that a similar, channel-

specific constraint operates for hedonic content when viewing complex natural scenes that are emotionally arousing. Evidence derived from the LPP amplitudes as well as from the affective ratings of the images, provided by the participants, suggests that the failure to observe ssVEP effects for the chromatic (red/green) stimuli is not explained by inadequate processing of the picture content.

There is considerable controversy among vision researchers regarding the technical possibility of cleanly separating the magno- and parvocellular pathways using non-invasive methods (Lee, 2011). Nevertheless, we have previously demonstrated using ssVEPs that emotional processing in lower-tier visual cortex is differentially affected by the physical parameters of incoming stimuli (Keil et al., 2013). The finding that ssVEP response augmentation for emotional content is specifically driven by low spatial frequency, luminance stimuli may have its basis in structural constraints that limit the capacity of pericalcarine cortex to establish flexible links with circuitry sensitive to emotional content. One example of a structural constraint is provided by fluorescent imaging of amygdalofugal tracts in macaque monkeys (Amaral et al., 2003), in which projections from the basal nucleus of the amygdala to primary and secondary visual cortex originate from large (magno-) cells. Modulatory input from core motivational circuits (including the amygdaloid complex) to early visual cortex is widely held to be the functional basis for amplified responses to cues with high biological significance (Zald, 2003), but see (Edmiston et al., 2013). Since fast-frequency ssVEPs at the first harmonic emanate primarily from neuronal populations in V1 and its close vicinity (Di Russo et al., 2007; Wieser & Keil, 2011), channel-specific amplification might be reflecting, at the neuronal population level, the underlying connectivity profile. Also consistent with this hypothesis is the observation that studies reporting a central role for spatially coarse images in eliciting strong emotional responses have almost all focused on electrophysiological components with main contributions from primary or secondary visual cortex (e.g., Alorda, Serrano-Pedraza, Campos-Bueno, Sierra-Vazquez, & Montoya, 2007; Carretie, Hinojosa, Lopez-Martin, & Tapia, 2007; Pourtois et al., 2005).

At higher levels of stimulus analysis, of course, there are contributions from a greater variety of brain regions, with considerable interlocking of cortico-subcortical and cortico-cortical connections. For example, projections from the parvocellular regions of the basal nucleus of the amygdala extend to ventral structures encompassing the temporo-parieto-occipital junctions (Amaral et al., 2003). One might therefore expect less sensitivity to variation in the physical composition of emotionally arousing pictures. In this respect, the insensitivity of the LPP to the specific visual channel through which the emotional image is conveyed replicates previous studies finding that this ERP component is relatively immune to low level physical characteristics such as physical composition (Bradley et al., 2007, De Cesarei & Codispoti, 2011) and stimulus size -- a proxy for viewing distance (De Cesarei & Codispoti, 2006).

As in previous work (Hajcak et al., 2013), emotion-related amplification of ssVEP and LPP responses varied independently, indicative of the fact that they represent measures of different neurophysiological processes. Functional brain activity reflected in the LPP response most likely reflects processes that have traditionally been defined as “post-

perceptual”, operating on more abstract, semantic representations of stimulus content (Cuthbert et al., 2000). Our findings reinforce the interpretation that ssVEP amplitude fluctuations elicited by fast-flickering stimuli mostly reflect synchronized volleys of neural excitation relatively early in the feed-forward sweep, while the latent computational processes indexed by the LPP represent the outcome of neural interactions between an extensive network of brain regions.

One critical question regarding the current results is whether the absence of ssVEP modulation in the chromatic condition is due to floor effects when using isoluminant stimuli delivered at fast reversal rates (Robson & Parry, 2008), which receives some support from the fact that ssVEP amplitude was smaller for isoluminant chromatic modulation compared with viewing luminance-modulated grayscale pictures. Explicit testing of the presence of a reliable ssVEP signal by means of the circular T-square statistic however suggests that reliable and regular entrainment occurred in the chromatic picture condition for each participant. This finding is in line with the visual inspection of the clear amplitude increase at stimulus onset, quantified by the complex demodulation analysis. The waveform suggests a 4-fold increase over the baseline noise, considered a satisfactory signal-to-noise ratio in human electrophysiology. Although a clear chromatic ssVEP signal was present, the means in Figure 2 do not suggest that modulation of the ssVEP signal occurred in the same direction as for the luminance stimuli, contradicting the interpretation that a weak signal prevented a demonstration of affect-driven modulation of the chromatic ssVEP.

In conclusion, the physical composition of an emotional picture influenced the extent of ssVEP amplification in human visual cortex. Emotional content conveyed via luminance channels appears to more strongly engage mechanisms that amplify the population activity of visual neurons in lower-tier sensory cortex. Facilitation of responses in early visual cortex potentially reflects important structural constraints that are less potent at subsequent stages of cortical processing.

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Highlights for Review

- Manipulated low-level physical parameters of natural scenes to emphasize the relative contributions of luminance based versus chromatic visual channels to emotional perception.
- Quantified evoked electrocortical responses reflecting the contribution of neuronal populations at low tiers of the visual cortex as well as those reflecting more globally distributed cerebral sources.
- Steady-state visual evoked potential enhancement for emotional content was present only for low spatial frequency, grayscale stimuli, and not for high spatial frequency, red/green stimuli.
- Late positive potential was always immune to manipulation of scene physical properties.

Figure 1.

Illustration of the transformation applied to original color pictures from the IAPS. A non-IAPS picture (not used in the study) is shown in panel A in its original form. Panel B shows the spectrum of the original (normalized to its maximum contrast energy, obtained with the FFT2 function in Matlab) as well as the low-pass filtered (blurry) grayscale version (C) and the red-green high-pass filtered version (D).

Figure 2.

Time course of ssVEP spectral amplitude revealed by a complex demodulation analysis averaged across all subjects for a subset of posterior electrodes (top middle panel), sorted by hedonic valence content and shown separately for the luminance (left) and chromatic (right) viewing conditions.

Figure 3.

Grand mean ERP waveforms averaged by hedonic valence (pleasant, neutral, unpleasant pictures) over three centro-parietal electrodes (right middle panel). Note the larger LPP amplitudes for both pleasant (dashed) and unpleasant (black) pictures when compared to neutral (gray), visible for both luminance and chromatic stimuli (top right inset).