



# 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.

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## 1. Introduction

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 environments (Lang & Bradley, 2010). Free viewing images that depict emotionally arousing content (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

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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 (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 networks, 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 re-entrant 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, Behniea, & 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 toward 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 ms 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 toward 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 Cesarei & 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

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