



Neuronal generator patterns at scalp elicited by lateralized aversive pictures reveal consecutive stages of motivated attention



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ABSTRACT

Event-related potential (ERP) studies have provided evidence for an allocation of attentional resources to enhance perceptual processing of motivationally salient stimuli. Emotional modulation affects several consecutive components associated with stages of affective-cognitive processing, beginning as early as 100–200 ms after stimulus onset. In agreement with the notion that the right parietotemporal region is critically involved during the perception of arousing affective stimuli, some ERP studies have reported asymmetric emotional ERP effects. However, it is difficult to separate emotional from non-emotional effects because differences in stimulus content unrelated to affective salience or task demands may also be associated with lateralized function or promote cognitive processing. Other concerns pertain to the operational definition and statistical independence of ERP component measures, their dependence on an EEG reference, and spatial smearing due to volume conduction, all of which impede the identification of distinct scalp activation patterns associated with affective processing. Building on prior research using a visual half-field paradigm with highly controlled emotional stimuli (pictures of cosmetic surgery patients showing disordered [negative] or healed [neutral] facial areas before or after treatment), 72-channel ERPs recorded from 152 individuals (ages 13–68 years; 81 female) were transformed into reference-free current source density (CSD) waveforms and submitted to temporal principal components analysis (PCA) to identify their underlying neuronal generator patterns. Using both nonparametric randomization tests and repeated measures ANOVA, robust effects of emotional content were found over parietooccipital regions for CSD factors corresponding to N2 sink (212 ms peak latency), P3 source (385 ms) and a late centroparietal source (630 ms), all indicative of greater positivity for negative than neutral stimuli. For the N2 sink, emotional effects were right-lateralized and modulated by hemifield, with larger amplitude and asymmetry for left hemifield (right hemisphere) presentations. For all three factors, more positive amplitudes at parietooccipital sites were associated with increased ratings of negative valence and greater arousal. Distributed inverse solutions of the CSD-PCA-based emotional effects implicated a sequence of maximal activations in right occipitotemporal cortex, bilateral posterior cingulate cortex, and bilateral inferior temporal cortex. These findings are consistent with hierarchical activations of the ventral visual pathway reflecting subsequent processing stages in response to motivationally salient stimuli.

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Introduction

The detection of stimulus significance is a critical mechanism for survival, presumably constituted by two basic motivational systems mediating appetitive and defensive behavior (e.g., Bradley, 2009; Lang et al., 1998a). The necessary operations involve interactions between affective

and cognitive processing systems of the brain (e.g., Pessoa, 2008), which reach conscious awareness in the hierarchy of information processing when the products of affective and cognitive computations enter into working memory (e.g., LeDoux, 1989). Electrophysiological measures of ongoing brain activity, particularly event-related potentials (ERPs), are ideally suited to characterize consecutive stages of affective processing with millisecond temporal resolution, and ERP research with human populations has made considerable progress in this regard over the last two decades (e.g., see reviews by Hajcak et al., 2012; Olofsson et al., 2008). The most consistent finding has been an increased positivity to

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emotional (pleasant or unpleasant) compared to neutral pictures, often termed the late positive potential (LPP), which emerges around 200–300 ms after stimulus onset and affects several subcomponents of the late positive complex, including P3 and slow wave (e.g., Johnston et al., 1986). A broad topographical LPP maximum is typically observed over mid-parietal and centro-parietal scalp locations, with its amplitude closely covarying with the perceived arousal properties of a given stimulus (e.g., Cuthbert et al., 2000; Schupp et al., 2000), suggesting an increased allocation of attentional resources to stimuli that intrinsically engage motivational brain circuits (e.g., Bradley, 2009). Valence properties have less consistently been linked to the LPP; however, pictures of negative rather than positive affect tend to elicit a greater LPP (“negativity bias”; e.g., Ito et al., 1998b). As this may be due to their higher intrinsic motivational value, a systematic control of arousal and valence stimulus properties is an essential requirement for an interpretation of these findings (Olofsson et al., 2008). For example, no negativity bias is observed when unpleasant and pleasant pictures are matched for motivational saliency (Hajcak et al., 2012).

Affective stimulus significance has also been found to modulate earlier ERP components, including P1 (e.g., Pizzagalli et al., 1999; Smith et al., 2003), N1 (e.g., Keil et al., 2002), P2 (e.g., Delplanque et al., 2004) and N2 (e.g., Junghöfer et al., 2001). An ERP difference component, termed early posterior negativity (EPN; Schupp et al., 2003a, 2003b), revealing more negative-going waveforms for emotional than neutral stimuli at about 200–300 ms over bilateral occipital-temporal regions, has attracted considerable research over the last decade (e.g., Foti et al., 2009; Mavratsakis et al., 2016; Thom et al., 2014; Wiens et al., 2011). However, findings for these earlier ERP components that precede the LPP have been less consistent and notably varied with arousal and valence dimensions (see review by Olofsson et al., 2008), which may be in no small part attributable to differences in methodology, including—but not limited to—study paradigm (e.g., passive viewing, stimulus classification, target detection), stimulus characteristics (e.g., faces, scenes, words), EEG montage (e.g., ranging from selected midline sites to 129 sites or more) and reference (e.g., common average, linked mastoids), ERP component definition and measurement (e.g., peak amplitude, integrated time windows, temporal/spatial PCA), signal-to-noise ratio, and sample size. In contrast, emotional LPP effects, which are omnipresent in space (i.e., broad central-parietal topography) and time (i.e., spanning several hundred milliseconds or longer) and withstand habituation (e.g., Codispoti et al., 2007), are evidently too robust to be substantially affected by any differences in methodology.

Most affective ERP studies using visual stimuli have taken advantage of the International Affective Picture System (IAPS; Bradley and Lang, 2007; Lang et al., 2005), which comprises a large and diverse pool of affect-laden color photographs intended to evoke affective reactions, along with normative ratings of pleasure and arousal. While this allows the matching of valence categories for arousal (e.g., by equating the means of pleasant and unpleasant pictures selected for the experiment), other stimulus features, such as luminance, contrast, color, composition, content, complexity or spatial frequency, are often uncontrolled and constitute a possible confound (e.g., Delplanque et al., 2007; Wiens et al., 2011). Differences in physical stimulus properties will profoundly impact on early ERP components (P1, N1), whereas differences in stimulus content (e.g., animate or object) will likely impact on cognitive ERP components (N2, P3), all of which make it harder to separate genuine emotional from cognitive ERP effects. The problem is augmented when the study objectives include hemispheric differences of emotional processing (Kayser et al., 1997). There is ample clinical and experimental evidence indicating a differential involvement of the two hemispheres during affective states and affective processing (e.g., for reviews see Campbell, 1982; Davidson, 1995; Demaree et al., 2005; Gainotti, 1989; Heller, 1993), and observations for non-human primates suggest that emotional asymmetries may even predate human evolution (Lindell, 2013). Liotti and Tucker (1995) proposed that hemispheric

asymmetries in corticolimbic interaction arose from the evolution of functional differences involving dorsal (spatial) and ventral (object) processing streams (e.g., Ungerleider and Haxby, 1994), resulting in a lateralized representation and regulation of both motivational and cognitive domains across multiple levels of the brain hierarchy. Notwithstanding the intricate relationship between emotional and cognitive processes, the mere co-existence of hemispheric differences that should be primarily regarded as cognitive functions, most prominently a left-lateralization of language-related processes and a right hemispheric advantage for processing visuospatial stimuli, particularly of faces (e.g., Gainotti, 2015; Springer and Deutsch, 1989), presents a considerable challenge for the experimental separation of emotional from non-emotional lateralized ERP effects.

In three ERP studies (Kayser et al., 1997, 2000, 2001), we have directly addressed this challenge by employing a set of highly controlled stimuli, which largely isolate emotional content (negative valence, high arousal) from other confounding variables. Affective stimuli were intentionally limited to negative valence as this choice constituted the least common denominator of competing models of emotional lateralization (i.e., valence or approach/withdrawal vs. right hemisphere or dominance hypothesis): a right hemispheric advantage for the perception of negative versus neutral stimuli. This was further reinforced by the fact that negative stimuli were more arousing than their neutral counterparts, because right parietal regions are presumed to also mediate autonomic arousal processes (e.g., Heller, 1993). Furthermore, we used a passive viewing hemifield paradigm with separate stimulus presentations to the right or left visual field to directly probe lateralized hemispheric activity (e.g., McKeever, 1986; Young, 1982). For three different samples of healthy adults, we found enhanced P3 and slow wave amplitudes for negative compared to neutral stimuli. Hemispheric asymmetries in emotional processing were restricted to ERP components of the N2–P3 complex, with maximal effects over the right parietotemporal region. The right temporoparietal junction has been recognized as a key cortical region for detecting affective stimulus significance and modulating associated autonomic arousal (e.g., Caltagirone et al., 1989; Gainotti, 1987; Heller, 1993; Tranel and Damasio, 1994) and has since been linked to a brain network involving cortical (anterior insula, anterior cingulate cortex [ACC]) and subcortical (amygdala, striatum) structures for detecting emotional and reward saliency (Corbetta and Shulman, 2002; Lutz et al., 2015). Similar right-greater-than-left asymmetries of emotional content for ERP components preceding LPP have been reported by others (e.g., Junghöfer et al., 2001; Keil et al., 2001, 2002), but this has not been a consistent finding or central research objective for the majority of ERP studies using IAPS pictures (Olofsson et al., 2008).

One crucial feature of our affective ERP studies has been the systematic use of temporal principal components analysis (PCA) as a comprehensive approach to obtain unbiased, data-driven measures (e.g., Donchin and Heffley, 1978; Kayser and Tenke, 2003), which allowed an improved characterization of LPP subcomponents and earlier ERPs related to affective picture responsivity. Notwithstanding the recognized merits of multivariate data decomposition approaches for affective ERP research (e.g., Delplanque et al., 2006; Olofsson et al., 2008; Pourtois et al., 2008), these techniques do not resolve the interpretational ambiguity of ERP signals caused by the EEG reference (e.g., Junghöfer et al., 2006a; Kayser and Tenke, 2010) or their spatial smearing due to volume conduction (e.g., Tenke and Kayser, 2012). However, these limitations can be conveniently overcome by incorporating a surface Laplacian, or current source density (CSD; e.g., Perrin et al., 1989), transformation of surface potentials in the data processing pipeline, which renders a unique, reference-free representation of radial current flow (sinks and sources) underlying the scalp-recorded EEG (e.g., Carvalhaes and de Barros, 2015; Nunez and Srinivasan, 2006; Tenke and Kayser, 2012). Compared to ERPs, CSDs provide higher spatial and temporal resolution (i.e., a more distinct time course; Burle et al., 2015). Unlike more complex inverse source localization techniques (e.g., Michel et al., 2004), which are likewise reference-independent, CSDs do not require any additional assumptions

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