

## REVIEW

# Alpha-band oscillations and emotion: A review of studies on picture perception

Maurizio Codispoti<sup>1</sup>  | Andrea De Cesare<sup>1</sup>  | Vera Ferrari<sup>2</sup> 

<sup>1</sup>Department of Psychology, University of Bologna, Bologna, Italy

<sup>2</sup>Department of Medicine and Surgery, University of Parma, Parma, Italy

## Correspondence

Maurizio Codispoti, Department of Psychology, Alma Mater Studiorum – University of Bologna, Viale Berti Pichat 5, Bologna 40127, Italy.  
Email: [maurizio.codispoti@unibo.it](mailto:maurizio.codispoti@unibo.it)

## Funding information

Fundação Bial, Grant/Award Number: 287/ 2020 awarded to Maurizio Codispoti.

[Correction added on September 29, 2023, after first online publication: “Evidence suggests that this effect involves a desynchronization of the upper alpha band and of the lower beta frequencies (10–20 Hz)” has been changed to “Evidence suggests that this effect is not confined to the alpha band but that it also involves a desynchronization of the lower beta frequencies (8–20 Hz)” in Abstract section].

## Abstract

Although alpha-band activity has long been a focus of psychophysiological research, its modulation by emotional value during picture perception has only recently been studied systematically. Here, we review these studies and report that the most consistent alpha oscillatory pattern indexing emotional processing is an enhanced desynchronization (ERD) over posterior sensors when viewing emotional compared with neutral pictures. This enhanced alpha ERD is not specific to unpleasant picture content, as previously proposed for other measures of affective response, but has also been observed for pleasant stimuli. Evidence suggests that this effect is not confined to the alpha band but that it also involves a desynchronization of the lower beta frequencies (8–20 Hz). The emotional modulation of alpha ERD occurs even after massive stimulus repetition and when emotional cues serve as task-irrelevant distractors, consistent with the hypothesis that evaluative processes are mandatory in emotional picture processing. A similar enhanced ERD has been observed for other significant cues (e.g., conditioned aversive stimuli, or in anticipation of a potential threat), suggesting that it reflects cortical excitability associated with the engagement of the motivational systems.

## KEYWORDS

alpha oscillations, emotion, orienting response, picture processing

## 1 | INTRODUCTION

Emotional stimuli activate cortico-limbic appetitive and defensive systems, which, in turn, elicit an orienting response, and allow for adaptive behavior when opportunities and threats are detected (Bradley, 2009; Codispoti et al., 2016; Gottlieb, 2012; Keil et al., 2008; LeDoux, 2012; Öhman, 1992). Electrocardiac activity during emotional processing has been extensively investigated through electroencephalography (EEG), by averaging time-locked electrical changes and determining the amplitude, timing, and topography of the resulting event-related potentials (ERP).

Cortical responses, recorded through electroencephalography, can be characterized not only in the time domain for the study of ERPs but also in the time-frequency domain in order to study oscillatory activity (Cohen, 2017; Herrmann et al., 2016; Klimesch, 2018). EEG oscillations represent periodic decrements and increases, with different time scales, in the electrical activity of populations of neurons. The past twenty years have seen increased interest in human brain oscillations, and it has been suggested that they are a potentially useful tool with which to understand the neural mechanisms involved in cognitive and emotional processes (Cohen, 2017). However, whereas both early and late ERPs

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Psychophysiology* published by Wiley Periodicals LLC on behalf of Society for Psychophysiological Research.

at occipito-parietal sensor sites are reliably modulated when viewing emotional, compared with neutral, scenes (Codispoti et al., 2007; Keil et al., 2002; Schupp et al., 2006), oscillatory changes during emotional picture processing have been less widely investigated.

Alpha activity is closely associated with many basic aspects of perception (Busch et al., 2009; Mathewson et al., 2009), and in the past 20 years, several studies have examined its functional meaning in visual processing (Jensen & Mazaheri, 2010; Woodman et al., 2022). As pointed out by Klimesch (2012), alpha band activity is the only oscillatory band (with the exception of low beta; see also “fast alpha variant” Mazaheri & Picton, 2005) that responds to a stimulus and/or task demands either with a decrease or an increase in amplitude (relative to a baseline level measured preceding the event), termed event-related desynchronization and synchronization, or ERD and ERS, respectively (Klimesch, 2012). In terms of cortical mechanisms, it has been suggested that alpha increase (ERS) indicates cortical inhibition, while alpha decrease reflects cortical excitability (Klimesch, 2012; Lorincz et al., 2009). According to the “information via desynchronization” account (Michelmann et al., 2022), and building on information theory (Shannon & Weaver, 1949), alpha/beta power decreases are functionally involved in neural computations. Following this account, synchronous (and therefore informationally redundant) neural activity does not provide enough coding space for information representation, while desynchronized neural activity (power decreases in the alpha/beta band) provides the required coding space through locally decoupled neural assemblies (Hanslmayr et al., 2012; Michelmann et al., 2022). Moreover, it has also been suggested that power decreases in the alpha/beta band reduce the background noise in the cortex, allowing for key signals to be more clearly communicated (Michelmann et al., 2022; Mitchell et al., 2009).

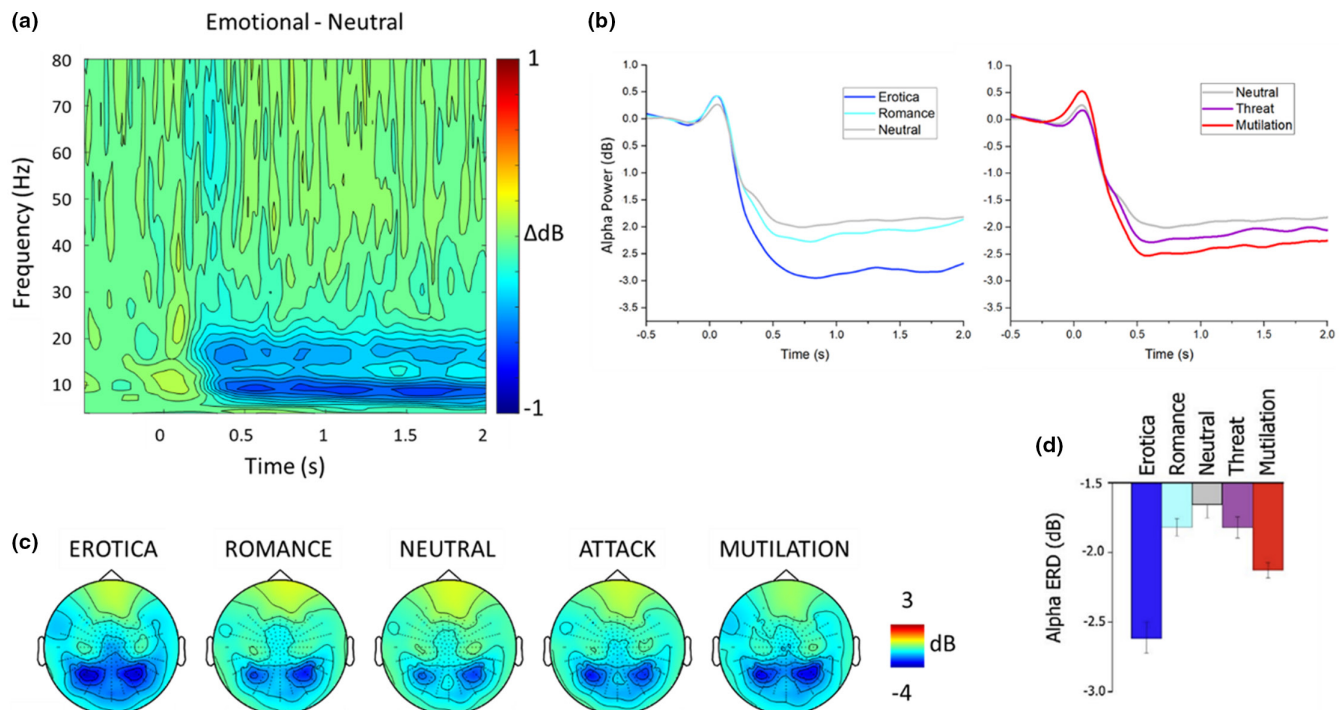
Focusing on the functional significance of alpha oscillations, in their seminal work, Ray and Cole (1985) found that alpha power is lower in sensory-intake tasks (i.e., tasks requiring attention to external stimuli) as compared to rejection tasks (i.e., tasks not requiring attention to the environment, such as mathematical tasks or imagery tasks). It has recently been proposed that alpha power is suppressed when new incoming stimuli need to be processed, whereas it is increased to maintain existing representations in the presence of competing processing streams (Gratton, 2018). Moreover, research has shown that alpha power also decreases phasically when a task-relevant visual stimulus appears or when visual attention is engaged (Bacigalupo & Luck, 2019; Mazaheri & Picton, 2005; Woodman et al., 2022; Yordanova et al., 2001). While previous research examined the effects of directed attention on alpha oscillations, with “top-down” signals

deriving from task demands (Klimesch, 2012; Woodman et al., 2022), less is known about the effects of the intrinsic relevance of a stimulus, i.e., its emotional significance.

In a previous literature review assessing EEG oscillatory activity during emotional visual perception, Güntekin and Başar concluded that the effects of emotional processing on alpha band activity were unclear and inconsistent (Başar & Güntekin, 2012; Güntekin & Başar, 2014; Güntekin et al., 2017; see also Bekkedal et al., 2011; Knyazev, 2007; Masood & Farooq, 2021). However, despite many studies on alpha activity being available, they were not included in the reviews mentioned above. The primary goal of the current review is to determine whether there are reliable patterns in alpha activity during emotional visual processing.

In the literature on emotion, it has been proposed that unpleasant events tend to have larger effects than pleasant ones do (put simply, “Bad is stronger than good”; Baumeister et al., 2001; Rozin & Royzman, 2001). This phenomenon is called “Negative bias” and appears to be pervasive, as evidence has been found in a number of domains (Baumeister et al., 2001; Hilgard et al., 2014). While no conclusive evidence was reported in previous reviews of alpha activity (Başar & Güntekin, 2012; Güntekin & Başar, 2014; Masood & Farooq, 2021), a large and consistent body of evidence has demonstrated that emotional engagement modulates both cortical and autonomic responses, and this modulation is primarily driven by motivational intensity (or arousal) induced by visual stimuli, regardless of hedonic content (i.e., similar reactivity for unpleasant and pleasant, compared with neutral, stimuli; Adolphs & Anderson, 2018; Bradley et al., 2001, 2012; Codispoti & De Cesare, 2007; Keil et al., 2008; Sabatinelli et al., 2005; Schupp et al., 2006; Zald, 2003). Therefore, one focus of the present review will be the valence-specificity of alpha emotional modulation, i.e., whether alpha activity is modulated only by unpleasant stimuli or also by those that are pleasant and whether the modulation is more pronounced for unpleasant, compared with pleasant, stimuli.

Previous research examined alpha changes when viewing emotional pictures in different experimental conditions; participants could be performing a task on the pictures (or on other stimuli) or simply asked to look at them (free viewing). It has been suggested that emotional effects on alpha activity vary with task conditions (Luther et al., 2023; Noguchi & Kubo, 2020; Strube et al., 2021; Uusberg et al., 2013). Uusberg et al. (2013) reported enhanced alpha ERS for emotional compared to neutral stimuli, and this effect was particularly pronounced during an emotional task (rating the valence and arousal of the affective state induced by the picture), compared with a non-emotional task (evaluating physical properties of the pictures), leading the authors to suggest that emotion-modulated alpha



**FIGURE 1** Affective modulation of alpha-ERD. Data from Ferrari et al., 2020 (overall blocks). (a) Time-frequency plot of the emotional-neutral difference at occipitotemporal sensor sites. (b) Waveform of the power changes in the alpha range (8–12 Hz, baseline corrected from −0.5 to −0.2 s). (c) Topography of alpha power changes for each stimulus category during the 400–800 ms interval. (d) Alpha power changes for each stimulus category at occipitotemporal sensor sites in the 400–800 time interval.

power changes may be sensitive to task requirements. Can affective modulation of alpha activity be observed only in free viewing or only when participants are asked to focus on the emotional content of the stimuli? How is alpha activity modulated by task requirements and emotion? In order to answer these questions, the present review summarizes findings for experiments that used free-viewing paradigms (in which no specific instruction was given to participants), emotional tasks (in which the participants' attention was directed to the emotional characteristics of a stimulus), and non-emotional tasks (in which the participants were asked to judge a non-affective feature of an emotional stimulus, such as its luminance, or were asked to focus on a separate neutral target stimulus, such as a Gabor patch). Finally, since the most common visual stimuli presented when studying emotion are natural scenes and images of facial expressions, oscillatory data measured when viewing either type of cue will be assessed and included in separate sections of the present review.

## 1.1 | Emotional processing of natural scenes and alpha changes

Across studies, the processing of emotional, compared to neutral, pictures was reliably associated with an enhanced

power decrease in the alpha band (“emotional modulation of alpha ERD” hereafter) over posterior sensors<sup>1</sup> (see Figure 1; Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2015, 2020, 2022; Meng et al., 2016; Messerotti Benvenuti et al., 2019; Murphy et al., 2020; Parvaz et al., 2015; Scharinger, 2023; Schubring & Schupp, 2019, 2021; Simons et al., 2003; Wang et al., 2021).

In terms of the time course, the emotional modulation of alpha ERD was observed in the time window beginning around 300–400 ms after stimulus onset and lasted approximately until 900–1000 ms or longer after stimulus onset. Several studies report the emotional modulation of alpha ERD only in the time window in which the effect was larger (or in which it overlapped with the affective modulation of the Late Positive Potential; Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2015, 2020,

<sup>1</sup> Few studies reported affective modulation of alpha power over frontal regions, in the direction of a larger alpha ERS for emotional, compared to neutral, stimuli (Aftanas et al., 2001, 2002; Uusberg et al., 2013), or a larger ERD for emotional, compared to neutral, stimuli (Balconi et al., 2009; Schubring & Schupp, 2019; Weinreich et al., 2016), while a substantial number of studies analyzing frontal regions failed to report affective modulation in the alpha range, or found weaker effects compared to posterior areas (Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2020; Ferrari et al., 2022; Keil et al., 2001; Lee et al., 2017; Messerotti Benvenuti et al., 2019; Müller et al., 1999; Schubring & Schupp, 2019, 2021).

2022); however, other experiments clarified the time course by assessing the whole time interval (Messerotti Benvenuti et al., 2019; Schubring & Schupp, 2019, 2021). Interestingly, the emotional modulation of alpha ERD mostly involved the upper alpha band, consistent with previous studies on visual processing (Klimesch, 2018). Moreover, this effect seems not to be confined to the upper alpha band, but also involves the lower beta band (Ferrari et al., 2020, 2022; Schubring & Schupp, 2019, 2021). The emotional modulation of alpha ERD was found even for stimuli that were only briefly presented (150ms or longer, Ferrari et al., 2022; Murphy et al., 2020; Schubring & Schupp, 2019), suggesting that it is triggered by the rapid detection of stimulus significance and does not rely on sustained picture scanning and processing (similar findings have been reported for the affective modulation of the Late Positive potential; Codispoti, Ferrari, & De Cesarei, 2009, 2012; Ferrari et al., 2008).

The emotional modulation of alpha ERD seems to reflect the engagement of the motivational systems when a significant/arousing stimulus is detected. Consistently, a modulation of alpha ERD was also observed in studies that manipulated stimulus significance (arousal) by conditioning neutral stimuli (Bacigalupo & Luck, 2022; Bierwirth et al., 2023), and in anticipation paradigms, in which participants had to anticipate negative events, painful/aversive stimulation or possible threats (Del Percio et al., 2006; Onoda et al., 2007). Several conditioning studies reported greater alpha-band suppression following a conditioned stimulus (CS) that was paired with an aversive (CS+) vs. neutral (CS-) outcome (Bacigalupo & Luck, 2022; Chien et al., 2017; Friedl & Keil, 2020, 2021; Panitz et al., 2019; Yin et al., 2020). It is worth mentioning that enhanced alpha desynchronization was also found during the anticipation of significant stimuli, not only when stimuli were visually available (Bacigalupo & Luck, 2022; Balderston et al., 2017; Onoda et al., 2007). The anticipation of a painful stimulus prompted larger suppression of alpha activity (Babiloni et al., 2003; Del Percio et al., 2006; on the subject of pain perception, see also Li et al., 2020) compared to a non-painful stimulus; likewise, in a “threat of shock” paradigm (also called “instructed threat paradigm”, Grillon et al., 1991), the threatening context was associated with a sustained larger alpha reduction compared to a safe context (Balderston et al., 2017). Interestingly, Balderston et al. (2017) found that threat reduced parietal alpha oscillations and increased functional connectivity (measured with fMRI) in the intraparietal sulcus and in other regions known to play a key role in attention orienting. Taken together, these findings suggest that enhanced alpha desynchronization following arousing/significant cues reflects the engagement of the motivational systems.

A similar pattern of findings was also observed in previous research using dynamic stimuli (film clips, or looming stimuli), in which it was reported that emotional stimuli trigger a greater alpha sustained decrease compared to neutral stimuli (Kim et al., 2021; Romeo et al., 2022; Sarlo et al., 2005; Vagnoni et al., 2015). The impact of unpleasant film clips on oscillatory activity was investigated by Sarlo et al. (2005) who wanted to clarify the specificity of alpha changes induced by different unpleasant contents. Consistent with picture processing studies, a film clip depicting the early phases of a thoracic surgical procedure (open wounds, a category akin to mutilations) elicited larger alpha ERD compared to other unpleasant and neutral contents (Sarlo et al., 2005). Recently, Kim et al. (2021) examined the impact of 32 emotional videos on EEG oscillations. A larger alpha and beta desynchronization was found in widely distributed areas of the cortex for film clips containing high, compared to low, arousal scenes (Kim et al., 2021). Moreover, it has been reported that threatening looming stimuli, compared with non-threatening ones, induced larger alpha ERD (Vagnoni et al., 2015).

While larger alpha ERD for emotional compared to neutral stimuli is the most replicated pattern during the processing of natural scenes, one study observed larger alpha power (ERS) for unpleasant, compared to neutral pictures, within the first second of viewing over posterior regions (Uusberg et al., 2013; see section 5.0 for a discussion on the task effects), and another two studies over frontal areas (Aftanas et al., 2001, 2002).

Finally, a few studies did not observe any significant emotional effects over posterior regions (Aftanas et al., 2001; Arana et al., 2022; Dell’Acqua et al., 2022; Lee et al., 2017; Luther et al., 2023; Müller et al., 1999; Noguchi & Kubo, 2020), while one only reported an early and short-lived (280 – 340ms) alpha power affective modulation, in the direction of larger desynchronization for unpleasant compared with neutral and pleasant stimuli but only when pictures were presented in the right hemifield (Keil et al., 2001). Notably, in some of these studies, the most arousing stimulus categories, such as erotic scenes and/or mutilation/injury, were not used (Dell’Acqua et al., 2022; Lee et al., 2017; Luther et al., 2023; Noguchi & Kubo, 2020), or a combination of different picture categories, such as babies, family, animals, sport, romance, and erotica, were included for the pleasant condition, while pollution, human attack, animal attack, and mutilation/injury were used as stimuli for the unpleasant category (Aftanas et al., 2001; Arana et al., 2022; Dell’Acqua et al., 2022; Müller et al., 1999). As erotic and mutilation/injury scenes have been shown to be the strongest elicitors of emotional alpha-ERD modulation (Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2020, see also Figure 1), consistent with other cortical and autonomic measures



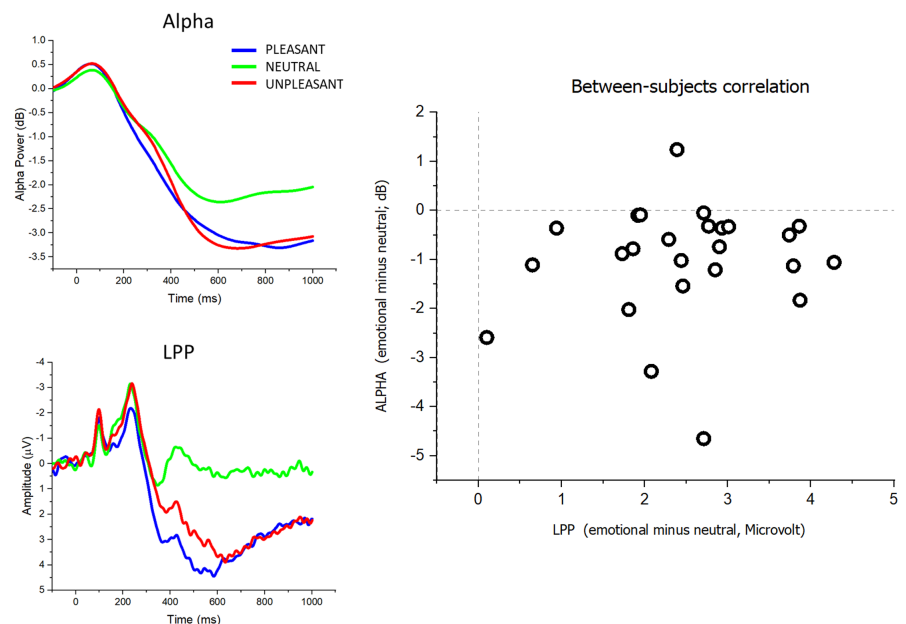
(Bradley et al., 2017; De Cesarei & Codispoti, 2010; Sabatinelli et al., 2005; Schupp et al., 2004; Stevens et al., 2019; Weinberg & Hajcak, 2010), it is possible that the absence (or low percentage) of highly engaging pictures from the emotional categories might be a factor (among others) in determining the findings.

Previous research has shown that emotional cues, especially pictures of mutilation/injury and erotic scenes, activate cortical and subcortical processes, and engage a cascade of orienting, metabolic mobilization, and action preparation. Brain responses to emotional stimuli have been widely investigated via the presentation of pictures evoking a broad range of subjective and autonomic reactions, varying in intensity (Bradley, 2000; Keil et al., 2008; Schupp et al., 2006). fMRI studies showed enhanced activation for emotional pictures in secondary visual processing sites in the lateral occipital cortex, extending up the dorsal stream to the parietal cortex (Bradley et al., 2003; Keil et al., 2012; Lang & Bradley, 2010; Pessoa, 2008; Pourtois et al., 2013; Sabatinelli et al., 2007; Satpute et al., 2015). In a MEG study, Popov et al. (2012) found that the larger alpha (again in the upper range) reduction for unpleasant, compared to neutral, pictures involved the parietal and occipital areas.

The emotional modulation of alpha ERD that was reliably reported within the first second of viewing emotional pictures largely overlapped with the late positive potential (LPP) in terms of timing (De Cesarei & Codispoti, 2011; see Figure 2). The LPP affective modulation reflects both motivational significance and attention allocation (Codispoti et al., 2007, 2016; De Cesarei et al., 2017; Ferrari et al., 2020; Schupp et al., 2006; Weinberg & Hajcak, 2010).

Although these two brain markers of emotional processing share some similarities (De Cesarei & Codispoti, 2011; Ferrari et al., 2022), increasing evidence has also shown that emotional modulation of alpha ERD and of the LPP are differentially affected by stimulus novelty, especially in terms of habituation pattern across picture repetitions: whereas the enhanced LPP for emotional pictures reliably decreases with stimulus repetition, the emotional modulation of alpha ERD remains stable across repetitions (Codispoti et al., 2007; Ferrari et al., 2015, 2020; Schubring & Schupp, 2021), suggesting that it reflects the engagement of motivational systems when a significant stimulus is detected, rather than attentional processes that are expected to decrease with stimulus repetition. Moreover, no correlation was found across participants between the emotional modulation of the LPP and the alpha ERD effect (De Cesarei & Codispoti, 2011; Parvaz et al., 2015; see also Figure 2, and Li et al., 2020, for dissociation in pain perception). Furthermore, these patterns have been replicated in several studies and suggest that the affective modulation of these two measures (LPP and alpha ERD) reflect partially distinct mechanisms engaged in emotional picture processing (see Valentini et al., 2017, for similar findings on death-related cues in nociceptive processing). It should be noted that the dominant spectral components of the LPP (and P300) belongs to delta and theta frequency ranges (e.g., Wang & Ding, 2011). Several mechanisms might be involved in the relationship between oscillatory EEG activity and LPP affective modulation (e.g. baseline-shift mechanism; Nikulin et al., 2010), and more research is needed to clarify it.

### Alpha ERD and Late Positive Potential: Emotional Modulation



**FIGURE 2** Relationship between affective modulation of LPP and alpha-ERD. Data from Ferrari et al., 2020 (Novel blocks). Left panels: waveforms for affective modulation of LPP and alpha-ERD, separately for emotional and neutral novel pictures. Right panel: scatterplot of the relationship between affective modulation (emotional – neutral) of LPP and alpha-ERD across participants (Pearson  $r = .12$ ;  $p = .56$ ); each dot refers to a single participant.

Alpha ERD has been interpreted as an electrocortical component of the orienting response to environmental events (Barry & Beh, 1972; Sokolov, 1963). Consistently, previous research has shown that both top-down cognitive demands and bottom-up visual stimulation impact measurements of alpha oscillations (Klimesch, 2012; Rizzuto et al., 2003). In picture processing paradigms, the overall alpha ERD was affected by top-down/attentional processes (with a greater desynchronization for targets vs. non-targets; Schubring & Schupp, 2019), as well as by sensory/perceptual manipulations, such as picture size and exposure duration (less pronounced desynchronization for smaller or briefly presented pictures; Codispoti, Ferrari, & De Cesarei, 2009; De Cesarei & Codispoti, 2011). However, affective modulation of alpha ERD (i.e., emotion vs. neutral difference) was independent of task (e.g., Schubring & Schupp, 2019), picture size, and exposure time. Consistently, when pictures were presented lateralized (left and right), the overall alpha ERD, but not the emotional modulation of alpha ERD, was greater in the contralateral hemisphere compared to the ipsilateral hemisphere (notably, the lateralized pattern of alpha ERD differed from the topography of the LPP; Ferrari et al., 2022). Altogether, these results seem to indicate that while the overall change in alpha ERD may reflect a cortical activation that is modulated by contextual or perceptual features, its affective modulation constitutes a further modulatory and independent factor, which is likely to be related to the engagement of motivational systems (appetitive and defensive) in reaction to emotional contents.

## 1.2 | The processing of emotional facial expressions and alpha changes

The current review also summarizes studies that used facial expressions as stimuli to assess emotional modulation of oscillatory alpha activity. Overall, studies using faces as induction stimuli reported mixed results. Only a few studies reported a larger alpha ERD for emotional compared with neutral facial expressions (Balconi & Mazza, 2009; Chen et al., 2012; Sollfrank et al., 2021). On the other hand, two studies reported the opposite pattern, that is, a larger alpha power for emotional compared with neutral expressions (Almeida et al., 2016; Fisher et al., 2015), while others failed to observe significant alpha modulation (Balconi & Lucchiari, 2006; Balconi & Pozzoli, 2007; Baumgartner et al., 2006; González-Roldán et al., 2011; González-Roldán et al., 2013; Knyazev et al., 2008). These mixed findings are consistent with previous research, suggesting that static emotional facial expressions are weak stimuli in the induction of reliable emotional effects in autonomic responses (Alpers et al., 2011; Bublatzky

et al., 2019; Fisher et al., 2015; Surcinelli & Codispoti, 2007; Vrana & Gross, 2004; Wangelin et al., 2012; for a similar argument see Levenson et al., 2017) and, at least in part, in cortical responses (Bradley et al., 2003; Thom et al., 2014; Wangelin et al., 2012). Interestingly, in a recent study by Schubring et al. (2020), facial expressions seem to engage alpha power changes in a late time window (1000–1800 ms) when immersion is enhanced in a virtual reality (VR) environment. In this study, the authors found more pronounced alpha ERD for angry avatar faces compared to neutral faces, suggesting that an enhanced immersion with avatar expressions enabled by VR technology can affect alpha activity in the same direction as pictures of natural scenes (Schubring et al., 2020).

## 2 | NEGATIVE BIAS IN AFFECTIVE MODULATION OF ALPHA ERD?

It has been proposed that effects of emotion on attention are specific to unpleasant stimuli (e.g., Koster et al., 2004; Ohman et al., 2001; Pratto & John, 1991). A previous review (Güntekin & Başar, 2014) that summarized the studies on neural oscillations and affective visual processing that were available at the time concluded that a negative bias could exist concerning other oscillatory bands, but no conclusion was reached concerning alpha activity. Does emotional modulation of alpha ERD occur only for unpleasant stimuli? What about responses to pleasant stimuli? Does alpha ERD modulation differ in response to pleasant and unpleasant stimuli?

A larger alpha ERD has been observed for unpleasant compared to neutral images (Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2015, 2020, 2022; Meng et al., 2016; Messerotti Benvenuti et al., 2019; Parvaz et al., 2015; Scharinger, 2023; Schubring et al., 2020, Exp. 2 and 3; Wang et al., 2021), but also for pleasant compared to neutral pictures (Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2015, 2020, 2022; Messerotti Benvenuti et al., 2019; Schubring & Schupp, 2019, 2021, in Exp. 1. and 3; Wang et al., 2021). Most studies failed to find a difference between pleasant and unpleasant contents (Cui et al., 2013; De Cesarei & Codispoti, 2011; Messerotti Benvenuti et al., 2019; Murphy et al., 2020; Wang et al., 2021), while in two studies erotica elicited a larger alpha ERD than mutilation/injury (Ferrari et al., 2020, 2022). Consistently, this pattern of ERD findings has been observed not only with pictures but also with other emotional reactivity induction techniques, such as film clips (Romeo et al., 2022). Romeo et al. (2022) reported a larger alpha ERD for erotic and fear-inducing film clips compared to neutral ones, and, in addition, a larger alpha

ERD for erotic compared to fear-inducing film clips over posterior regions. Although picture repetition does not affect the alpha ERD for either pleasant or unpleasant stimuli, an enhanced alpha ERD has been observed when novel emotional stimuli (pleasant and unpleasant), but not neutral ones, are presented after an extensive phase of stimulus repetition. This suggests that the detection of any specific perceptual change in pleasant and unpleasant stimuli results in an enhanced alpha ERD (Ferrari et al., 2020). Altogether, the available evidence does not support the possibility of emotional modulation of alpha ERD being specific for unpleasant stimuli compared with pleasant and neutral stimuli. The negativity bias may be involved in several processes – including attitudes, social contagion, and contamination (Ito et al., 1998; Rozin & Royzman, 2001) – however, the current review does not reach the same conclusion regarding the existence of this negativity bias on emotional modulation of alpha ERD during picture processing.

Modulatory patterns as a function of stimulus intensity, driven mostly by mutilation/injury and erotic scenes, have been consistently reported for other physiological measures of emotional reactivity, including skin conductance, pupil dilation, late positive potential, and functional changes in the amygdala and visual cortex (Bernat et al., 2006; Bradley et al., 2001; Bradley et al., 2017; Codispoti & De Cesarei, 2007; Keil et al., 2008; Stevens et al., 2019; Weinberg & Hajcak, 2010; Sabatinelli et al., 2005; Schupp et al., 2004), suggesting that alpha activity, similarly to other physiological components of the orienting response (see also similar findings for attentional interference/capture by emotion in Codispoti et al., 2016; De Cesarei & Codispoti, 2008; Ferrari et al., 2017; Most et al., 2007; Schimmack, 2005), varies with motivational significance of the stimuli, more than with their hedonic content (i.e., valence).

### 3 | FRONTAL ALPHA ASYMMETRY AND EMOTION

Since the 1980s, a large body of research has examined frontal alpha asymmetry in relation to emotion and psychopathology (Ahern & Schwartz, 1985; Coan & Allen, 2004; Davidson, 1992; Harmon-Jones, 2003; Reznik & Allen, 2018). The “approach-withdrawal motivational” hypothesis of frontal asymmetry proposes a lateralization of emotion across the left and right frontal hemispheres; appetitive motivation and approach-related affect are associated with greater left-frontal activity, whereas withdrawal motivation and negative motivation are linked to greater right-frontal activity (Coan & Allen, 2004; Harmon-Jones, 2003). Several studies examined frontal

alpha asymmetry as an individual difference variable (resting activity) related to emotional responses and disorders (for reviews on this specific topic see Coan & Allen, 2004; Davidson, 1992; Hagemann, 2004; Harmon-Jones & Gable, 2018; Reznik & Allen, 2018). Concerning frontal alpha asymmetry as a state-dependent concomitant of emotional responding (“activation”) to visual stimuli, the studies failed to observe any effect of emotional picture content (Adolph et al., 2017; Deng et al., 2021; Elgavish et al., 2003; Gable & Harmon-Jones, 2008; Güntekin et al., 2017; Hagemann et al., 1998; Harmon-Jones, 2007; Harmon-Jones et al., 2010; Harmon-Jones et al., 2022; Pönkänen & Hietanen, 2012; Poole & Gable, 2014; Uusberg et al., 2014; for reviews, see Sabu et al., 2022). Consistently, most of the studies examined in the present review did not report any hemispheric difference in alpha activity for pleasant and unpleasant stimuli, and neuroimaging studies (fMRI and PET) failed to find asymmetrical frontal activation differences as a function of type of affective stimuli (García-García et al., 2016; Kober et al., 2008; Murphy et al., 2003; Pizzagalli et al., 2003; Xu et al., 2021; Wager et al., 2015). Several studies on alpha activity assessed frontal asymmetry during emotional picture processing, but the findings did not support the “approach-withdrawal motivational” hypothesis, and this focus on frontal asymmetry for pleasant and unpleasant contents might have contributed to the emotional modulation ERD effect being somewhat neglected.

### 4 | ALPHA ACTIVITY AND EMOTION: THE EFFECT OF TASK

It has been suggested that the pattern of alpha modulation as a function of stimulus emotionality may depend on the task the system is carrying out (Strube et al., 2021; Uusberg et al., 2013). More specifically, it has been proposed that while larger alpha ERD for unpleasant compared to neutral pictures may be observed during free viewing, a different pattern (larger ERS for emotional compared to neutral) could be found during active tasks (Uusberg et al., 2013).

Most of the studies examining the free viewing of emotional and neutral pictures reported emotional modulation of alpha ERD over posterior sensor sites, with a sustained stronger ERD for emotional compared with neutral pictures from 300 to 400 ms to about 1000 ms after the onset of the pictures (Cui et al., 2013; De Cesarei & Codispoti, 2011; Ferrari et al., 2015; Messerotti Benvenuti et al., 2019; Parvaz et al., 2015; Schubring & Schupp, 2021; but see Dell'Acqua et al., 2022; Lee et al., 2017; Luther et al., 2023; Müller et al., 1999 for null findings in

free-viewing tasks). A similar emotional effect was also found when emotional pictures were presented while participants were asked to perform cognitive tasks, again showing a significant alpha ERD over posterior sensors between about 300 ms to 1000 ms post-picture onset (Ferrari et al., 2020, 2022; Murphy et al., 2020; Schubring & Schupp, 2019, 2021). Finally, in emotional tasks (i.e., either judging emotional picture content or rating one's affective reactions), two studies reported increased alpha power for emotional compared with neutral pictures (Aftanas et al., 2002; Uusberg et al., 2013), but a higher number of studies reported a larger alpha ERD for emotional compared with neutral pictures (Schubring & Schupp, 2019, 2021 [three independent experiments]; Simons et al., 2003; Strube et al., 2021). Altogether, these investigations indicate that the nature of the task does not seem to be crucial in affecting the emotional modulation of alpha ERD. A sustained posterior emotional modulation of alpha ERD is reliably observed during free viewing as well as in active task conditions, regardless of the fact that the emotional pictures were task relevant stimuli (Schubring & Schupp, 2019, 2021), or served as distractor stimuli during a main task (Ferrari et al., 2020, 2022; Schubring & Schupp, 2019, 2021). Enhanced alpha ERD for highly arousing compared with low arousing pictures was found with a variety of task conditions: a categorization task for the scenes that required an explicit decision to press one of two buttons (Schubring & Schupp, 2019); counting, in one's head, the number of scenes depicting a specific target category (Schubring & Schupp, 2021); tasks not specifically focused on the scene, such as detecting the appearance of a low-probability target (a geometric shape; Ferrari et al., 2020) or identifying the orientation of a centrally presented Gabor patch while emotional pictures were distractors presented in the peripheral visual field (4° from the inner edge of the distractor to the center of the Gabor patch, Ferrari et al., 2022). Taken together, the findings reported in the current review do not support the hypothesis that emotional (differential) effects (ERS vs. ERD) in the alpha band depend on the concurrent task in the picture-processing context. Furthermore, several studies indicate that the emotional modulation of alpha ERD occurs even when participants are performing a cognitive competing task on the images, or when emotional cues serve as task-irrelevant distractors and appear displaced in space compared to the target of the perceptual task at hand. These findings, together with evidence that the emotional modulation of alpha ERD occurs even after massive stimulus repetition, seem to be consistent with the hypothesis that evaluative processes and the engagement of motivational systems are mandatory in emotional picture processing.

## 5 | LIMITATIONS AND FUTURE DIRECTIONS

Some potential limitations of the current review need to be addressed. First, we were not able to assess the emotional modulation of alpha ERD in terms of onset time, length, and topography because most of the studies reported only a specific time interval and sensor selection (however, see Schubring & Schupp, 2019, 2021). Second, in the present review, we focused on the impact of static visual stimuli on alpha modulation, therefore future reviews and studies should examine whether similar findings are obtained for other modalities (e.g., acoustic, olfactory). Third, alpha oscillation was assessed using a variety of techniques (see baseline selection and quantification, e.g., Gyurkovics et al., 2022) across studies, that, together with missing methodological details (often basic statistical parameters, such as means and standard error, or partial eta squared), might have contributed to the underestimation/overestimation of possible “between studies” manipulations/comparisons (e.g., task requirements or exposure time) and prevent a meta-analysis from being performed. We believe future research would benefit from recent methodological recommendations on oscillations (Donoghue et al., 2020; Keil et al., 2022) and signal processing techniques (Cole & Voytek, 2019; Donoghue et al., 2020; Gyurkovics et al., 2022; Kosciessa et al., 2020).

The literature on EEG oscillatory activity and emotional processing has also been characterized by an inconsistent focus on various EEG bands, often without a specific rationale, and most of the studies analyzed each oscillatory band separately with few studies assessing the coherence between bands. Concerning other oscillatory bands, less systematic research has been reported; there is some evidence of emotional effects on delta, theta, and gamma bands (Güntekin & Başar, 2014; but see Schubring & Schupp, 2019, 2021, for null findings). Moreover, few studies have examined the electrocortical synchronization (spectral power and phase EEG coherence) of cortical regions/networks during emotional picture perception (Güntekin et al., 2017; Miskovic & Schmidt, 2010; Yang et al., 2020), again with no consistent findings. Future studies might clarify the neural mechanisms and processes (e.g., attention or memory) engaged by emotional stimuli by systematically examining the coherence between oscillatory bands (e.g., alpha and gamma; Ono et al., 2023; Srinivasan et al., 2007), and between cortical regions/networks.

Alpha ERD has repeatedly been shown to be related to heightened attentional engagement (Klimesch, 2012; Mazaheri & Picton, 2005; Yordanova et al., 2001) and it



was recently proposed that alpha oscillations might reflect “a cognitive mechanism of attention that not only works to select new, important inputs from our visual field, but also operates to activate memory representations” (Woodman et al., 2022). Since emotional stimuli capture attention (Micucci et al., 2020; Mulckhuyse, 2018; Öhman, 1992), the emotional modulation of alpha ERD is consistent with these previous EEG studies on attentional selection. However, it has been shown that stimulus repetition does not reduce the emotional modulation of alpha ERD (Ferrari et al., 2020, 2022), and future studies should clarify how attention affects alpha ERD in emotional processing.

In the present review, we focused on emotional picture perception, and although a similar alpha ERD effect has been observed for other significant/arousing stimuli (e.g., anticipation of threat), or during the processing of dynamic stimuli (film-clips or looming images), less is known regarding acoustic stimuli and naturalistic multi-sensory stimulation/contexts. The emotional modulation of alpha ERD has mostly been assessed and reported using static visual stimuli, and, even though it is a reliable effect, an open question for future research would be to examine EEG oscillations in emotionally intense quasi-naturalistic settings. Experimental control is a problem with everyday-life conditions, but new technologies, such as immersive virtual reality (VR), allow individuals to experience dynamic/interactive situations and might represent an extraordinary tool to improve the tradeoff between internal and external validity in psychophysiological research (and neuroscience). Recently, Hofmann et al. (2021) pioneered this new field and used VR to investigate EEG oscillations during an intense emotional situation (a roller coaster ride with high immersion). Signal processing of EEG activity through statistical modeling revealed an inverse relationship between subjective emotional arousal and alpha power over parieto-occipital regions, consistent with the emotional modulation alpha ERD effect reported in picture perception studies. Future research should examine EEG oscillations in other high and low arousing pleasant and unpleasant contexts in everyday-life conditions.

## 5.1 | Summary and conclusions

Alpha band activity has long been examined in psychophysiological research in the context of the orienting response to visual and acoustic stimuli (e.g., geometric figures and tones); however, oscillatory activity during emotional processing has been less widely investigated. Previous literature reviews assessing EEG oscillatory activity during picture perception focused on a small number of studies showing inconsistent findings, and concluded that the emotional effects on alpha band activity were unclear

(Güntekin et al., 2017; Güntekin & Başar, 2014; Masood & Farooq, 2021). Recently, systematic research has been conducted, and the studies reviewed here indicate that alpha desynchronization (ERD) over posterior sensors is reliably enhanced when viewing emotional compared with neutral pictures. Consistent with other measures of emotional reactivity, alpha ERD is modulated by highly arousing picture contents, such as stimuli depicting mutilation/injury and erotic scenes, suggesting that it is triggered by the high motivational significance of the stimuli more than with their hedonic content (i.e., valence). Evidence indicates that the emotional modulation of alpha ERD occurs even after massive stimulus repetition (Ferrari et al., 2020; Schubring & Schupp, 2021), when participants are asked to perform a perceptual task, and when emotional cues serve as task-irrelevant distractors and appear displaced in space compared to the target of the task at hand (Ferrari et al., 2022; Murphy et al., 2020), consistent with the hypothesis that evaluative processes are mandatory: that is, they are not affected by ongoing top-down goal settings in emotional picture processing when enough time is available for stimulus identification (Reisenzein & Franikowski, 2022).

A similar enhanced ERD has been observed for other significant stimuli (e.g., conditioned threat stimuli, or in anticipation of a potential threat), suggesting that it reflects cortical excitability associated with the engagement of the motivational systems (Bacigalupo & Luck, 2022; Balderston et al., 2017; Friedl & Keil, 2021). Michelmann et al. (2022) pointed out that alpha activity, similar to any other neural phenomenon (Cacioppo & Tassinary, 1990; Tassinary et al., 2023), does not reflect a specific cognitive process (i.e., attention, memory; see the “reverse inference error”, Poldrack, 2011) but is more likely to indicate a basic mechanism involved in different contexts and processes (Klimesch, 2012; Michelmann et al., 2022). One possibility is that the enhanced alpha/beta ERD might reflect a basic mechanism associated with the engagement of the motivational systems, which is mandatory in the processing of stimulus significance.

## AUTHOR CONTRIBUTIONS

**Maurizio Codispoti:** Conceptualization; methodology; validation; visualization; writing – original draft; writing – review and editing. **Andrea De Cesare:** Conceptualization; methodology; validation; visualization; writing – original draft; writing – review and editing. **Vera Ferrari:** Conceptualization; methodology; validation; visualization; writing – original draft; writing – review and editing.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

## ORCID

Maurizio Codispoti  <https://orcid.org/0000-0002-7285-4342>

Andrea De Cesarei  <https://orcid.org/0000-0002-6624-5006>

Vera Ferrari  <https://orcid.org/0000-0003-1070-6691>

## REFERENCES

- Adolph, D., von Glischinski, M., Wannemüller, A., & Margraf, J. (2017). The influence of frontal alpha-asymmetry on the processing of approach- and withdrawal-related stimuli—A multichannel psychophysiology study. *Psychophysiology*, 54(9), 1295–1310. <https://doi.org/10.1111/psyp.12878>
- Adolphs, R., & Anderson, D. J. (2018). *The neurobiology of emotion: A new synthesis*. Princeton University Press.
- Aftanas, L., Varlamov, A., Pavlov, S., Makhnev, V., & Reva, N. (2001). Event-related synchronization and desynchronization during affective processing: Emergence of valence-related time-dependent hemispheric asymmetries in theta and upper alpha band. *The International Journal of Neuroscience*, 110(3–4), 197–219. <https://doi.org/10.3109/00207450108986547>
- Aftanas, L. I., Varlamov, A. A., Pavlov, S. V., Makhnev, V. P., & Reva, N. V. (2002). Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *International Journal of Psychophysiology*, 44(1), 67–82. [https://doi.org/10.1016/s0167-8760\(01\)00194-5](https://doi.org/10.1016/s0167-8760(01)00194-5)
- Ahern, G. L., & Schwartz, G. E. (1985). Differential lateralization for positive and negative emotion in the human brain: EEG spectral analysis. *Neuropsychologia*, 23(6), 745–755. [https://doi.org/10.1016/0028-3932\(85\)90081-8](https://doi.org/10.1016/0028-3932(85)90081-8)
- Almeida, P. R., Ferreira-Santos, F., Chaves, P. L., Paiva, T. O., Barbosa, F., & Marques-Teixeira, J. (2016). Perceived arousal of facial expressions of emotion modulates the N170, regardless of emotional category: Time domain and time-frequency dynamics. *International Journal of Psychophysiology*, 99, 48–56. <https://doi.org/10.1016/j.ijpsycho.2015.11.017>
- Alpers, G. W., Adolph, D., & Pauli, P. (2011). Emotional scenes and facial expressions elicit different psychophysiological responses. *International Journal of Psychophysiology*, 80(3), 173–181. <https://doi.org/10.1016/j.ijpsycho.2011.01.010>
- Arana, L., Melcón, M., Kessel, D., Hoyos, S., Albert, J., Carretié, L., & Capilla, A. (2022). Suppression of alpha-band power underlies exogenous attention to emotional distractors. *Psychophysiology*, 59(9), e14051. <https://doi.org/10.1111/psyp.14051>
- Babiloni, C., Brancucci, A., Babiloni, F., Capotosto, P., Carducci, F., Cincotti, F., Arendt-Nielsen, L., Chen, A. C. N., & Rossini, P. M. (2003). Anticipatory cortical responses during the expectancy of a predictable painful stimulation. A high-resolution electroencephalography study. *European Journal of Neuroscience*, 18, 1692–1700. <https://doi.org/10.1046/j.1460-9568.2003.02851.x>
- Bacigalupo, F., & Luck, S. J. (2019). Lateralized suppression of alpha-band EEG activity As a mechanism of target processing. *The Journal of Neuroscience*, 39(5), 900–917. <https://doi.org/10.1523/JNEUROSCI.0183-18.2018>
- Bacigalupo, F., & Luck, S. J. (2022). Alpha-band EEG suppression as a neural marker of sustained attentional engagement to conditioned threat stimuli. *Social Cognitive and Affective Neuroscience*, 17(12), 1101–1117. <https://doi.org/10.1093/scan/nsac029>
- Balconi, M., Brambilla, E., & Falbo, L. (2009). BIS/BAS, cortical oscillations and coherence in response to emotional cues. *Brain Research Bulletin*, 80(3), 151–157. <https://doi.org/10.1016/j.brainresbull.2009.07.001>
- Balconi, M., & Lucchiari, C. (2006). EEG correlates (event-related desynchronization) of emotional face elaboration: A temporal analysis. *Neuroscience Letters*, 392(1–2), 118–123. <https://doi.org/10.1016/j.neulet.2005.09.004>
- Balconi, M., & Mazza, G. (2009). Brain oscillations and BIS/BAS (behavioral inhibition/activation system) effects on processing masked emotional cues. ERS/ERD and coherence measures of alpha band. *International journal of psychophysiology: Official journal of the international organization of. Psychophysiology*, 74(2), 158–165. <https://doi.org/10.1016/j.ijpsycho.2009.08.006>
- Balconi, M., & Pozzoli, U. (2007). Event-related oscillations (EROs) and event-related potentials (ERPs) comparison in facial expression recognition. *Journal of Neuropsychology*, 1(2), 283–294. <https://doi.org/10.1348/174866407x184789>
- Balderston, N. L., Hale, E., Hsiung, A., Torrisi, S., Holroyd, T., Carver, F. W., Coppola, R., Ernst, M., & Grillon, C. (2017). Threat of shock increases excitability and connectivity of the intraparietal sulcus. *eLife*, 6, e23608. <https://doi.org/10.7554/eLife.23608>
- Barry, R. J., & Beh, H. C. (1972). Desynchronization of the alpha rhythm of the EEG as a function of intensity of visual stimulation. *Psychonomic Science*, 26(5), 241–242.
- Başar, E., & Güntekin, B. (2012). A short review of alpha activity in cognitive processes and in cognitive impairment. *International Journal of Psychophysiology*, 86(1), 25–38. <https://doi.org/10.1016/j.ijpsycho.2012.07.001>
- Baumeister, R. F., Bratslavsky, E., Finkenauer, C., & Vohs, K. D. (2001). Bad is stronger than good. *Review of General Psychology*, 5(4), 323–370. <https://doi.org/10.1037/1089-2680.5.4.323>
- Baumgartner, T., Valko, L., Esslen, M., & Jäncke, L. (2006). Neural correlate of spatial presence in an arousing and non-interactive virtual reality: An EEG and psychophysiology study. *Cyberpsychology & Behavior*, 9(1), 30–45. <https://doi.org/10.1089/cpb.2006.9.30>
- Bekkedal, M. Y., Rossi, J., 3rd, & Panksepp, J. (2011). Human brain EEG indices of emotions: Delineating responses to affective vocalizations by measuring frontal theta event-related synchronization. *Neuroscience and Biobehavioral Reviews*, 35(9), 1959–1970. <https://doi.org/10.1016/j.neubiorev.2011.05.001>
- Bernat, E., Patrick, C. J., Benning, S. D., & Tellegen, A. (2006). Effects of picture content and intensity on affective physiological response. *Psychophysiology*, 43(1), 93–103. <https://doi.org/10.1111/j.1469-8986.2006.00380.x>
- Bierwirth, P., Antov, M. I., & Stockhorst, U. (2023). Oscillatory and non-oscillatory brain activity reflects fear expression in an immediate and delayed fear extinction task. *Psychophysiology*, 60, e14283. <https://doi.org/10.1111/psyp.14283>
- Bradley, M. M. (2000). Emotion and motivation. In J. T. Cacioppo, L. G. Tassinary, & G. Berntson (Eds.), *Handbook of psychophysiology* (pp. 602–642). Cambridge University Press.
- Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology*, 46, 1–11. <https://doi.org/10.1111/j.1469-8986.2008.00702.x>

- Bradley, M. M., Codispoti, M., Cuthbert, B., & Lang, P. J. (2001). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion*, 1(3), 276–298. <https://doi.org/10.1037/1528-3542.1.3.276>
- Bradley, M. M., Keil, A., & Lang, P. J. (2012). Orienting and emotional perception: Facilitation, attenuation, and interference. *Frontiers in Psychology*, 3, 493. <https://doi.org/10.3389/fpsyg.2012.00493>
- Bradley, M. M., Sabatinelli, D., Lang, P. J., Fitzsimmons, J. R., King, W., & Desai, P. (2003). Activation of the visual cortex in motivated attention. *Behavioral Neuroscience*, 117(2), 369–380. <https://doi.org/10.1037/0735-7044.117.2.369>
- Bradley, M. M., Sapigao, R. G., & Lang, P. J. (2017). Sympathetic ANS modulation of pupil diameter in emotional scene perception: Effects of hedonic content, brightness, and contrast. *Psychophysiology*, 54(10), 1419–1435. <https://doi.org/10.1111/psyp.12890>
- Bublitzky, F., Riemer, M., & Guerra, P. (2019). Reversing threat to safety: Incongruence of facial emotions and instructed threat modulates conscious perception but not physiological responding. *Frontiers in Psychology*, 10, 2091. <https://doi.org/10.3389/fpsyg.2019.02091>
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, 29(24), 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>
- Cacioppo, J. T., & Tassinary, L. G. (1990). Inferring psychological significance from physiological signals. *American Psychologist*, 45(1), 16–28. <https://doi.org/10.1037/0003-066X.45.1.16>
- Chen, S., Sun, J., & Tong, S. (2012). Delayed attentional disengagement from sad face: A study of alpha rhythm by event-related desynchronization. Annual international conference of the IEEE engineering in medicine and biology society. IEEE engineering in medicine and biology society. *Annual International Conference, 2012*, 6776–6779. <https://doi.org/10.1109/EMBC.2012.6347550>
- Chien, J. H., Colloca, L., Korzeniewska, A., Cheng, J. J., Campbell, C. M., Hillis, A. E., & Lenz, F. A. (2017). Oscillatory EEG activity induced by conditioning stimuli during fear conditioning reflects salience and valence of these stimuli more than expectancy. *Neuroscience*, 346, 81–93. <https://doi.org/10.1016/j.neuroscience.2016.12.047>
- Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, 67(1–2), 7–49. <https://doi.org/10.1016/j.biopsycho.2004.03.002>
- Codispoti, M., & De Cesarei, A. (2007). Arousal and attention: Picture size and emotional reactions. *Psychophysiology*, 44(5), 680–686. <https://doi.org/10.1111/j.1469-8986.2007.00545.x>
- Codispoti, M., De Cesarei, A., Biondi, S., & Ferrari, V. (2016). The fate of unattended stimuli and emotional habituation: Behavioral interference and cortical changes. *Cognitive, Affective, & Behavioral Neuroscience*, 16, 1063–1073. <https://doi.org/10.3758/s13415-016-0453-0>
- Codispoti, M., De Cesarei, A., & Ferrari, V. (2012). The influence of color on emotional perception of natural scenes. *Psychophysiology*, 49(1), 11–16. <https://doi.org/10.1111/j.1469-8986.2011.01284.x>
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2007). Repetition and event-related potentials: Distinguishing early and late processes in affective picture perception. *Journal of Cognitive Neuroscience*, 19, 577–586. <https://doi.org/10.1162/jocn.2007.19.4.577>
- Codispoti, M., Ferrari, V., & De Cesarei, A. (2009). The influence of color on the perception of briefly presented emotional scenes. *Psychophysiology*, 46, S97.
- Codispoti, M., Mazzetti, M., & Bradley, M. M. (2009). Unmasking emotion: Exposure duration and emotional engagement. *Psychophysiology*, 46(4), 731–738. <https://doi.org/10.1111/j.1469-8986.2009.00804.x>
- Cohen, M. X. (2017). Where does EEG come from and what does it mean? *Trends in Neurosciences*, 40(4), 208–218. <https://doi.org/10.1016/j.tins.2017.02.004>
- Cole, S., & Voytek, B. (2019). Cycle-by-cycle analysis of neural oscillations. *Journal of Neurophysiology*, 122(2), 849–861. <https://doi.org/10.1152/jn.00273.2019>
- Cui, Y., Versace, F., Engelmann, J. M., Minnix, J. A., Robinson, J. D., Lam, C. Y., Karam-Hage, M., Brown, V. L., Wetter, D. W., Dani, J. A., Kosten, T. R., & Cinciripini, P. M. (2013). Alpha oscillations in response to affective and cigarette-related stimuli in smokers. *Nicotine & Tobacco Research: Official Journal of the Society for Research on Nicotine and Tobacco*, 15(5), 917–924. <https://doi.org/10.1093/ntr/nts209>
- Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, 151(20), 125–151. [https://doi.org/10.1016/0278-2626\(92\)90065-T](https://doi.org/10.1016/0278-2626(92)90065-T)
- De Cesarei, A., & Codispoti, M. (2008). Fuzzy picture processing: Effects of size reduction and blurring on emotional processing. *Emotion*, 8, 352–363. <https://doi.org/10.1037/1528-3542.8.3.352>
- De Cesarei, A., & Codispoti, M. (2010). Effects of picture size reduction and blurring on emotional engagement. *PLoS One*, 5(10), e13399. <https://doi.org/10.1371/journal.pone.0013399>
- De Cesarei, A., & Codispoti, M. (2011). Affective modulation of the LPP and  $\alpha$ -ERD during picture viewing. *Psychophysiology*, 48, 1397–1404. <https://doi.org/10.1111/j.1469-8986.2011.01204.x>
- De Cesarei, A., Loftus, G. R., Mastroia, S., & Codispoti, M. (2017). Understanding natural scenes: Contributions of image statistics. *Neuroscience & Biobehavioral Reviews*, 74, 44–57. <https://doi.org/10.1016/j.neubiorev.2017.01.012>
- Del Percio, C., Le Pera, D., Arendt-Nielsen, L., Babiloni, C., Brancucci, A., Chen, A. C., De Armas, L., Miliucci, R., Restuccia, D., Valeriani, M., & Rossini, P. M. (2006). Distraction affects frontal alpha rhythms related to expectancy of pain: An EEG study. *NeuroImage*, 31(3), 1268–1277. <https://doi.org/10.1016/j.neuroimage.2006.01.013>
- Dell'Acqua, C., Dal Bò, E., Moretta, T., Palomba, D., & Messerotti Benvenuti, S. (2022). EEG time-frequency analysis reveals blunted tendency to approach and increased processing of unpleasant stimuli in dysphoria. *Scientific Reports*, 12(1), 8161. <https://doi.org/10.1038/s41598-022-12263-9>
- Deng, Y., Hou, L., Chen, X., & Zhou, R. (2021). Working memory training improves emotion regulation in drug abstiners: Evidence from frontal alpha asymmetry. *Neuroscience Letters*, 742, 135513. <https://doi.org/10.1016/j.neulet.2020.135513>
- Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A. H., Wallis, J. D., Knight, R. T., Shestyuk, A., & Voytek, B. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, 23(12), 1655–1665. <https://doi.org/10.1038/s41593-020-00744-x>
- Elgavish, E., Halpern, D., Dikman, Z., & Allen, J. J. B. (2003). Does frontal EEG asymmetry moderate or mediate responses to the international affective picture system (IAPS)? *Psychophysiology*, 40, 38.



- Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2015). Massed and distributed repetition of natural scenes: Brain potentials and oscillatory activity. *Psychophysiology*, 52, 865–872. <https://doi.org/10.1111/psyp.12424>
- Ferrari, V., Bruno, N., Chattat, R., & Codispoti, M. (2017). Evaluative ratings and attention across the life span: Emotional arousal and gender. *Cognition & Emotion*, 31(3), 552–563. <https://doi.org/10.1080/02699931.2016.1140020>
- Ferrari, V., Canturi, F., & Codispoti, M. (2022). Stimulus novelty and emotionality interact in the processing of visual distractors. *Biological Psychology*, 167, 108238. <https://doi.org/10.1016/j.biopsycho.2021.108238>
- Ferrari, V., Codispoti, M., Cardinale, R., & Bradley, M. M. (2008). Directed and motivated attention during processing of natural scenes. *Journal of Cognitive Neuroscience*, 20, 1753–1761. <https://doi.org/10.1162/jocn.2008.20121>
- Ferrari, V., Mastria, S., & Codispoti, M. (2020). The interplay between attention and long-term memory in affective habituation. *Psychophysiology*, 57(6), e13572. <https://doi.org/10.1111/psyp.13572>
- Fisher, A. C., Rushby, J. A., McDonald, S., Parks, N., & Piguet, O. (2015). Neurophysiological correlates of dysregulated emotional arousal in severe traumatic brain injury. *Clinical Neurophysiology*, 126(2), 314–324. <https://doi.org/10.1016/j.clinph.2014.05.033>
- Friedl, W. M., & Keil, A. (2020). Effects of experience on spatial frequency tuning in the visual system: Behavioral, Visuocortical, and alpha-band responses. *Journal of Cognitive Neuroscience*, 32(6), 1153–1169. [https://doi.org/10.1162/jocn\\_a\\_01524](https://doi.org/10.1162/jocn_a_01524)
- Friedl, W. M., & Keil, A. (2021). Aversive conditioning of spatial position sharpens neural population-level tuning in visual cortex and selectively alters alpha-band activity. *The Journal of Neuroscience*, 41(26), 5723–5733. <https://doi.org/10.1523/JNEUROSCI.2889-20.2021>
- Gable, P., & Harmon-Jones, E. (2008). Relative left frontal activation to appetitive stimuli: Considering the role of individual differences. *Psychophysiology*, 45(2), 275–278. <https://doi.org/10.1111/j.1469-8986.2007.00627.x>
- García-García, I., Kube, J., Gaebler, M., Horstmann, A., Villringer, A., & Neumann, J. (2016). Neural processing of negative emotional stimuli and the influence of age, sex and task-related characteristics. *Neuroscience and Biobehavioral Reviews*, 68, 773–793. <https://doi.org/10.1016/j.neubiorev.2016.04.020>
- González-Roldán, A. M., Martínez-Jauand, M., Muñoz-García, M. A., Sitges, C., Cifre, I., & Montoya, P. (2011). Temporal dissociation in the brain processing of pain and anger faces with different intensities of emotional expression. *Pain*, 152(4), 853–859. <https://doi.org/10.1016/j.pain.2010.12.037>
- González-Roldán, A. M., Muñoz, M. A., Cifre, I., Sitges, C., & Montoya, P. (2013). Altered psychophysiological responses to the view of others' pain and anger faces in fibromyalgia patients. *The Journal of Pain*, 14(7), 709–719. <https://doi.org/10.1016/j.jpain.2013.01.775>
- Gottlieb, J. (2012). Attention, learning, and the value of information. *Neuron*, 76(2), 281–295. <https://doi.org/10.1016/j.neuron.2012.09.034>
- Gratton, G. (2018). Brain reflections: A circuit-based framework for understanding information processing and cognitive control. *Psychophysiology*, 55(3), e13038. <https://doi.org/10.1111/psyp.13038>
- Grillon, C., Ameli, R., Woods, S. W., Merikangas, K., & Davis, M. (1991). Fear-potentiated startle in humans: Effects of anticipatory anxiety on the acoustic blink reflex. *Psychophysiology*, 28(5), 588–595. <https://doi.org/10.1111/j.1469-8986.1991.tb01999.x>
- Güntekin, B., & Başar, E. (2014). A review of brain oscillations in perception of faces and emotional pictures. *Neuropsychologia*, 58, 33–51. <https://doi.org/10.1016/j.neuropsychologia.2014.03.014>
- Güntekin, B., Femir, B., Gölbaşı, B. T., Tülay, E., & Başar, E. (2017). Affective pictures processing is reflected by an increased long-distance EEG connectivity. *Cognitive Neurodynamics*, 11(4), 355–367. <https://doi.org/10.1007/s11571-017-9439-z>
- Gyurkovics, M., Clements, G. M., Low, K. A., Fabiani, M., & Gratton, G. (2022). Stimulus-induced changes in 1/f-like background activity in EEG. *The Journal of Neuroscience*, 42(37), 7144–7151. <https://doi.org/10.1523/JNEUROSCI.0414-22.2022>
- Hagemann, D. (2004). Individual differences in anterior EEG asymmetry: Methodological problems and solutions. *Biological Psychology*, 67(1–2), 157–182. <https://doi.org/10.1016/j.biopsycho.2004.03.006>
- Hagemann, D., Naumann, E., Becker, G., Maier, S., & Bartussek, D. (1998). Frontal brain asymmetry and affective style: A conceptual replication. *Psychophysiology*, 35(4), 372–388.
- Hanslmayr, S., Staudigl, T., & Fellner, M. C. (2012). Oscillatory power decreases and longterm memory: The information via desynchronization hypothesis. *Frontiers in Human Neuroscience*, 6, 74. <https://doi.org/10.3389/fnhum.2012.00074>
- Harmon-Jones, E. (2003). Early career award. Clarifying the emotive functions of asymmetrical frontal cortical activity. *Psychophysiology*, 40(6), 838–848. <https://doi.org/10.1111/1469-8986.00121>
- Harmon-Jones, E. (2007). Trait anger predicts relative left frontal cortical activation to anger-inducing stimuli. *International Journal of Psychophysiology*, 66(2), 154–160. <https://doi.org/10.1016/j.ijpsycho.2007.03.020>
- Harmon-Jones, E., & Gable, P. A. (2018). On the role of asymmetric frontal cortical activity in approach and withdrawal motivation: An updated review of the evidence. *Psychophysiology*, 55(1), e12879. <https://doi.org/10.1111/psyp.12879>
- Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology*, 84(3), 451–462. <https://doi.org/10.1016/j.biopsycho.2009.08.010>
- Harmon-Jones, E., Popp, T., & Gable, P. A. (2022). Theory and research on asymmetric frontal cortical activity as assessed by EEG frequency analyses. In P. A. Gable, M. W. Miller, & E. M. Bernat (Eds.), *The Oxford handbook of eeg frequency*. Oxford Library of Psychology.
- Herrmann, C. S., Strüder, D., Helfrich, R. F., & Engel, A. K. (2016). EEG oscillations: From correlation to causality. *International Journal of Psychophysiology*, 103, 12–21. <https://doi.org/10.1016/j.ijpsycho.2015.02.003>
- Hilgard, J., Weinberg, A., Hajcak Proudfit, G., & Bartholow, B. D. (2014). The negativity bias in affective picture processing depends on top-down and bottom-up motivational significance. *Emotion*, 14(5), 940–949. <https://doi.org/10.1037/a0036791>
- Hofmann, S. M., Klotzsche, F., Mariola, A., Nikulin, V., Villringer, A., & Gaebler, M. (2021). Decoding subjective emotional arousal from EEG during an immersive virtual reality experience. *eLife*, 10, e64812. <https://doi.org/10.7554/eLife.64812>



- Ito, T. A., Larsen, J. T., Smith, N. K., & Cacioppo, J. T. (1998). Negative information weighs more heavily on the brain: The negativity bias in evaluative categorizations. *Journal of Personality and Social Psychology*, 75(4), 887–900. <https://doi.org/10.1037//0022-3514.75.4.887>
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: Gating by inhibition. *Frontiers in Human Neuroscience*, 4, 186. <https://doi.org/10.3389/fnhum.2010.00186>
- Keil, A., Bernat, E. M., Cohen, M. X., Ding, M., Fabiani, M., Gratton, G., Kappenman, E. S., Maris, E., Mathewson, K. E., Ward, R. T., & Weisz, N. (2022). Recommendations and publication guidelines for studies using frequency domain and time-frequency domain analyses of neural time series. *Psychophysiology*, 59(5), e14052. <https://doi.org/10.1111/psyp.14052>
- Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. *Psychophysiology*, 39(5), 641–649. <https://doi.org/10.1017/S0048577202394162>
- Keil, A., Costa, V., Smith, J. C., Sabatinelli, D., McGinnis, E. M., Bradley, M. M., & Lang, P. J. (2012). Tagging cortical networks in emotion: A topographical analysis. *Human Brain Mapping*, 33(12), 2920–2931. <https://doi.org/10.1002/hbm.21413>
- Keil, A., Müller, M. M., Gruber, T., Wienbruch, C., Stolarova, M., & Elbert, T. (2001). Effects of emotional arousal in the cerebral hemispheres: A study of oscillatory brain activity and event-related potentials. *Clinical Neurophysiology*, 112(11), 2057–2068. [https://doi.org/10.1016/s1388-2457\(01\)00654-x](https://doi.org/10.1016/s1388-2457(01)00654-x)
- Keil, A., Smith, J. C., Wangelin, B. C., Sabatinelli, D., Bradley, M. M., & Lang, P. J. (2008). Electrocutaneous and electrodermal responses covary as a function of emotional arousal: A single-trial analysis. *Psychophysiology*, 45(4), 516–523. <https://doi.org/10.1111/j.1469-8986.2008.00667.x>
- Kim, H., Seo, P., Choi, J. W., & Kim, K. H. (2021). Emotional arousal due to video stimuli reduces local and inter-regional synchronization of oscillatory cortical activities in alpha- and beta-bands. *PLoS One*, 16(7), e0255032. <https://doi.org/10.1371/journal.pone.0255032>
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, 16(12), 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>
- Klimesch, W. (2018). The frequency architecture of brain and brain body oscillations: An analysis. *The European Journal of Neuroscience*, 48(7), 2431–2453. <https://doi.org/10.1111/ejn.14192>
- Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience and Biobehavioral Reviews*, 31(3), 377–395. <https://doi.org/10.1016/j.neubiorev.2006.10.004>
- Knyazev, G. G., Bocharov, A. V., Levin, E. A., Savostyanov, A. N., & Slobodskoj-Plusnin, J. Y. (2008). Anxiety and oscillatory responses to emotional facial expressions. *Brain Research*, 1227, 174–188. <https://doi.org/10.1016/j.brainres.2008.06.108>
- Kober, H., Barrett, L. F., Joseph, J., Bliss-Moreau, E., Lindquist, K., & Wager, T. D. (2008). Functional grouping and cortical-subcortical interactions in emotion: A meta-analysis of neuroimaging studies. *NeuroImage*, 42(2), 998–1031. <https://doi.org/10.1016/j.neuroimage.2008.03.059>
- Kosciessa, J. Q., Grandy, T. H., Garrett, D. D., & Werkle-Bergner, M. (2020). Single-trial characterization of neural rhythms: Potential and challenges. *NeuroImage*, 206, 116331. <https://doi.org/10.1016/j.neuroimage.2019.116331>
- Koster, E. H., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion (Washington, D.C.)*, 4(3), 312–317. <https://doi.org/10.1037/1528-3542.4.3.312>
- Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology*, 84(3), 437–450. <https://doi.org/10.1016/j.biopsycho.2009.10.007>
- LeDoux, J. (2012). Rethinking the emotional brain. *Neuron*, 73(5), 1052. <https://doi.org/10.1016/j.neuron.2012.02.018>
- Lee, J. Y., Lindquist, K. A., & Nam, C. S. (2017). Emotional granularity effects on event-related brain potentials during affective picture processing. *Frontiers in Human Neuroscience*, 11, 133. <https://doi.org/10.3389/fnhum.2017.00133>
- Levenson, R. W., Lwi, S. J., Brown, C. L., Ford, B. Q., Otero, M. C., & Verstaen, A. (2017). Emotion. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology* (4th ed., pp. 444–464). Cambridge University Press.
- Li, X., Liu, Y., Ye, Q., Lu, X., & Peng, W. (2020). The linkage between first-hand pain sensitivity and empathy for others' pain: Attention matters. *Human Brain Mapping*, 41(17), 4815–4828. <https://doi.org/10.1002/hbm.25160>
- Lorincz, M. L., Kékesi, K. A., Juhász, G., Crunelli, V., & Hughes, S. W. (2009). Temporal framing of thalamic relay-mode firing by phasic inhibition during the alpha rhythm. *Neuron*, 63(5), 683–696. <https://doi.org/10.1016/j.neuron.2009.08.012>
- Luther, L., Horschig, J. M., van Peer, J. M., Roelofs, K., Jensen, O., & Hagenaars, M. A. (2023). Oscillatory brain responses to emotional stimuli are effects related to events rather than states. *Frontiers in Human Neuroscience*, 16, 868549. <https://doi.org/10.3389/fnhum.2022.868549>
- Masood, N., & Farooq, H. (2021). Comparing neural correlates of human emotions across multiple stimulus presentation paradigms. *Brain Sciences*, 11(6), 696. <https://doi.org/10.3390/brainsci11060696>
- Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. *The Journal of Neuroscience*, 29(9), 2725–2732. <https://doi.org/10.1523/JNEUROSCI.3963-08.2009>
- Mazaheri, A., & Picton, T. W. (2005). EEG spectral dynamics during discrimination of auditory and visual targets. *Cognitive Brain Research*, 24(1), 81–96. <https://doi.org/10.1016/j.cogbr.2004.12.013>
- Meng, X., Liu, W., Zhang, L., Li, X., Yao, B., Ding, X., Yuan, J., & Yang, J. (2016). EEG oscillation evidences of enhanced susceptibility to emotional stimuli during adolescence. *Frontiers in Psychology*, 7, 616. <https://doi.org/10.3389/fpsyg.2016.00616>
- Messerotti Benvenuti, S., Buodo, G., Mennella, R., Dal Bò, E., & Palomba, D. (2019). Appetitive and aversive motivation in depression: The temporal dynamics of task-elicited asymmetries in alpha oscillations. *Scientific Reports*, 9(1), 17129. <https://doi.org/10.1038/s41598-019-53639-8>
- Michelmann, S., Griffiths, B., & Hanslmayr, S. (2022). The role of alpha and beta oscillations in the human EEG during perception and memory processes. In P. A. Gable, M. W. Miller, & E. M. Bernat (Eds.), *The Oxford handbook of eeg frequency*. Oxford Library of Psychology.
- Micucci, A., Ferrari, V., De Cesare, A., & Codispoti, M. (2020). Contextual modulation of emotional distraction: Attentional capture and motivational significance. *Journal of Cognitive Neuroscience*, 32(4), 621–633. [https://doi.org/10.1162/jocn\\_a\\_01505](https://doi.org/10.1162/jocn_a_01505)



- Miskovic, V., & Schmidt, L. A. (2010). Cross-regional cortical synchronization during affective image viewing. *Brain Research*, 1362, 102–111. <https://doi.org/10.1016/j.brainres.2010.09.102>
- Mitchell, J. F., Sundberg, K. A., & Reynolds, J. H. (2009). Spatial attention decorrelates intrinsic activity fluctuations in macaque area V4. *Neuron*, 63(6), 879–888. <https://doi.org/10.1016/j.neuron.2009.09.013>
- Most, S. B., Smith, S. D., Cooter, A. B., Levy, B. N., & Zald, D. H. (2007). The naked truth: Positive, arousing distractors impair rapid target perception. *Cognition and Emotion*, 21(5), 964–981. <https://doi.org/10.1080/02699930600959340>
- Mulckhuysen, M. (2018). The influence of emotional stimuli on the oculomotor system: A review of the literature. *Cognitive, Affective, & Behavioral Neuroscience*, 18(3), 411–425. <https://doi.org/10.3758/s13415-018-0590-8>
- Müller, M. M., Keil, A., Gruber, T., & Elbert, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band EEG activity. *Clinical Neurophysiology*, 110(11), 1913–1920. [https://doi.org/10.1016/s1388-2457\(99\)00151-0](https://doi.org/10.1016/s1388-2457(99)00151-0)
- Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: A meta-analysis. *Cognitive, Affective & Behavioral Neuroscience*, 3(3), 207–233. <https://doi.org/10.3758/cabn.3.3.207>
- Murphy, J., Devue, C., Corballis, P. M., & Grimshaw, G. M. (2020). Proactive control of emotional distraction: Evidence from EEG alpha suppression. *Frontiers in Human Neuroscience*, 14, 318. <https://doi.org/10.3389/fnhum.2020.00318>
- Nikulin, V. V., Linkenkaer-Hansen, K., Nolte, G., & Curio, G. (2010). Non-zero mean and asymmetry of neuronal oscillations have different implications for evoked responses. *Clinical Neurophysiology*, 121(2), 186–193. <https://doi.org/10.1016/j.clinph.2009.09.028>
- Noguchi, Y., & Kubo, S. (2020). Changes in latency of brain rhythms in response to affective information of visual stimuli. *Biological Psychology*, 149, 107787. <https://doi.org/10.1016/j.biopsycho.2019.107787>
- Öhman, A. (1992). Orienting and attention: Preferred preattentive processing of potentially phobic stimuli. In B. A. Campbell, H. Haynes, & R. Richardson (Eds.), *Attention and information processing in infants and adults. Perspectives from human and animal research*. Erlbaum.
- Ohman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, 130(3), 466–478. <https://doi.org/10.1037/0096-3445.130.3.466>
- Ono, H., Sonoda, M., Sakakura, K., Kitazawa, Y., Mitsuhashi, T., Firestone, E., Luat, A. F., Marupudi, N. I., Sood, S., & Asano, E. (2023). Dynamic cortical and tractography atlases of proactive and reactive alpha and high-gamma activities. *Brain Communications*, 5, fca111. <https://doi.org/10.1101/2022.07.16.500323v>
- Onoda, K., Okamoto, Y., Shishida, K., Hashizume, A., Ueda, K., Yamashita, H., & Yamawaki, S. (2007). Anticipation of affective images and event-related desynchronization (ERD) of alpha activity: An MEG study. *Brain Research*, 1151, 134–141. <https://doi.org/10.1016/j.brainres.2007.03.026>
- Panitz, C., Keil, A., & Mueller, E. M. (2019). Extinction-resistant attention to long-term conditioned threat is indexed by selective visuocortical alpha suppression in humans. *Scientific Reports*, 9(1), 15809. <https://doi.org/10.1038/s41598-019-52315-1>
- Parvaz, M. A., Moeller, S. J., Goldstein, R. Z., & Proudfit, G. H. (2015). Electrocortical evidence of increased post-reappraisal neural reactivity and its link to depressive symptoms. *Social Cognitive and Affective Neuroscience*, 10(1), 78–84. <https://doi.org/10.1093/scan/nsu027>
- Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews. Neuroscience*, 9(2), 148–158. <https://doi.org/10.1038/nrn2317>
- Pizzagalli, D., Shackman, A. J., & Davidson, R. J. (2003). The functional neuroimaging of human emotion: Asymmetric contributions of cortical and subcortical circuitry. In K. Hugdahl & R. J. Davidson (Eds.), *The asymmetrical brain* (pp. 511–532). Boston Review.
- Poldrack, R. A. (2011). Inferring mental states from neuroimaging data: From reverse inference to large-scale decoding. *Neuron*, 72(5), 692–697. <https://doi.org/10.1016/j.neuron.2011.11.001>
- Pönkänen, L. M., & Hietanen, J. K. (2012). Eye contact with neutral and smiling faces: Effects on autonomic responses and frontal EEG asymmetry. *Frontiers in Human Neuroscience*, 6, 122. <https://doi.org/10.3389/fnhum.2012.00122>
- Poole, B. D., & Gable, P. A. (2014). Affective motivational direction drives asymmetric frontal hemisphere activation. *Experimental Brain Research*, 232(7), 2121–2130. <https://doi.org/10.1007/s00221-014-3902-4>
- Popov, T., Steffen, A., Weisz, N., Miller, G. A., & Rockstroh, B. (2012). Cross-frequency dynamics of neuromagnetic oscillatory activity: Two mechanisms of emotion regulation. *Psychophysiology*, 49(12), 1545–1557. <https://doi.org/10.1111/j.1469-8986.2012.01484.x>
- Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*, 92(3), 492–512. <https://doi.org/10.1016/j.biopsycho.2012.02.007>
- Pratto, F., & John, O. P. (1991). Automatic vigilance: The attention-grabbing power of negative social information. *Journal of Personality and Social Psychology*, 61(3), 380–391. <https://doi.org/10.1037/0022-3514.61.3.380>
- Ray, W. J., & Cole, H. W. (1985). EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. *Science*, 228(4700), 750–752. <https://doi.org/10.1126/science.3992243>
- Reisenzein, R., & Franikowski, P. (2022). On the latency of object recognition and affect: Evidence from temporal order and simultaneity judgments. *Journal of Experimental Psychology: General*, 151(12), 3060–3081. <https://doi.org/10.1037/xge0001244>
- Reznick, S. J., & Allen, J. J. B. (2018). Frontal asymmetry as a mediator and moderator of emotion: An updated review. *Psychophysiology*, 55(1), e12965. <https://doi.org/10.1111/psyp.12965>
- Rizzuto, D. S., Madsen, J. R., Bromfield, E. B., Schulze-Bonhage, A., Seelig, D., Aschenbrenner-Scheibe, R., & Kahana, M. J. (2003). Reset of human neocortical oscillations during a working memory task. *Proceedings of the National Academy of Sciences of the United States of America*, 100(13), 7931–7936. <https://doi.org/10.1073/pnas.0732061100>
- Romeo, Z., Fusina, F., Semenzato, L., Bonato, M., Angrilli, A., & Spironelli, C. (2022). Comparison of slides and video clips as different methods for inducing emotions: An electroencephalographic alpha modulation study. *Frontiers in*

- Human Neuroscience*, 16, 901422. <https://doi.org/10.3389/fnhum.2022.901422>
- Rozin, P., & Royzman, E. B. (2001). Negativity bias, negativity dominance, and contagion. *Personality and Social Psychology Review*, 5(4), 296–320. [https://doi.org/10.1207/S15327957PSPR0504\\_2](https://doi.org/10.1207/S15327957PSPR0504_2)
- Sabatinelli, D., Bradley, M. M., Fitzsimmons, J. R., & Lang, P. J. (2005). Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. *NeuroImage*, 24(4), 1265–1270. <https://doi.org/10.1016/j.neuroimage.2004.12.015>
- Sabatinelli, D., Lang, P. J., Keil, A., & Bradley, M. M. (2007). Emotional perception: Correlation of functional MRI and event-related potentials. *Cerebral Cortex*, 17(5), 1085–1091. <https://doi.org/10.1093/cercor/bhl017>
- Sabu, P., Stuldreher, I. V., Kaneko, D., & Brouwer, A.-M. (2022). A review on the role of affective stimuli in event-related frontal alpha asymmetry. *Frontiers in Computer Science*, 4, 869123. <https://doi.org/10.3389/fcomp.2022.869123>
- Sarlo, M., Buodo, G., Poli, S., & Palomba, D. (2005). Changes in EEG alpha power to different disgust elicitors: The specificity of mutilations. *Neuroscience Letters*, 382(3), 291–296. <https://doi.org/10.1016/j.neulet.2005.03.037>
- Satpute, A. B., Kang, J., Bickart, K. C., Yardley, H., Wager, T. D., & Barrett, L. F. (2015). Involvement of sensory regions in affective experience: A meta-analysis. *Frontiers in Psychology*, 6, 1860. <https://doi.org/10.3389/fpsyg.2015.01860>
- Scharinger, C. (2023). Effects of emotional decorative pictures on cognitive load as assessed by pupil dilation and EEG frequency band power. *Applied Cognitive Psychology*, 37, 861–875. <https://doi.org/10.1002/acp.4087>
- Schimmack, U. (2005). Attentional interference effects of emotional pictures: Threat, negativity, or arousal? *Emotion*, 5(1), 55–66. <https://doi.org/10.1037/1528-3542.5.1.55>
- Schubring, D., Kraus, M., Stolz, C., Weiler, N., Keim, D. A., & Schupp, H. (2020). Virtual reality potentiates emotion and task effects of alpha/beta brain oscillations. *Brain Sciences*, 10(8), 537. <https://doi.org/10.3390/brainsci10080537>
- Schubring, D., & Schupp, H. T. (2019). Affective picture processing: Alpha- and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology*, 56, e13386. <https://doi.org/10.1111/psyp.13386>
- Schubring, D., & Schupp, H. T. (2021). Emotion and brain oscillations: High arousal is associated with decreases in alpha- and lower Beta-band power. *Cerebral Cortex*, 31, 1597–1608. <https://doi.org/10.1093/cercor/bhaa312>
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Hillman, C. H., Hamm, A. O., & Lang, P. J. (2004). Brain processes in emotional perception: Motivated attention. *Cognition and Emotion*, 18, 593–611. <https://doi.org/10.1080/02699930341000239>
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: Event-related brain potential studies. *Progress in Brain Research*, 156, 31–51. [https://doi.org/10.1016/S0079-6123\(06\)56002-9](https://doi.org/10.1016/S0079-6123(06)56002-9)
- Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. University of Illinois Press.
- Simons, R. F., Detenber, B. H., Cuthbert, B. N., Schwartz, D. D., & Reiss, J. E. (2003). Attention to television: Alpha power and its relationship to image motion and emotional content. *Media Psychology*, 5, 283–301.
- Sokolov, E. N. (1963). *Perception and the conditioned reflex*. Macmillan.
- Sollfrank, T., Kohnen, O., Hilfiker, P., Kegel, L. C., Jokeit, H., Brugger, P., Loertscher, M. L., Rey, A., Mersch, D., Sternagel, J., Weber, M., & Grunwald, T. (2021). The effects of dynamic and static emotional facial expressions of humans and their avatars on the EEG: An ERP and ERD/ERS study. *Frontiers in Neuroscience*, 15, 651044. <https://doi.org/10.3389/fnins.2021.651044>
- Srinivasan, R., Winter, W. R., Ding, J., & Nunez, P. L. (2007). EEG and MEG coherence: measures of functional connectivity at distinct spatial scales of neocortical Dynamics. *Journal of Neuroscience Methods*, 166(1), 41–52.
- Stevens, E. M., Frank, D., Codispoti, M., Kypriotakis, G., Cinciripini, P. M., Claiborne, K., Dewese, M. M., Engelmann, J. M., Green, C. E., Karam-Hage, M., Minnix, J. A., Ng, J., Robinson, J. D., Tyndale, R. F., Vidrine, D. J., & Versace, F. (2019). The late positive potentials evoked by cigarette-related and emotional images show no gender differences in smokers. *Scientific Reports*, 9(1), 3240. <https://doi.org/10.1038/s41598-019-39954-0>
- Strube, A., Rose, M., Fazeli, S., & Büchel, C. (2021). Alpha-to-beta- and gamma-band activity reflect predictive coding in affective visual processing. *Scientific Reports*, 11(1), 23492. <https://doi.org/10.1038/s41598-021-02939-z>
- Surcinelli, P., & Codispoti, M. (2007). Autonomic changes during the perception of emotional facial expressions. *Psychophysiology*, 44(S1), S108.
- Tassinary, L. G., Hess, U., Carcoba, L. M., & Orr, J. M. (2023). The perimetric physiological measurement of psychological constructs. In H. Cooper, M. N. Coutanche, L. M. McMullen, A. T. Panter, D. Rindskopf, & K. J. Sher (Eds.), *APA handbook of research methods in psychology: Foundations, planning, measures, and psychometrics* (pp. 531–564). American Psychological Association. <https://doi.org/10.1037/0000318-025>
- Thom, N., Knight, J., Dishman, R., Sabatinelli, D., Johnson, D. C., & Clementz, B. (2014). Emotional scenes elicit more pronounced self-reported emotional experience and greater EPN and LPP modulation when compared to emotional faces. *Cognitive, Affective, & Behavioral Neuroscience*, 14(2), 849–860. <https://doi.org/10.3758/s13415-013-0225-z>
- Uusberg, A., Uibo, H., Kreegipuu, K., & Allik, J. (2013). EEG alpha and cortical inhibition in affective attention. *International Journal of Psychophysiology*, 89(1), 26–36. <https://doi.org/10.1016/j.ijpsycho.2013.04.020>
- Uusberg, A., Uibo, H., Tiimus, R., Sarapuu, H., Kreegipuu, K., & Allik, J. (2014). Approach-avoidance activation without anterior asymmetry. *Frontiers in Psychology*, 5, 192. <https://doi.org/10.3389/fpsyg.2014.00192>
- Vagnoni, E., Lourenco, S. F., & Longo, M. R. (2015). Threat modulates neural responses to looming visual stimuli. *The European Journal of Neuroscience*, 42(5), 2190–2202. <https://doi.org/10.1111/ejn.12998>
- Valentini, E., Nicolardi, V., & Aglioti, S. M. (2017). Visual reminders of death enhance nociceptive-related cortical responses and event-related alpha desynchronisation. *Biological Psychology*, 129, 121–130. <https://doi.org/10.1016/j.biopsycho.2017.08.055>
- Vrana, S. R., & Gross, D. (2004). Reactions to facial expressions: Effects of social context and speech anxiety on responses to neutral, anger, and joy expressions. *Biological Psychology*, 66(1), 63–78. <https://doi.org/10.1016/j.biopsycho.2003.07.004>
- Wager, T. D., Kang, J., Johnson, T. D., Nichols, T. E., Satpute, A. B., & Barrett, L. F. (2015). A Bayesian model of category-specific



- emotional brain responses. *PLoS Computational Biology*, 11(4), e1004066. <https://doi.org/10.1371/journal.pcbi.1004066>
- Wang, X., & Ding, M. (2011). Relation between P300 and event-related theta-band synchronization: A single-trial analysis. *Clinical Neurophysiology*, 122(5), 916–924. <https://doi.org/10.1016/j.clinph.2010.09.011>
- Wang, X., Jin, J., Liu, W., Liu, Z., & Yin, T. (2021). Emotional processing of sadness and disgust evoked by disaster scenes. *Brain and Behavior*, 11(12), e2421. <https://doi.org/10.1002/brb3.2421>
- Wangelin, B. C., Bradley, M. M., Kastner, A., & Lang, P. J. (2012). Affective engagement for facial expressions and emotional scenes: The influence of social anxiety. *Biological Psychology*, 91(1), 103–110. <https://doi.org/10.1016/j.biopsycho.2012.05.002>
- Weinberg, A., & Hajcak, G. (2010). Beyond good and evil: The time-course of neural activity elicited by specific picture content. *Emotion*, 10(6), 767–782. <https://doi.org/10.1037/a0020242>
- Weinreich, A., Stephani, T., & Schubert, T. (2016). Emotion effects within frontal alpha oscillation in a picture oddball paradigm. *International Journal of Psychophysiology*, 110, 200–206. <https://doi.org/10.1016/j.ijpsycho.2016.07.517>
- Woodman, G. F., Wang, S., Sutterer, D. W., Reinhart, R. M. G., & Fukuda, K. (2022). Alpha suppression indexes a spotlight of visual-spatial attention that can shine on both perceptual and memory representations. *Psychonomic Bulletin & Review*, 29(3), 681–698. <https://doi.org/10.3758/s13423-021-02034-4>
- Xu, P., Peng, S., Luo, Y. J., & Gong, G. (2021). Facial expression recognition: A meta-analytic review of theoretical models and neuroimaging evidence. *Neuroscience and Biobehavioral Reviews*, 127, 820–836. <https://doi.org/10.1016/j.neubiorev.2021.05.023>
- Yang, K., Tong, L., Shu, J., Zhuang, N., & Zeng, Y. (2020). High gamma band EEG closely related to emotion: Evidence from functional network. *Frontiers in Human Neuroscience*, 14, 89. <https://doi.org/10.3389/fnhum.2020.00089>
- Yin, S., Bo, K., Liu, Y., Thigpen, N., Keil, A., Ding, M., Crayton Pruitt, J., & Pruitt, C. (2020). Fear conditioning prompts sparser representations of conditioned threat in primary visual cortex. *Social Cognitive and Affective Neuroscience*, 15(9), 950–964. <https://doi.org/10.1093/scan/nsaa122>
- Yordanova, J., Kolev, V., & Polich, J. (2001). P300 and alpha event-related desynchronization (ERD). *Psychophysiology*, 38(1), 143–152.
- Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research. Brain Research Reviews*, 41(1), 88–123. [https://doi.org/10.1016/s0165-0173\(02\)00248-5](https://doi.org/10.1016/s0165-0173(02)00248-5)

**How to cite this article:** Codispoti, M., De Cesarei, A., & Ferrari, V. (2023). Alpha-band oscillations and emotion: A review of studies on picture perception. *Psychophysiology*, 60, e14438. <https://doi.org/10.1111/psyp.14438>