

Emotion and Brain Oscillations: High Arousal is Associated with Decreases in Alpha- and Lower Beta-Band Power

David Schubring^{id} and Harald T. Schupp

Department of Psychology, University of Konstanz, Konstanz, Germany

Address correspondence to Harald Schupp, General & Biological Psychology, University of Konstanz, P.O. Box 36, 78457 Konstanz, Germany.
Tel: +49-(0)7531-88-2504; Email: harald.schupp@uni-konstanz.de.

Abstract

The study of brain oscillations associated with emotional picture processing has revealed conflicting findings. Although many studies observed a decrease in power in the alpha- and lower beta band, some studies observed an increase. Accordingly, the main aim of the present research series was to further elucidate whether emotional stimulus processing is related to an increase or decrease in alpha/beta power. In Study 1, participants ($N = 16$) viewed briefly presented (150 ms) high-arousing erotic and low-arousing people pictures. Picture presentation included a passive viewing condition and an active picture categorization task. Study 2 ($N = 16$) replicated Study 1 with negative valence stimuli (mutilations). In Study 3 ($N = 18$), stimulus materials of Study 1 and 2 were used. The main finding is that high-arousing pictures (erotica and mutilations) are associated with a decrease of power in the alpha/beta band across studies and task conditions. The effect peaked in occipitoparietal sensors between 400 and 800 ms after stimulus onset. Furthermore, a late (>1000 ms) alpha/beta power increase to mutilation pictures was observed, possibly reflecting top-down inhibitory control processes. Overall, these findings suggest that brain oscillations in the alpha/beta-band may serve as a useful measure of emotional stimulus processing.

Key words: attention, arousal, EEG, emotion, ERD

Introduction

Evidence has accumulated in the past 2 decades that brain oscillations in the alpha and lower beta range (~8–30 Hz) provide windows into attention and memory processes in humans. Responses to stimuli or task demands in the alpha and lower beta band can be reflected by both, increases or decreased in power, denoted as event-related desynchronization (ERD) or synchronization (ERS). The various accounts considering the functional significance of ERD/ERS share the notion that power increases relate to a state of inhibition of neural networks whereas ERD reflects the release from inhibition (Klimesch et al. 2007; Foxe and Snyder 2011; Hanslmayr et al. 2012; Klimesch 2012; Frey et al. 2015; Sadaghiani and Kleinschmidt 2016). Three experiments are reported here aiming to further

elucidate whether emotional stimulus processing is reliably and consistently related to ERD/ERS responses.

The majority of studies investigating emotional stimulus processing observed that emotional compared with neutral stimulus processing is associated with an ERD response in the alpha and lower beta range. These studies examined different emotional stimulus materials including pictures from the International Affective Picture Series (de Cesarei and Codispoti 2011; Cui et al. 2013; Meng et al. 2016, Ferrari, Mastria, and Codispoti, 2020), and facial expression (Knyazev et al. 2008; Balconi and Mazza 2009; Popov et al. 2012a, 2013; Schneider et al. 2018). However, even although many studies reported that emotional stimulus processing is associated with decreased power in the alpha and lower beta range, there is considerable

variability in findings in terms of onset latency (e.g., ~200 vs. 800 ms) and topography (anterior vs. centroparietal vs. occipital). Differences in findings across studies can be in part attributed to different experimental protocols, e.g. duration of stimulus presentation, and methodological differences, e.g. evoked versus induced event-related oscillations, and different scaling of responses (decibel, percentage, and absolute). To address some of these methodological issues, [Schubring and Schupp \(2019\)](#) presented erotica and romantic stimuli varying in arousal with brief presentation times focusing on induced event-related oscillations. A robust ERD response to erotic images was observed for decibel and absolute power and various baseline measures addressing the concern that low baseline activity may prevent the detection of alpha-ERD ([Başar and Güntekin 2012](#)). Overall, the finding of an ERD response to emotional stimuli has been observed across the range of emotional stimulus materials used in affective neuroscience research.

However, the finding that emotional stimulus processing is associated with an ERD response is challenged by results from studies which reported an increase rather than decrease in alpha power for emotionally significant stimuli. Some discrepancies may be accounted for by methodological differences. For instance, several studies reported increased alpha/beta power to unpleasant compared with neutral or positive images analyzing event-related spectral perturbations including evoked and induced oscillations in an earlier time window (0–400 ms), ([Güntekin and Başar 2007](#); [Güntekin and Başar 2010](#); [Güntekin and Tülay 2014](#); [Mennella et al. 2017](#)). Thus, it is likely that these responses indicate evoked rather than induced oscillations. However, analyzing event-related spectral perturbations, several studies report increased power in the alpha and/or lower beta range in later time windows (>500 ms) to emotionally arousing (pleasant and unpleasant compared with neutral IAPS pictures ([Aftanas et al. 2002, 2004](#)), particularly apparent for aversive stimulus materials ([Uusberg et al. 2013](#)). Thus, further research is needed to resolve conflicting evidence on the issue whether emotional stimulus processing is associated with ERS or ERD responses indicating inhibitory or release from inhibitory neural states respectively.

Here, we present 3 experiments aiming to determine whether emotional stimulus processing is associated with an ERD or ERS response in the alpha and lower beta range. Providing a conceptual replication of our previous study ([Schubring and Schupp 2019](#)), Study 1 explored the processing of high arousing pleasant that is, erotica, compared with control pictures in a free viewing paradigm as well as an explicit categorization task demanding working memory capacity (see also [Hajcak et al. 2007](#); [Schupp et al. 2007](#)). Study 2 aimed to demonstrate generality of findings across stimulus valence examining mutilations as a high arousing negative picture category. Erotica and mutilations were selected as high-arousing pleasant and unpleasant picture categories based on an array of studies showing that these picture contents prompt largest modulations in emotional response measures including physiological arousal (e.g., skin conductance) and defensive reflex activity, fMRI-BOLD signal changes in inferotemporal cortex and amygdala, and ERP components (e.g., [Bradley et al. 2001](#); [Sabatinelli et al. 2005](#); [Schupp et al. 2004](#)). Finally, Study 3 presented both, erotic and mutilation images, alongside to less arousing control stimuli. This design was chosen to follow-up new findings from Study 2 showing that aversive images prompted a late ERS response subsequent to the earlier ERD. In all 3 studies, power analysis focused on induced oscillations which are not phase-locked to the stimulus event.

Thus, the contribution of stimulus-evoked oscillations reflecting ERP components such as the late positive potential was minimized. In addition, although previous research often focused on the specific frequency bands, that is, alpha activity, we investigated a broader frequency range, that is, 1–40 Hz, including both alpha- and beta-band activity. Furthermore, in order to increase interpretability of emotional modulation effects, all 3 studies included the replication of a cognitive task manipulation, that is, alpha/beta power decrease to target stimuli, which served as a within-study check that the cognitive task manipulation was successful. Finally, the stability of emotional modulation effects was explored as a function of stimulus repetition. Overall, our primary aim was to examine the hypothesis that emotional stimulus processing (pleasant and unpleasant) is associated with power decreases in the alpha and lower beta range during free viewing and an explicit categorization task.

Study 1

The main aim of Study 1 was to provide a conceptual replication of our previous research observing robust power decreases for high-arousing erotic compared with less arousing romantic stimuli across different scaling and baseline measures ([Schubring and Schupp 2019](#)). This research examined picture processing in free viewing conditions as well as an explicit categorization task, that is, asking participants to press a button when the target stimuli (either erotic or romantic images in different blocks) appeared on the screen. The present research presented pictures of couples either in erotic or everyday situations and used a different explicit categorization task. Specifically, rather than pressing a button to the target stimuli, participants were asked to count the target stimuli. On the one hand, this task rules out possible confounds by motor responses, on the other hand, the task taxes working memory resources as the target count has to be kept in mind across trials ([Polich 2007](#); [Schupp et al. 2007](#)). Overall, we predicted to replicate decreased alpha- and lower beta-band power for erotic stimuli for both, free viewing and active task conditions.

Study 1: Materials and Methods

Participants

Sixteen healthy volunteers (8 men/8 women) with a mean age of 25.7 years ($SD = 7.2$) were recruited on the campus of the University of Konstanz. All participants had normal or corrected-to-normal vision. Sample size was determined based on previous research on emotional modulation of brain oscillations ([Schubring and Schupp 2019](#)). Power estimation indicated that a large sized effect can be detected with $\alpha = 0.05$, and a power of 0.9 with a sample size of $N = 15$ ([Faul et al. 2007](#)). Participants received monetary compensation or course credit for participation. The ethical committee of the University of Konstanz approved the experimental procedure in accordance with the regulations of the Declaration of Helsinki. All participants provided informed consent.

Stimuli

The stimuli comprised 2 picture categories, that is, “erotic” and “neutral”, which were selected from the International Affective Picture System (IAPS; [Lang, Bradley, and Cuthbert, 2008](#)) and public domain pictures available on the Internet. The erotic picture series comprised 20 color images of nude couples in erotic, interacting poses (“erotic”) with 8 pictures drawn from the IAPS

library (4658, 4659, 4664, 4672, 4680, 4693, 4694, and 4695). The neutral control category included 20 images of dressed couples in neutral, noninteracting situations, which were selected to promote the comparability of the 2 picture categories in terms of picture composition and categorical homogeneity. Additionally, the pictures were normalized in terms of mean color and luminosity. Each picture was equally often presented both normally and as a mirror image with flipped left–right axis to prevent a bias in lateralization.

Self-report data on valence and arousal were obtained at the end of the experiment using the self-assessment manikin (Bradley and Lang, 1994). Replicating previous findings (Schubring and Schupp 2019), erotic ($M = 5.46$, $SD = 2.20$) images were evaluated as more arousing than neutral images ($M = 3.06$, $SD = 1.35$, $t(15) = 5.06$, $P = 0.001$) and there were no significant differences in valence for the 2 categories (erotic: $M = 5.87$, $SD = 1.84$; neutral: $M = 5.86$, $SD = 0.88$; $t(15) = 0.04$, $P = 0.97$).

Experimental Conditions

The experiment consisted of 2 conditions: Passive and active picture viewing. Order of active and passive viewing conditions was balanced across participants.

Passive Viewing Condition. In the passive viewing condition, participants viewed the pictures in random order without explicit task instruction. Each picture was shown 8 times for 150 ms which resulted in a total of 320 trials. The trials were separated with an intertrial-interval (ITI) of 3500–4200 ms. To ensure a similar procedure as in the active task condition, the passive condition was divided into 5 blocks with 48–80 trials each, separated by a short break of approximately 1 min.

Active Task Condition. In the active task condition, participants viewed the pictures in random order while silently counting the occurrences of 1 of the 2 picture categories. The presentation was divided into 10 blocks with 48–80 trials each. After each block, the experimenter asked for the number of target images counted. Afterwards, the target category changed, with half of the participants starting with “erotic” as target category and the other half with “neutral”.

Presentation times and intertrial intervals were identical to the passive condition. Each picture was shown 8 times as a nontarget and 8 times as a target, which resulted in a total of 640 trials. The order of presentation both for targets and pictures was randomized with restrictions to minimize priming effects because of preceding trials (Flaisch et al. 2016). All possible orders of target and nontarget pictures were realized equally often, i.e., the 4 possible orders (target–target, target–nontarget, nontarget–target, and nontarget–nontarget) each made up approximately 25% (minimum 24%–maximum 26%) of all transitions. Furthermore, the entire picture set was presented before the picture series was presented again in a different order. A different picture presentation order was generated for each participant.

Participants would receive an additional 1€ bonus for each correctly counted block and 0.50€ for each block with a $+1$ margin of error as incentive. On average, the majority of blocks were counted correctly or within a $+1$ margin of error with comparable task performance for both picture categories (neutral targets: $M = 89\%$, $SD = 14\%$; erotic targets: 88% , $SD = 18\%$; $t(15) = 0.29$, $P = 0.77$).

EEG Data Acquisition and Main Analysis

Brain and ocular scalp potential fields were measured with a 257 lead geodesic sensor net, on-line bandpass filtered from 0.01 to 100 Hz, and sampled at 1000 Hz using Netstation acquisition software and Electrical Geodesics (EGI; Eugene, OR) amplifiers. Data were recorded continuously with the vertex sensor as the reference electrode. Stimulus synchronized epochs lasting from 1000 ms before until 2000 ms after picture onset were extracted. Heart and eye-blink artifacts were corrected by independent component analysis. Trials containing movement artifacts and noisy channels were rejected based on visual inspection of variance. For each participant, trials and channels with extreme variance were removed. On average, 94.4% ($SD = 1.9\%$) of the channels were used per participant. Removed EEG channels were interpolated by the mean of their neighboring sensors. The mean waveforms were calculated using on average 93.8% ($SD = 2.5\%$) of the trials. After artifact correction, data were converted to an average reference. EEG data analysis was conducted using the open-source signal processing toolbox FieldTrip (Oostenveld et al. 2011) and in-house functions using MATLAB 9.3.0 R2017b (MathWorks Inc., Natick, MA).

Frequency Analysis. Based on the results from Schubring and Schupp (2019), EEG frequency analysis focused on induced brain activity in the alpha/beta band. Accordingly, in a first step, the ERP average of each condition was computed and subtracted from the single trials comprising this condition. In a second step, a fast fourier transform was calculated for single trial data in the frequency range from 1 to 30 Hz. Specifically, a sliding window of 200 ms was multiplied by a Hanning taper resulting in a spectral resolution of 5 Hz and a time resolution of ± 100 ms. The sliding window advanced in 24 ms and 1 Hz increments to estimate changes in power over time and frequency. For each condition, single-trial power estimates were then averaged across trials and expressed as a decibel change from prestimulus baseline (-300 ms to 0 ms).

Statistics. To determine the main effects of emotion (erotic vs. neutral) and task (target vs. nontarget), data from each time point (0–2000 ms), sensor, and frequency bin (1–30 Hz) of the respective picture/task condition were submitted separately to a dependent sample t-test. The interaction of task by emotion was examined with the contrast ($\text{Erotic}_{\text{Target}} - \text{Neutral}_{\text{Target}}$) vs. ($\text{Erotic}_{\text{Nontarget}} - \text{Neutral}_{\text{Nontarget}}$). To account for the multiple comparisons problem, a cluster-based permutation test (Maris and Oostenveld 2007) was performed. In short, this procedure clusters adjacent t-values (in time, frequency, and sensor space) to a single summed cluster test statistic. Clusters were formed when they had at least 2 neighbors that reached a cluster-forming threshold of $P < 0.05$. These clusters were then tested against a Monte Carlo approximation of the test statistic, which was formed by randomly shuffling the data for 1000 permutations and reporting the proportion of random shuffles that were bigger than the actual observed cluster test statistic as a cluster P value.

Furthermore, exploratory follow-up tests were conducted to reproduce the effects separately in each condition and test for interactions between conditions using the main effects of emotion and task as a region of interest. Toward this end, for each condition, all sensors, time points, and frequencies forming a significant cluster effect were summed up and submitted to a dependent sample t-test.

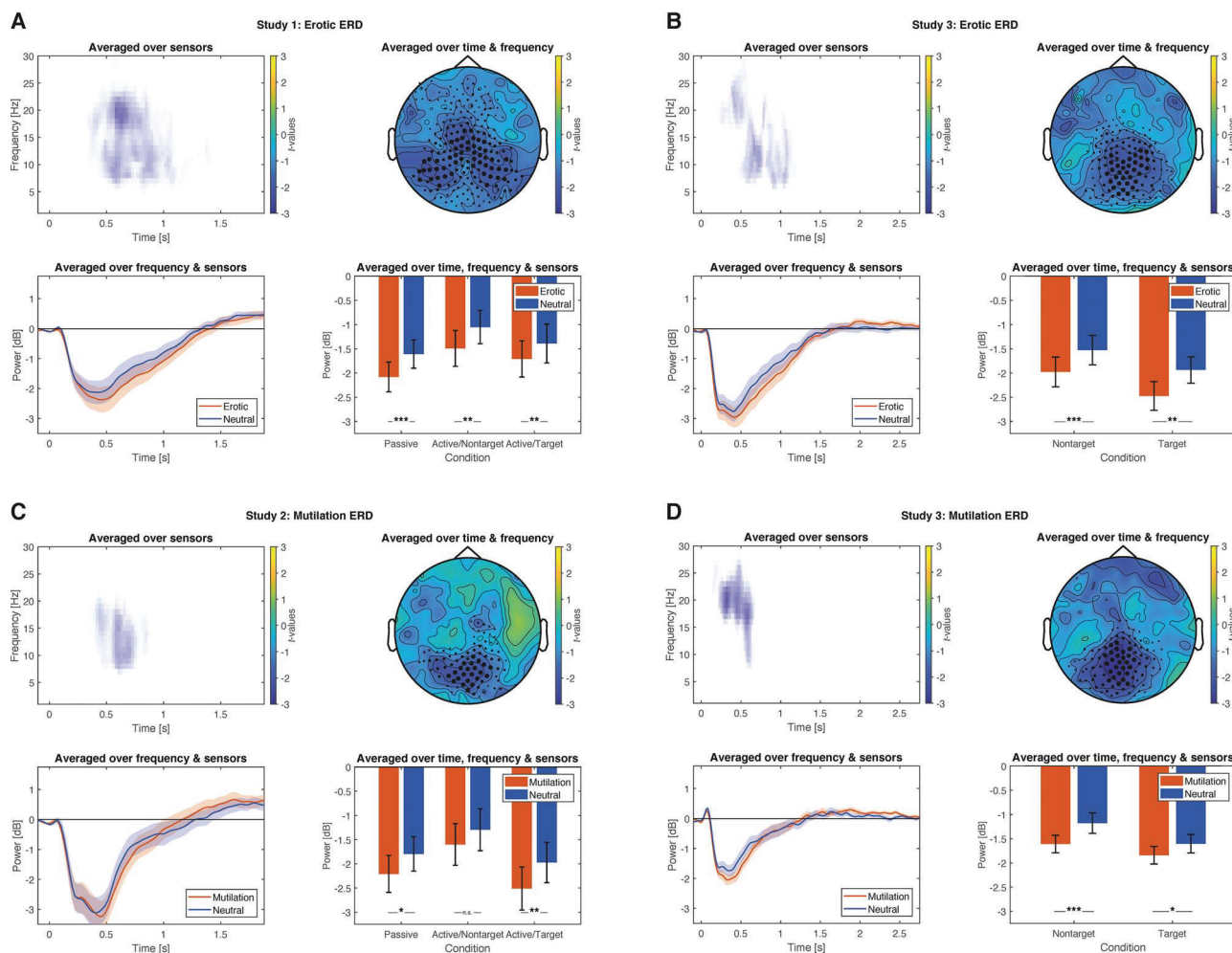


Figure 1. Illustration of the emotional ERD. Emotional pictures elicit a stronger ERD than neutral pictures in Study 1, 2, and 3. (A, B, C, and D): Top left: time–frequency plot of t -values, averaged across sensors of the respective cluster (see top right). Only time–frequency bins which are part of the cluster are displayed. Opacity represents the percentage of sensors showing the effect, e.g., nearly opaque time–frequency bins indicate that only few sensors contribute to this effect. Top right: topography of t -values averaged across the significant time points and frequency bins (see top left). The size of the marked sensors is displayed proportional to their contribution to the cluster. Bottom left: time course of the respective ERD cluster. Values were averaged over the respective sensors (see top right) and frequencies (see top left). Colored shaded areas signify standard errors. Gray shaded areas signify the extent of the cluster. Bottom right: bar plot from the respective cluster averaged across time, sensors, and frequency, separately for the different task conditions. Error bars signify standard errors. Asterisks indicate the significance of exploratory post-hoc subgroup comparisons: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Study 1: Results

Emotion Main Effect for Erotic Pictures

A first analysis determined emotional modulation effects combined across passive viewing and active task conditions. As shown in Figure 1A (top left), erotic compared with control pictures elicited an overall stronger ERD response ($P = 0.004$), which was most pronounced in the alpha and lower beta band (~8–22 Hz). The effect was found over extended posterior and central regions (Fig. 1A top right). Although the peak of the overall ERD in both conditions was around 500 ms (Fig. 1A bottom left), the difference between conditions was sustained longer and observed in a time window lasting from approximately 400 to 1100 ms.

Exploratory post-hoc tests within this cluster (Fig. 1A bottom right) reproduced the effect separately for passive ($t(15) = 4.15$, $P < 0.001$), active/nontarget ($t(15) = 3.60$, $P = 0.003$) and active/target conditions ($t(15) = 3.63$, $P = 0.002$).

Target ERD

Serving as a manipulation check, target and nontarget picture conditions were compared. As expected, combined across erotic and neutral pictures, target as compared with nontarget picture processing was associated with a stronger ERD. The effect was most in the alpha and lower beta band (~9–15 Hz) pronounced over extended central sensor regions from approximately 500–800 ms (see Fig. 2 top).

Emotion \times Target Interaction

No significant cluster effect for an emotion \times target interaction was found in Study 1.

Study 2

Study 1 replicated the main findings from Schubring and Schupp (2019) in reporting distinct effects of emotional arousal and task

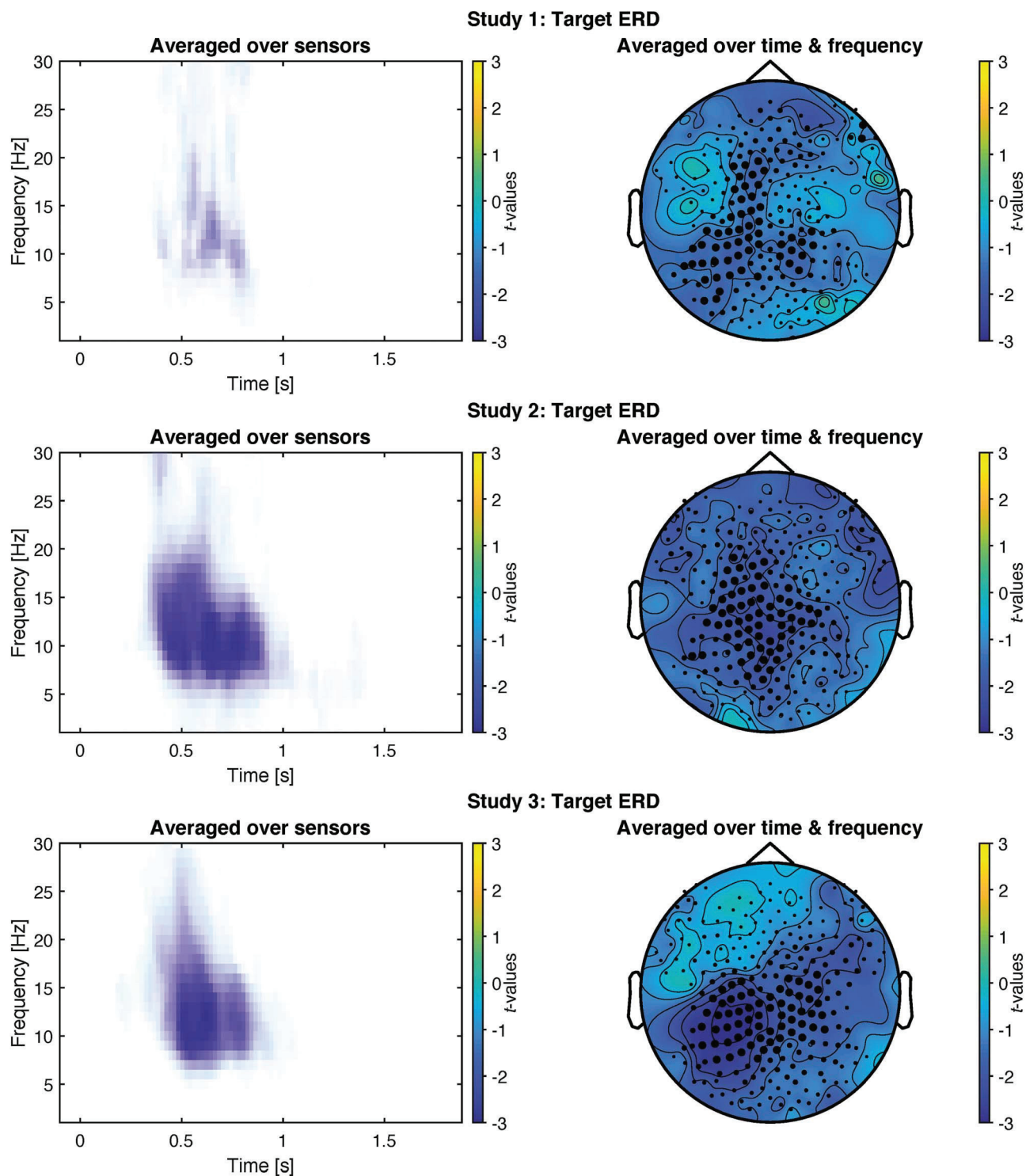


Figure 2. Illustration of the target ERD. Target pictures elicit a stronger ERD than nontarget pictures in Study 1, 2, and 3.

relevance, that is, a decrease of alpha- and lower beta power to erotic and target stimuli, in free viewing and active task conditions. Relying on the same experimental protocol, the main aim of Study 2 was to extend the results of Study 1 to unpleasant stimulus materials. Thus, rather than presenting high-arousing positive images, the stimulus categories comprised

high-arousing mutilation and neutral control stimuli. Given that these picture contents have produced conflicting findings in previous research with strong ERD (de Cesarei and Codispoti 2011) and ERS responses in the alpha-band (Uusberg et al. 2013), the main aim was to determine whether mutilation pictures elicit an ERD or an ERS response.

Study 2: Materials and Methods

Participants

Sixteen participants (8 women, 8 men) between 18 and 30 years of age ($M = 22.4$, $SD = 3.3$) participated in the study. All participants had normal or corrected-to-normal vision. Participants received monetary compensation or course credit for participation. The ethical committee of the University of Konstanz approved the experimental procedure in accordance with the regulations of the Declaration of Helsinki. All participants provided informed consent.

Stimulus Materials

Participants viewed 20 pictures from the IAPS (Lang et al. 2008). The 2 picture categories consisted of 10 picture contents showing scenes of mutilation and injury (mutilation category: 3010, 3030, 3051, 3061, 3069, 3071, 3101, 3120, 3225, and 3550), and 10 pictures showing individual people in everyday life situations (people category: 2019, 2102, 2104, 2190, 2200, 2221, 2372, 2383, 2850, and 5410). Stimulus selection was based on previous studies showing that images of mutilation compared with people are associated with pronounced differences across various emotional response measures (Bradley et al. 2001; Sabatinelli et al. 2005; Schupp et al. 2007). As expected, mutilation pictures were rated as significantly more unpleasant compared with pictures of people (valence $M = 3.09$ and 5.93 , $SD = 0.85$ and 0.42 , respectively; $t(15) = 16.5$, $P < 0.001$). Furthermore, mutilation pictures were rated as more arousing compared with pictures of people ($M = 5.56$ and 2.80 , $SD = 1.36$ and 1.25 , respectively; $t(15) = 7.60$, $P < 0.001$).

Experimental Conditions and EEG Data Acquisition and Analysis

Active and passive task conditions, experimental methodology, EEG data collection, and analysis were the same as in Study 1.

Regarding task performance, most blocks were counted correctly or within a ± 1 margin of error (94%). However, performance was better for the neutral people (correct $M = 99\%$, $SD = 5\%$) compared with the mutilation category ($M = 90\%$, $SD = 16\%$; $t(15) = 2.4$, $P = 0.029$).

Study 2: Results

Emotion Main Effects for Mutilation Pictures

As shown in Figures 1C and 3A, emotional modulation in the alpha/lower beta band varied across time. Specifically, although mutilation pictures initially resulted in an ERD, the effect reversed direction later in time leading to an increased synchronization.

Combined across active and passive task conditions, mutilation pictures compared with images depicting people in neutral situations elicited a significant ERD response ($P = 0.044$) in the alpha- and lower beta-band (~ 8 – 18 Hz) over posterior regions between approximately 400–800 ms (Fig. 1C). Furthermore, exploratory post-hoc tests within this cluster reproduced the effect separately for the passive ($t(15) = 2.34$, $P = 0.034$) and active/target conditions ($t(15) = -3.78$, $P = 0.002$). However, as shown in Figure 1C (bottom right), the effect of a larger ERD response to mutilation images only approached significance for the active/nontarget condition ($t(15) = -1.77$, $P = 0.097$; Fig. 1C bottom right).

The later mutilation ERS was highly significant ($P < 0.001$) and centered in the upper alpha and lower beta band (~ 10 – 20 Hz) appearing over anterior and posterior regions around

approximately 1100–1600 ms (Fig. 3A). In addition, exploratory post-hoc testing reproduced the effect within each conditions (passive $t(15) = 3.55$, $P = 0.003$; active/nontarget $t(15) = 7.98$, $P < 0.001$; active/target $t(15) = 3.02$, $P = 0.009$).

Target ERD

Combined across mutilation and neutral conditions, target as compared with nontarget picture processing was associated with a stronger ERD response ($P < 0.001$) in the alpha/lower beta band (~ 8 – 16 Hz) over central sensor sites in a time window from approximately 400 to 900 ms (see Fig. 2 middle).

Emotion \times Target Interaction

As in Study 1, the interaction of task by emotion was examined with a contrast comparing the emotional modulation (mutilation—neutral) separately for target and nontarget stimuli. As shown in Figure 4 (top panels), a significant interaction effect ($P = 0.027$) was observed in the alpha/low beta range (~ 8 – 18 Hz) over central regions. The interaction appeared between approximately 900 and 1200 ms, subsequent to ERD emotion and task effects, and preceding the emotional ERS effect. Exploratory follow-up testing revealed a significant event-related synchronization to mutilation pictures when they were nontargets ($t(15) = 5.97$, $P < 0.001$), contrasting to an desynchronization when they were targets ($t(15) = -2.35$, $P = 0.033$; Fig. 4 top right).

Study 3

Study 2 provided further support for the notion that unpleasant picture processing is associated with a power decrease in the alpha- and lower beta band between 400 and 800 ms after stimulus onset. Thus, an ERD response is observed for arousing stimuli with positive (Study 1) and negative (Study 2) stimulus valence. However, an unexpected finding was that mutilation picture elicited an ERS response between 1100 and 1600 ms. To replicate this finding and to directly compare differences among positive and negative valenced stimulus materials, Study 3 presented the stimulus materials of Study 1 (erotic vs. everyday couples) and Study 2 (mutilation vs. neutral people).

Study 3: Materials and Methods

Participants

Eighteen participants (15 women) with a mean age of 23.1 years ($SD = 1.9$) participated in the study. All participants had normal or corrected-to-normal vision. Participants received course credit for participation. The ethical committee of the University of Konstanz approved the experimental procedure in accordance with the regulations of the Declaration of Helsinki. All participants provided informed consent.

Stimulus Materials

Stimulus materials comprised 3 categories of pictures. For the erotic and mutilation categories, 10 exemplars were selected used in Study 1 and 2. Similarly, for the neutral picture category ($n = 10$), half the exemplars were selected from the neutral categories of Study 1 and 2, respectively. As expected, stimulus categories differed in arousal ratings with both erotic and mutilation pictures rated as more arousing compared with the neutral category (erotic: $M = 5.88$, $SD = 1.47$, neutral: $M = 2.26$, $SD = 0.97$, mutilation: $M = 6.55$, $SD = 1.08$; erotic vs. neutral: $t(17) = 11.8$, $P < 0.001$; erotic vs. mutilation: $t(17) = 1.60$, $P = 0.13$, mutilation vs.

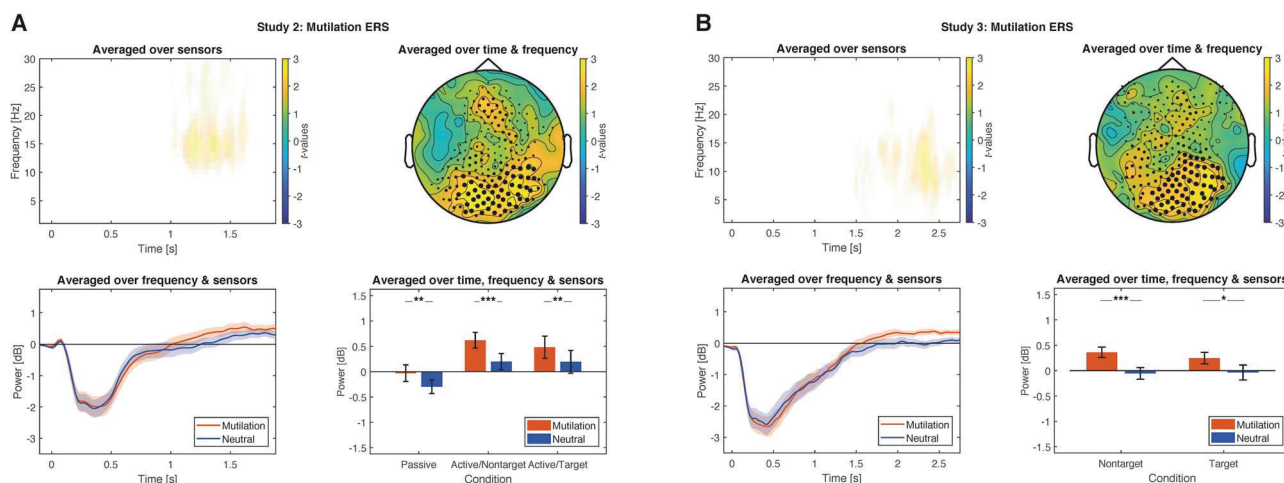


Figure 3. Illustration of the mutilation ERS. Mutilation pictures elicit a stronger ERS than neutral pictures in a later time window in Study 2 and 3. (A and B): Top left: time–frequency plot of t -values, averaged across sensors of the respective cluster (see top right). Only time–frequency bins which are part of the cluster are displayed. Opacity represents the percentage of sensors showing the effect, e.g., nearly opaque time–frequency bins indicate that only few sensors contribute to this effect. Top right: topography of t -values averaged across the significant time points and frequency bins (see top left). The size of the marked sensors is displayed proportional to their contribution to the cluster. Bottom left: time course of the respective ERD cluster. Values were averaged over the respective sensors (see top right) and frequencies (see top left). Colored shaded areas signify standard errors. Grey shaded areas signify the extent of the cluster. Bottom right: bar plot from the respective cluster averaged across time, sensors, and frequency, separately for the different task conditions. Error bars signify standard errors. Asterisks indicate the significance of exploratory post-hoc subgroup comparisons: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

neutral: $t(17) = 23.0$, $P < 0.001$). Regarding valence, a decrease in pleasantness was observed from erotic to neutral to mutilation pictures (erotic: $M = 6.57$, $SD = 1.08$, neutral: $M = 5.24$, $SD = 0.29$, mutilation: $M = 2.09$, $SD = 0.62$; erotic vs. neutral: $t(17) = 5.25$, $P < 0.001$, erotic vs. mutilation: $t(17) = 24.9$, $P < 0.001$, mutilation vs. neutral: $t(17) = 30.9$, $P < 0.001$).

Experimental Conditions and EEG Data Acquisition and Analysis

The experiment consisted of the active task condition. Methodology was similar as in Study 1 and 2, with the difference that the picture stream comprised 3 rather than 2 stimulus categories, and, consequently, participants asked to count in separate blocks either erotica, mutilation, or neutral pictures. Specifically, the picture stream was divided into 15 blocks with 48–80 trials each with a short pause after the eighth block. Picture presentation time was again 150 ms, however, to reduce the length of the study, the intertrial interval was shortened to 2500–3200 ms. Overall, the study comprised 900 trials. The order of presentation was randomized with restrictions to minimize priming effects because of preceding trials (Flaisch et al. 2016). All possible orders of picture categories were realized equally often, i.e., the 9 possible orders (3 picture categories \times 3 picture categories) each made up approximately 11% (minimum 10%—maximum 12.5%) of all transitions. Additionally, no picture category could occur more than 6 times in succession. Furthermore, the entire picture set was presented before the picture series was presented again in a different order.

Similar to Study 1 and 2, the majority of blocks were counted correctly or within ± 1 margin of error (neutral target: $M = 92\%$, $SD = 14\%$; erotic target: $M = 92\%$, $SD = 15\%$; mutilation target: $M = 86\%$, $SD = 27\%$) which did not differ significantly between groups ($F(2,54) = 0.46$, $P = 0.63$).

EEG data collection and analysis were the same as in Study 1 and 2, except for an extended time window (0–2750 ms) for the frequency analysis.

Study 3: Results

Erotic ERD

Replicating the results of Study 1, erotic picture processing induced a significantly ($P = 0.013$) larger ERD response compared with control pictures in the alpha and lower beta band (~ 8 –15 Hz). The effect appeared over extended centroparietal regions in a time window lasting from ~ 500 to 1000 ms (see Fig. 1B). Exploratory post-hoc analyses reproduced the effect separately for nontarget ($t(17) = 5.81$, $P < 0.001$) and target conditions ($t(17) = 3.68$, $P = 0.002$).

Furthermore, a slight resynchronization/ERS after the emotional ERD effect was observed in a later time window around approximately 2000–2500 ms (Fig. 1B bottom left). However, the effect approached significance only in an exploratory post-hoc analysis of this time window and cluster ($P = 0.086$).

Mutilation ERD and ERS

As shown in Figure 1D and Figure 3B, the findings of significant ERD and ERS modulation in earlier (ERD) and later (ERS) time windows for mutilation pictures was replicated.

Regarding the early effect, a significant ERD response ($P = 0.024$) to mutilation compared with neutral pictures was observed in the beta-frequency range (~ 16 –23 Hz) over centroparietooccipital sensor regions, peaking between approximately 300 to 600 ms. Exploratory post-hoc analysis reproduced the ERD effect for nontarget ($t(17) = 5.82$, $P < 0.001$) and target conditions ($t(17) = 2.47$, $P = 0.024$).

Regarding the later effect, a significantly increased ($P = 0.002$) synchronization was induced by mutilation compared with neutral pictures in the alpha/low beta-frequency range (~ 8 –15 Hz) over posterior sensor regions in a time window from approximately 1800 to 2600 ms. Exploratory post-hoc testing reproduced the effect within each condition (nontarget $t(17) = 5.63$, $P < 0.001$; target $t(17) = 2.37$, $P = 0.030$).

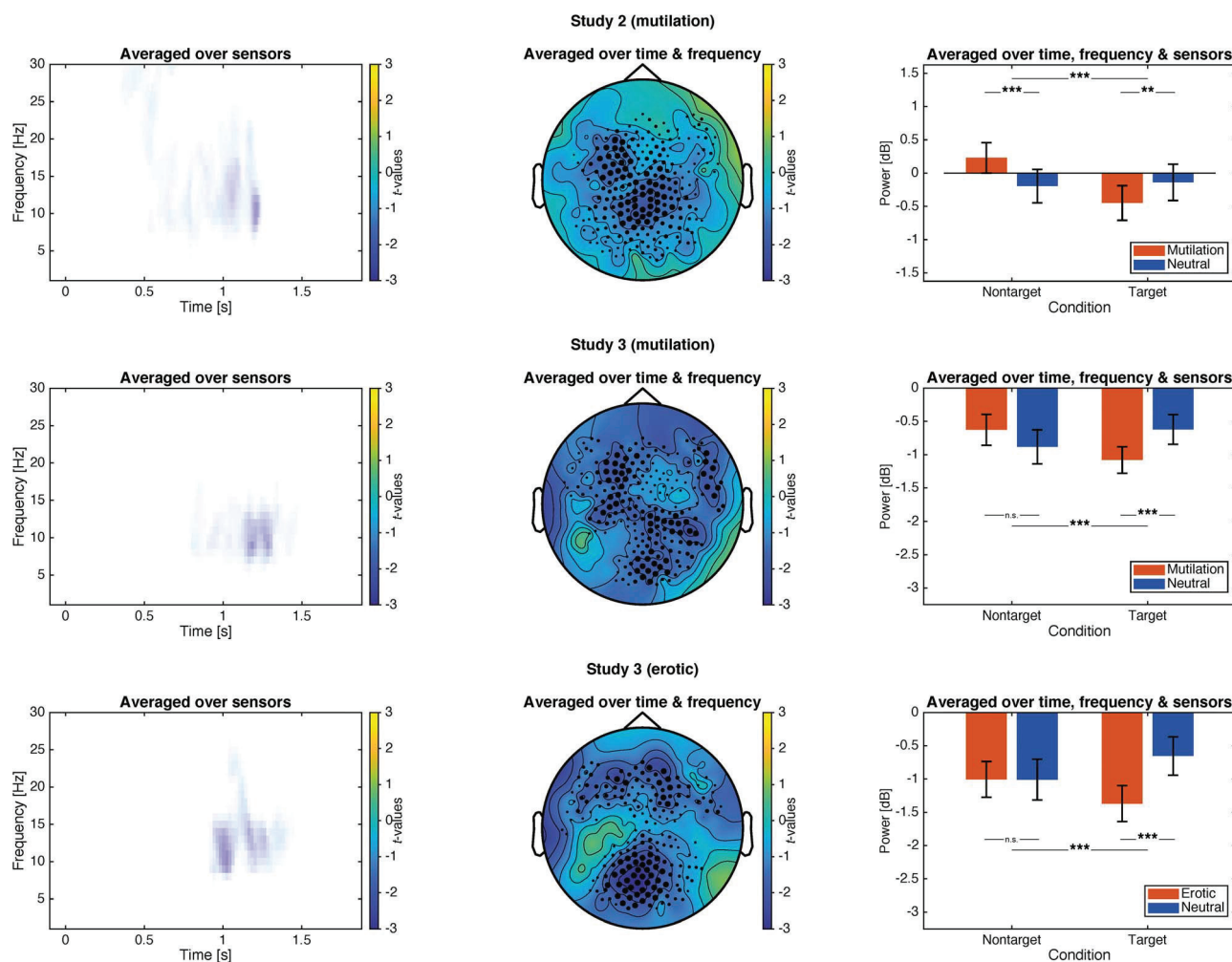


Figure 4. Illustration of the emotion \times target interaction for Study 2 (top), Study 3 for mutilation pictures (middle) and Study 3 for erotic pictures (bottom). Target pictures show an emotional ERD whereas nontarget pictures show a mutilation ERS (Study 2) or no emotional modulation (Study 3).

Target ERD

Combined across erotic and neutral target conditions, target as compared with nontarget picture processing was associated with a stronger ERD, peaking in the alpha/lower beta band over central regions around 500–800 ms (see Fig. 2 bottom).

Emotion \times Target Interaction

When comparing the emotional difference for target and nontarget task conditions, an emotion \times target interaction was found separately for mutilation ($P = 0.035$; Fig. 4 middle) and erotic ($P = 0.024$; Fig. 4 bottom) picture conditions indicating a stronger emotional ERD for targets than for nontargets. Both interactions were largely similar, peaking in the upper alpha and lower beta-range (~ 9 – 15 Hz) over extended posterior-central sensor areas around 1000–1400 ms. No significant 3-way interaction of Emotion \times Target \times Valence was found.

Study 1–3: Effects of Stimulus Repetition

A recent study observed that the alpha power decrease associated with the processing of high arousing pleasant and unpleasant pictures was stable across stimulus repetitions (Ferrari et al.

2020). Building upon these findings, emotional modulation of erotica and mutilation pictures was examined as a function of stimulus repetition, separately for passive viewing and active task conditions. Specifically, alpha/beta power activity within significant clusters (see Fig. 1) were extracted for single trials, task conditions, and participants. To achieve equal trial numbers for each analysis, passive and active task conditions were interpolated to 100 trials for each participant and condition. Finally, to assess the interaction of emotion by stimulus repetition, a linear regression analysis was conducted based on the ERD difference between emotional and neutral pictures across trials. The main finding is that the emotional modulation appeared stable across stimulus repetition. Specifically, across emotional stimulus categories, that is, erotica and mutilation, task condition, that is, passive viewing and active categorization task, and studies, the interaction of emotion by stimulus repetition was not significant ($|b_s| < 0.0025$, $|t_s| < 0.84$, $P_s > 0.40$). Furthermore, there was some evidence for effects of stimulus repetition, which differed across studies, task conditions, and emotion categories (see Fig. 5). Specifically, in Study 1, the ERD diminished with repetition of stimuli for both erotica ($b = 0.0056$, $t(98) = 3.65$, $P < 0.001$) and neutral images ($b = 0.0053$, $t(98) = 2.96$, $P = 0.004$). In contrast,

in Study 3 examining active task conditions, the overall ERD increased with stimulus repetition for all picture categories ($b_s < -0.0043$, $t_s > 3.89$, $P_s < 0.001$). However, no significant main effect of stimulus repetition was observed in Study 1 for the active task condition and in Study 2 for neither passive nor active task conditions ($|b_s| < 0.0031$, $|t_s| < 1.60$, $P_s > 0.11$).

General Discussion

The main aim of the present research series was to examine the hypothesis that the processing of high-arousing pleasant and unpleasant pictures is associated with power decreases in the alpha and lower beta range. Toward this end, a research series was conducted building on conceptual replication of the effect including experimental paradigms relying on potent emotional stimulus materials, that is, erotica and mutilations, and passive and active task instructions as means to provide strong measurements and control of error variance (Anderson and Maxwell 2016; Smith and Little 2018). Across studies, the processing of highly pleasant and unpleasant pictures (erotica and mutilations) was consistently associated with a decrease of power in the alpha- and lower beta band. The effect was broadly distributed with a focus on occipitoparietal sensors extending to central sites and most pronounced between 400 and 800 ms after stimulus onset. Furthermore, the effect was seen across conditions and observed in the context of passive viewing and an explicit categorization task assuring active processing of the pictures and appeared stable across stimulus repetition. In sum, evidence accumulates that high-arousing emotional stimulus processing is reliably associated with power decreases in the alpha and lower beta range. Furthermore, a new finding emerged as our data indicate a late ERS response to mutilation pictures, possibly indicating an inhibited state of neural networks involved in perceptual stimulus processing.

A main aim of the present study series was to resolve conflicting findings on power increases and decreases elicited by emotional stimulus processing. Specifically, although the majority of studies reported power decreases when processing emotionally arousing stimuli (de Cesare and Codispoti 2011; Knyazev et al. 2008; Balconi et al. 2009; Popov et al. 2012b, 2013; Cui et al. 2013; Meng et al. 2016; Furl et al. 2017; Schneider et al. 2018; Ferrari et al. 2020), some studies observed an increase in power in the alpha- and lower beta band, in particular when processing aversive images (Aftanas et al. 2002, 2004; Uusberg et al. 2013; Mennella et al. 2017). In Study 1 and 2, we replicated our previous findings that highly arousing pleasant pictures, that is, erotica, elicit a larger ERD compared with low-arousing control stimuli (Schubring and Schupp 2019). Extending these findings to unpleasant picture contents, a power decrease in the alpha- and lower beta band was observed in Study 2 and 3 when participants viewed mutilation pictures. These findings suggest that the processing of emotionally arousing pictures is associated with an ERD rather than ERS in the alpha- and lower beta band.

This conclusion is further supported when considering the various conceptual replications of this research series. To secure reproducibility of findings, Study 1 provided a conceptual replication of our previous research using a different set of picture stimuli, an active task posing working memory demands, and different interstimulus intervals. Study 2 used the same experimental paradigm as Study 1 providing a conceptual extension of the findings to unpleasant stimulus contents. Finally, Study 3 focused on active picture processing examining both

high-arousing pleasant and unpleasant pictures within 1 study. These 3 studies revealed significant main effects of emotion with an ERD rather than ERS response to emotionally arousing images (pleasant and unpleasant), distributed over broad posterior sensor regions, and most apparent between 400 and 800 ms. Furthermore, exploratory follow-up testing revealed significant power decreases to emotionally arousing pictures in 9 out of 10 simple effect analyses, adding to the robustness of the findings. One exception regarded mutilation picture processing in the active task condition focusing on nontarget stimuli. Again, a power decrease to mutilation pictures was observed, however, the effect only approached significance ($t(15) = -1.77$, $P = 0.097$). Collectively, conceptual replication of the main findings across studies and conditions provides strong support that the processing of emotionally arousing pictures is associated with a decrease in power in the alpha- and lower beta band during initial perceptual stimulus processing.

The analysis of stimulus repetition and possible affective habituation effects provides further insights into the modulation of alpha/beta power by emotional stimulus processing. A recent study observed that the alpha power decrease to high-arousing emotional stimuli was stable across stimulus repetition (Ferrari et al. 2020). This study involved massive repetitions (80 repeats) and the assessment of long-term habituation effects by repeating the session after a 24 h delay. Here, with a more modest number of repetitions, that is, 24 (Study 1 and 2), we replicated the findings regarding the passive viewing condition. Furthermore, analysis of the active task condition revealed a similar pattern of finding, that is, a stable effect of decreased alpha/beta power to high-arousing emotional stimuli across stimulus repetition. Overall, evidence accumulates that emotional modulation of the ERD is sustained across stimulus repetition.

The current findings may be discussed from a functional perspective on the meaning of ERD and a conceptual model on how emotional stimuli are represented in memory. Hanslmayr et al. (2012) suggested that memory processes are facilitated by neural desynchronization in the alpha/beta range. Specifically, increasing richness and amount of information represented in the brain is associated with power decreases. The information via desynchronization hypothesis can be related to the network model of emotion which assumes that emotional and neutral memory representations differ in terms of number of elements and strength of interconnectivity (Lang, 1993). Accordingly, we hypothesized that the richer memory representation of emotionally significant stimulus contents leads to power decreases in the alpha- and lower beta-frequency band. On the one hand, the present findings are consistent with this reasoning regarding the direction of power modulation, that is, a power decrease to erotica and mutilations across studies. However, on the other hand, there was variability of effects within and across erotic and mutilation picture categories regarding the boundaries of frequency bands, topography, and timing points toward differences. For instance, the latency of the effect differed for erotic and mutilation pictures, appearing earlier in time and less sustained for mutilation pictures. Furthermore, although the topography of the effect included occipital and parietal sensors for erotica and mutilations, the effect appeared with broader distribution including central sensor sites for erotic pictures, possibly reflecting overall stronger effects for this category. In addition, although erotic picture modulations were observed in Study 1 and 3 in highly overlapping frequency bands ranging from 8 to 25 Hz, processing of mutilation pictures revealed a more variable

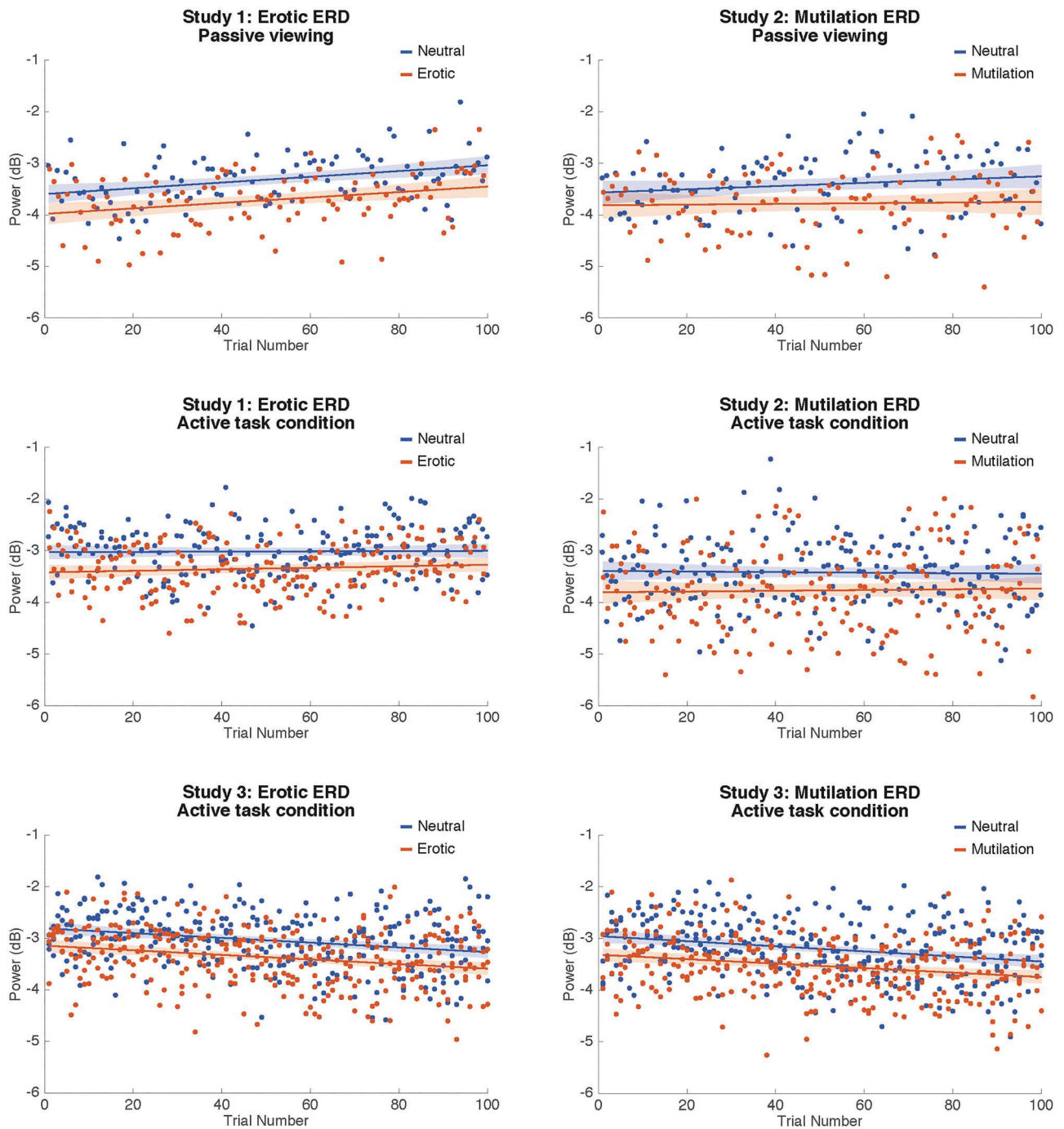


Figure 5. Emotional modulation of alpha/beta power appeared stable across stimulus repetition in Studies 1–3. Single trial values were extracted based on the ERD main effects (see Fig. 1). Each colored dot represents the single trial alpha/beta-frequency activity, interpolated to 100 trials, and averaged across participants. Colored lines represent the linear regression with colored shaded areas representing the 95% confidence interval.

pattern of modulation within the alpha- and lower beta band in Studies 2 (8–18 Hz) and 3 (15–25 Hz). Assuming that alpha/beta oscillations measured on the macroscopic level reflects synchronized firing of local cell ensembles (Hanslmayr et al. 2012), one may speculate that emotional stimulus categories differ in memory composition, that is, stimulus-meaning-response units and the temporal dynamics of network activation. Thus, future research needs to investigate the topography and latency of

alpha/beta power decreases as a function of different pleasant and unpleasant picture contents, different exposure times, and optimized designs for source analysis, that is, combining EEG and functional neuroimaging.

A new and surprising finding of the present research regards the observation that the ERD to mutilation pictures is followed by a significant increase in power. This late effect, observed between 1 and 1.5 s in Study 2 and 1.5 and 2.5 s in Study

3, may reflect resynchronization in the alpha- and lower beta band. Increases in the alpha-band have been discussed within cognitive research as a functional correlate of an inhibited state of neural networks. Examples for task conditions resulting in alpha power increases include the processing of task-irrelevant distractor stimuli in selective attention tasks (Foxye and Snyder 2011), increasing working memory load during encoding and retention, active forgetting of items (Bäumel et al. 2008; Waldhauser et al. 2012), and the withholding of responses within a motor task (Hummel et al. 2002; Klimesch et al. 2007). Accordingly, one may speculate that the late ERS elicited by mutilation pictures may indicate a state of inhibition in neural networks activated during initial perceptual stimulus processing associated with an ERD response. Consistent with this reasoning, ERD and ERS show a similar and highly overlapping posterior topography. Interestingly, the ERS was observed to mutilations but not erotic images. One hypothesis to account for the asymmetry builds on the hypothesis that the ERS reflects top-down inhibitory control processes, which, given the nature of the picture categories, may be more engaged during aversive picture viewing. Overall, the new finding of a late ERS response to mutilation pictures needs to be followed up by research examining a broader range of emotional stimulus categories in particular regarding unpleasant contexts (e.g., attack, disgust, and violence; de Cesare and Codispoti 2011).

Emotion-attention relationships have been assessed in previous research mainly with regard to event-relation components (e.g., Schupp et al. 2007; Ferrari et al. 2008; Weymar et al. 2011; Schindler and Straube 2020). Focusing on induced brain oscillations, the issue was examined in the present research series by including an active task condition directing attention to stimuli categories varying in emotional intensity. Previous findings regarding the main effect task were replicated (Yordanova et al. 2001; Bernat et al. 2007), with target compared with nontarget stimuli being associated with decreased power in the alpha- and lower beta band over occipitoparietocentral sensor sites in a time window from approximately 500 to 800 ms. However, although emotion and task effects overlapped in topography and were most pronounced between 500 and 800 ms, there was no interaction of emotion and task within the first second after stimulus onset. These findings replicate and extend the findings from Schubring and Schupp (2019) which also observed that task and emotion effects occurred independently from each other. However, although some evidence for emotion-attention interactions were observed between 1 and 1.5 s, the pattern of results provides little evidence for the potentiation of emotion processing when the stimuli were targets and the focus of attention. Rather, the interaction appeared to be driven by nontarget stimuli returning to baseline earlier than targets in the case of erotica and even showing an earlier ERS for mutilation pictures. Thus, perceptual stimulus processing indexed by brain oscillations provided no evidence for an interaction of emotion and attention within the first second after image presentation, but rather prolonged processing specifically for emotional target stimuli after the first second.

Summary

Three studies assessed induced frequency modulations by emotional stimuli in the context of an experimental design varying emotional picture contents, that is, erotica and mutilation, and task conditions, that is, free viewing and explicit categorization task. The main finding is that high arousing pleasant (erotica)

and unpleasant (mutilation) compared with low-arousing control stimuli decrease alpha- and beta-power across task contexts (free viewing and categorization task) during initial perceptual stimulus processing. Furthermore, a late (> 1 s) increase in alpha- and lower beta power was seen specifically for mutilation pictures, possibly reflecting top-down inhibitory control processes. Overall, these findings suggest that brain oscillations in the alpha- and lower beta-band may serve as a useful measure of emotional stimulus processing.

Notes

Conflict of interest: None declared.

Funding

This research was supported in part by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy - EXC2117 - 422037984 and the Research Unit FOR 2374 (granted to HS).

References

- Aftanas LI, Reva NV, Varlamov AA, Pavlov SV, Makhnev VP. 2004. Analysis of evoked EEG synchronization and desynchronization in conditions of emotional activation in humans: temporal and topographic characteristics. *Neurosci Behav Physiol.* 34:859–867.
- Aftanas LI, Varlamov AA, Pavlov SV, Makhnev VP, Reva NV. 2002. Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *Int J Psychophysiol.* 44:67–82.
- Anderson SF, Maxwell SE. 2016. There's more than one way to conduct a replication study: beyond statistical significance. *Psychol Methods.* 21(1):1–12.
- Balconi M, Brambilla E, Falbo L. 2009. Appetitive vs. defensive responses to emotional cues. Autonomic measures and brain oscillation modulation. *Brain Res.* 1296:72–84.
- 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. *Int J Psychophysiol.* 74:158–165.
- Başar E, Güntekin B. 2012. A short review of alpha activity in cognitive processes and in cognitive impairment. *Int J Psychophysiol.* 86:25–38.
- Bäumel KH, Hanslmayr S, Pastötter B, Klimesch W. 2008. Oscillatory correlates of intentional updating in episodic memory. *Neuroimage.* 41:596–604.
- Bernat EM, Malone SM, Williams WJ, Patrick CJ, Iacono WG. 2007. Decomposing delta, theta, and alpha time-frequency ERP activity from a visual oddball task using PCA. *Int J Psychophysiol.* 64:62–74.
- Bradley MM, Codispoti M, Cuthbert BN, Lang PJ. 2001. Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion.* 1:276–298.
- Bradley MM, Lang PJ. 1994. Measuring emotion: The self-assessment manikin and the semantic differential. *J Behav Ther Exp Psychiatry.* 25:49–59.
- Cui Y, Versace F, Engelmann JM, Minnix JA, Robinson JD, Lam CY, Karam-Hage M, Brown VL, Wetter DW, Dani JA et al. 2013. Alpha oscillations in response to affective and cigarette-related stimuli in smokers. *Nicotine Tob Res.* 15:917–924.

- de Cesarei A, Codispoti M. 2011. Affective modulation of the LPP and α -ERD during picture viewing. *Psychophysiology*. 48:1397–1404.
- Faul F, Erdfelder E, Lang A-G, Buchner A. 2007. G*power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav Res Methods*. 39: 175–191.
- Ferrari V, Codispoti M, Cardinale R, Bradley MM. 2008. Directed and motivated attention during processing of natural scenes. *J Cogn Neurosci*. 20:1753–1761.
- Ferrari V, Mastria S, Codispoti M. 2020. The interplay between attention and long-term memory in affective habituation. *Psychophysiology*. 57(6):e13572.
- Flaisch T, Steinhäuser M, Schupp HT. 2016. Emotional aftereffects: when emotion impairs subsequent picture recognition. *Emotion*. 16:987–996.
- Foxe JJ, Snyder AC. 2011. The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front Psychol*. 2:1–13.
- Frey JN, Ruhnau P, Weisz N. 2015. Not so different after all: the same oscillatory processes support different types of attention. *Brain Res*. 1626:183–197.
- Furl N, Lohse M, Pizzorni-Ferrarese F. 2017. Low-frequency oscillations employ a general coding of the spatio-temporal similarity of dynamic faces. *Neuroimage*. 157:486–499.
- Güntekin B, Başar E. 2007. Emotional face expressions are differentiated with brain oscillations. *Int J Psychophysiol*. 64:91–100.
- Güntekin B, Başar E. 2010. Event-related beta oscillations are affected by emotional eliciting stimuli. *Neurosci Lett*. 483:173–178.
- Güntekin B, Tülay E. 2014. Event related beta and gamma oscillatory responses during perception of affective pictures. *Brain Res*. 1577:45–56.
- Hajcak G, Dunning JP, Foti D. 2007. Neural response to emotional pictures is unaffected by concurrent task difficulty: an event-related potential study. *Behav Neurosci*. 121:1156–1162.
- Hanslmayr S, Staudigl T, Fellner M-C. 2012. Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Front Hum Neurosci*. 6:1–12.
- Hummel F, Andres F, Altenmüller E, Dichgans J, Gerloff C. 2002. Inhibitory control of acquired motor programmes in the human brain. *Brain*. 125:404–420.
- Klimesch W. 2012. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci*. 16:606–617.
- Klimesch W, Sauseng P, Hanslmayr S. 2007. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev*. 53:63–88.
- Knyazev GG, Bocharov AV, Levin EA, Savostyanov AN, Slobodskoj-Plusnin JY. 2008. Anxiety and oscillatory responses to emotional facial expressions. *Brain Res*. 1227:174–188.
- Lang PJ. 1993. The network model of emotion: motivational connections. In: Wyer R, Srull T, editors. *Advances in Social Cognition: Perspectives on Anger and Emotion*. Hillsdale, NJ: Lawrence Erlbaum Associate, pp. 109–133.
- Lang PJ, Bradley MM, Cuthbert BN. 2008. International affective picture system (IAPS): affective ratings of pictures and instruction manual. Technical Report. Gainesville (FL): University of Florida.
- Maris E, Oostenveld R. 2007. Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods*. 164:177–190.
- Meng X, Liu W, Zhang L, Li X, Yao B, Ding X, Yuan JJ, Yang J. 2016. EEG oscillation evidences of enhanced susceptibility to emotional stimuli during adolescence. *Front Psychol*. 7:1–9.
- Mennella R, Sarlo M, Messerotti Benvenuti S, Buodo G, Mento G, Palomba D. 2017. The two faces of avoidance: time-frequency correlates of motivational disposition in blood phobia. *Psychophysiology*. 54:1606–1620.
- Oostenveld R, Fries P, Maris E, Schoffelen J-M. 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci*. 2011:156869.
- Polich J. 2007. Updating P300: an integrative theory of P3a and P3b. *Clin Neurophysiol*. 118:2128–2148.
- Popov T, Miller GA, Rockstroh B, Weisz N. 2013. Modulation of alpha power and functional connectivity during facial affect recognition. *J Neurosci*. 33:6018–6026.
- Popov T, Steffen A, Weisz N, Miller GA, Rockstroh B. 2012a. Cross-frequency dynamics of neuromagnetic oscillatory activity: two mechanisms of emotion regulation. *Psychophysiology*. 49:1545–1557.
- Popov T, Steffen A, Weisz N, Miller GA, Rockstroh B. 2012b. Cross-frequency dynamics of neuromagnetic oscillatory activity: two mechanisms of emotion regulation. *Psychophysiology*. 49:1545–1557.
- Sabatinelli D, Bradley MM, Fitzsimmons JR, Lang PJ. 2005. Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. *Neuroimage*. 24: 1265–1270.
- Sadaghiani S, Kleinschmidt A. 2016. Brain networks and α -oscillations: structural and functional foundations of cognitive control. *Trends Cogn Sci*. 20:805–817.
- Schindler S, Straube T. 2020. Selective visual attention to emotional pictures: interactions of task-relevance and emotion are restricted to the late positive potential. *Psychophysiology*. 57:1–14.
- Schneider TR, Hipp JF, Domnick C, Carl C, Büchel C, Engel AK. 2018. Modulation of neuronal oscillatory activity in the beta- and gamma-band is associated with current individual anxiety levels. *Neuroimage*. 178:423–434.
- Schubring D, Schupp HT. 2019. Affective picture processing: alpha- and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology*. 56:1–13.
- Schupp HT, Stockburger J, Codispoti M, Junghofer M, Weike AI, Hamm AO. 2007. Selective visual attention to emotion. *J Neurosci*. 27:1082–1089.
- Schupp HT, Cuthbert BN, Bradley MM, Hillman CH, Hamm AO, Lang PJ. 2004. Brain processes in emotional perception: Motivated attention. *Cogn Emot*. 18:593–611.
- Smith PL, Little DR. 2018. Small is beautiful: in defense of the small-N design. *Psychon Bull Rev*. 25(6):2083–2101.
- Uusberg A, Uibo H, Kreegipuu K, Allik J. 2013. EEG alpha and cortical inhibition in affective attention. *Int J Psychophysiol*. 89:26–36.
- Waldhauser GT, Johansson M, Hanslmayr S. 2012. Alpha/beta oscillations indicate inhibition of interfering visual memories. *J Neurosci*. 32:1953–1961.
- Weymar M, Löw A, Öhman A, Hamm AO. 2011. The face is more than its parts - brain dynamics of enhanced spatial attention to schematic threat. *Neuroimage*. 76:211–220.
- Yordanova J, Kolev V, Polich J. 2001. P300 and alpha event-related desynchronization (ERD). *Psychophysiology*. 38:143–152.