

The influence of frontal alpha-asymmetry on the processing of approach- and withdrawal-related stimuli—A multichannel psychophysiology study

Dirk Adolph | Michael von Glischinski | André Wannemüller | Jürgen Margraf

Faculty of Psychology, Ruhr-Universität
Bochum, Bochum, Germany

Correspondence

Dr. Dirk Adolph, Ruhr-Universität
Bochum, Faculty of Psychology,
Department of Clinical Psychology and
Psychotherapy, Massenbergrstraße 9-13,
44787 Bochum, Germany.
Email: dirk.adolph@rub.de

Abstract

The approach-withdrawal model of hemispheric activation suggests that left frontal cortical areas mediate approach, while right frontal cortical areas mediate withdrawal motivation. Within this framework, the present study investigates the association of frontal cortical asymmetry with attentional and emotional responses toward approach- and withdrawal-related emotional stimuli. Resting frontal asymmetry was measured from 43 students before they passively viewed negative, neutral, and positive emotional pictures. The startle reflex, skin conductance response, and subjective ratings of valence and arousal were assessed to quantify emotional responding, while attention was assessed with ERPs. We also assessed frontal asymmetry in response to the pictures. Results indicated that relatively stronger right frontal cortical activation was associated with increased N1 amplitudes and more negative subjective emotional evaluation of all stimuli. Furthermore, enhanced right frontal asymmetry (state and trait) was associated with diminished emotional modulation of the late positive potential. In contrast, no association of frontal asymmetry with defensive reflex physiology or activation of sympathetic nervous system activity was found. The current data suggest dissociable influence of resting frontal brain asymmetry on attentional and physiological processing of withdrawal- and approach-related stimuli. That is, asymmetrical frontal cortical brain activation might not modulate approach-/withdrawal-related motor responses and sympathetic arousal directly, but instead enhances allocation of attentional resources to subjectively significant stimuli. The results are discussed in terms of their potential importance for emotion perception in anxiety disorders and their contribution to the understanding of frontal asymmetry.

KEYWORDS

approach and withdrawal, ERPs, frontal alpha asymmetry, skin conductance response, startle reflex

1 | INTRODUCTION

Individual responses to emotional stimuli vary greatly across individuals. Among the numerous individual differences (review in Hamann & Canli, 2004) influencing emotion processing, asymmetrical activation of the frontal cortex has received major attention over the past three decades (Harmon-Jones, Lueck, Fearn, & Harmon-Jones, 2006). For example, the approach-withdrawal model of hemispheric activation (Davidson, 1992) suggests that left frontal cortical

areas mediate approach, while right frontal cortical areas mediate withdrawal motivation (overview in Coan & Allen, 2004b; Leventhal & Tomarken, 1986; Silberman & Weingartner, 1986). Based on this dispositional model of hemispheric activation, it was predicted that trait-like individual differences in resting asymmetrical frontal brain activation (i.e., the individual's affective style, Davidson, 1992, 1998) cause individual differences in emotional processing (Coan & Allen, 2004b; Davidson, Jackson, & Kalin, 2000). In a conceptual extension, Coan, Allen, and McKnight (2006)

also highlighted the importance of situational factors. Following the capability model of hemispheric activation, the individual intensity of right or left frontal activation (i.e., state frontal asymmetry) during emotional situations modulates the individual's emotional responses in that situation (Coan, Allen, & McKnight, 2006). Put into concrete words, these models predict that persons showing larger right frontal cortical activation either at rest or while experiencing emotions are supposed to show enhanced withdrawal-related emotional responses toward withdrawal-related, negative stimuli. In contrast, persons showing a pattern of larger relative left frontal cortical activation (either at rest or during emotion processing) show more approach-related emotional responses toward approach-related, positive stimuli (Coan & Allen, 2004b; Davidson, 1992; Harmon-Jones, Gable, & Peterson, 2010). In addition, as proposed by Heller's two-dimensional model, anxiety manifesting predominantly with symptoms of anxious apprehension might also be characterized by enhanced relative left frontal activity, while persons with a trait-like disposition to react with anxious arousal (e.g., persons suffering from panic disorder) are supposed to show enhanced activity of right parietal as compared to left parietal regions (Heller, Nitschke, Etienne, & Miller, 1997; see Heller, 1993, for a theoretical overview).

However, supporting research involving models of frontal asymmetry has demonstrated an association between resting right and left frontal cortical activation and more negative evaluation of withdrawal-related film clips (Tomarken, Davidson, & Henriques, 1990; Wheeler, Davidson, & Tomarken, 1993) and more positive evaluation of approach-related film clips, respectively (Wheeler et al., 1993). In addition, right frontal asymmetry is associated with diminished emotion regulation abilities (Goodman, Rietschel, Lo, Costanzo, & Hatfield, 2013; Jackson et al., 2003), as well as attentional biases toward withdrawal-related stimuli (Grimshaw, Foster, & Corballis, 2014; Miskovic & Schmidt, 2010; Pérez-Edgar, Kujawa, Nelson, Cole, & Zapp, 2013). Finally, a series of studies on anger (i.e., an approach-oriented emotion) have shown that enhanced left frontal brain asymmetry during the perception of anger-evoking pictures is related to enhanced motivated attention (e.g., Gable & Poole, 2014; Poole & Gable, 2014; overview in Harmon-Jones et al., 2010). This gives evidence for an association of frontal asymmetry with motivational tendency elicited by the stimulus, rather than with its emotional valence (Harmon-Jones & Allen, 1998).

However, although these data are generally consistent with the approach-withdrawal model, there are also studies that failed to replicate (Hagemann, Naumann, Becker, Maier, & Bartussek, 1998) or found only partial support for the models' predictions (Coan & Allen, 2003; Goodman et al., 2013; Jackson, Malmstadt, Larson, & Davidson, 2000).

Moreover, only very few studies assessed the association of frontal asymmetry with psychophysiological reactivity, and to our knowledge no study to date assessed emotional reactivity with physiological, attentional, and self-report measures in one single paradigm. However, to understand the entire course of emotional responding (i.e., attentional processing of eliciting stimuli, bottom-up emotion generation processes, emotional evaluation/top-down emotion control; for details, see McRae, Misra, Prasad, Pereira, & Gross, 2012; Ochsner et al., 2009), the importance of multilevel response scoring, (i.e., behavior, self-report, and physiological reactions) has been highlighted repeatedly (e.g., Ekman, 1992; Fabiani, 2015; Izard, 1977; Lang, 1988; Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005). Thus, in sum, the present literature lacks final evidence of whether frontal asymmetry uniformly influences the entire course of emotion processing.

1.1 | The present study

The main aim of the present study was therefore to assess whether asymmetrical frontal brain activation uniformly modulates the different levels of emotion processing. To address this question adequately, (a) the different levels of stimulus processing had to be assessed in one single paradigm, and (b) we had to prove that approach and withdrawal emotion tendencies are elicited within the current paradigm.

To accomplish this, we used the passive viewing paradigm of approach- and withdrawal-related stimuli. This paradigm has been used extensively to test the assumptions from the biphasic or motivational model of emotion (Lang, Bradley, & Cuthbert, 1997). It is ideally suited for two reasons: (a) The model's key assumptions largely overlap those derived from the approach-withdrawal model (cf. Davidson et al., 2000).¹ (b) The passive viewing paradigm of approach- and withdrawal-related emotional pictures produces a reliable and replicable pattern of emotional responding including attention deployment, bottom-up emotion generation (McRae et al., 2012; Ochsner et al., 2009) as well as top-down processes, such as subjective emotion evaluation (e.g., Grimm et al., 2006; Taylor, Phan, Decker, & Liberzon, 2003).

¹The biphasic theory of emotion proposes two motivational systems (appetitive and aversive) guiding human behavior in light of evolutionary significant situations (Bradley et al., 2001; Fanselow, 1994; Lang, 2014; Lang & Bradley, 2013; Lang et al., 1997). Activation of these systems initiates increased sensory processing of target stimuli (i.e., attention modulation) as well as mobilization of the organism for action (Lang & Bradley, 2013), associated with an orchestrated response of underlying neural circuits of the brain, as well as corresponding autonomic responses (both from the sympathetic and the parasympathetic branch) and subjective emotional experience (e.g., Bradley et al., 2001; Lang & Bradley, 2013; Lang et al., 1998).

In detail, this pattern consists of an emotional modulation of early spatial attention allocation (as assessed with early ERPs, i.e., N1 and P1; see review in Olofsson, Nordin, Sequeira, & Polich, 2008) and an enhancement of late motivated attention (assessed with late positive potentials, LPP, of the EEG; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Olofsson et al., 2008; Schupp et al., 2000). Moreover, elevated arousal-related sympathetic autonomous responding (as assessed with the skin conductance response, SCR; see, e.g., Bradley et al., 2001) for positive and negative stimuli, as compared to neutral stimuli, are found consistently. Finally, numerous studies using appetitive and aversive stimuli from different modalities (Alpers, Adolph, & Pauli, 2011; Bradley, Codispoti, Cuthbert, & Lang, 2001; Miltner, Matjak, Braun, Diekmann, & Brody, 1994) showed potentiation of the startle reflex (i.e., see Bradley et al., 2001; Lang, Bradley, & Cuthbert, 1998a), indicating enhanced withdrawal motivation (Davis, 2006; Vrana, Spence, & Lang, 1988; overview in Bradley et al., 2001) and more negative subjective evaluation for threatening, and an attenuated startle response (indicating approach motivation) as well as more positive subjective evaluation for approach-related positive stimuli, as compared to neutral ones.

This response pattern—and most notably the emotional modulation of the startle reflex—indicates activation of the mammalian defensive or appetitive motivational systems, respectively (overview in Bradley et al., 2001, Lang, Bradley, & Cuthbert, 1998b; Löw, Lang, Carson Smith, & Bradley, 2008). For example, the startle reflex is a cross-species defensive reflex, with the purpose of facilitating flight or protecting the body from a sudden attack (e.g., Grillon & Baas, 2003). It is enhanced when the organism is exposed to threat, while it is attenuated in appetitive contexts. Consistent with this, in experimental contexts, it has been demonstrated that, rather than the hedonic valence of the emotional stimulus (e.g., a negative or positive picture), its motivational significance (e.g., if it signals threat or reward) is responsible for the modulation of the startle reflex (see Bradley, Moulder, & Lang, 2005; Grillon, 2002).

For the purpose of the present study, we presented approach- and withdrawal-related, as well as neutral control stimuli, and assessed responding of the sympathetic branch of the autonomous nervous system with the SCR, motivation-directed reflex action with the affect-modulated startle reflex, early automatic spatial (N1 component) and late motivational attention processes (LPP) with ERPs, as well as self-report measures of valence and arousal to assess the entire course of emotional responding. We then related these emotional responses to both trait-like resting frontal asymmetry (dispositional model) and frontal asymmetry during the perception of the stimuli (capability model).

Following the literature and theoretical considerations based on the models, we await relatively enhanced right frontal cortical activation to be associated with a negativity bias in emotion processing (i.e., enhanced startle responses), enhanced skin conductance responses, more negative self-report, and enhanced attention allocation toward withdrawal-related as compared to neutral or positive stimuli (negative emotion bias).

2 | METHODS AND MATERIAL

2.1 | Participants

Participants were 43 right-handed students (28 female, age range 19–34 years, $M = 24.1$, $SD = 3.7$) recruited at Ruhr-Universität Bochum. All participants reported normal or corrected-to-normal vision, no use of medication on the day of testing, as well as no current or history of neurological disorders. Participants scored within the normal range for depression (range 0–19, $M = 3.8$, $SD = 3.9$) and trait anxiety (range 23–61, $M = 35.4$, $SD = 7.4$). No participant was excluded due to his or her questionnaire scores. All gave written informed consent to procedures and were paid €20. Due to technical reasons, we lost electrodermal activity and startle data of two and ERP data of five participants. One participant discontinued the experiment without giving a reason. The study was conducted in accordance with the Declaration of Helsinki and was approved by the ethics review board of the Faculty of Psychology at Ruhr-Universität Bochum.

2.2 | Assessment of emotional responsivity

During startle assessment, 66 pictures from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008) and a custom picture set were presented in two blocks of 33 pictures each (11 positive, 11 neutral, and 11 negative).² The pictures successfully elicited approach and withdrawal motivation in a previous study at our lab and were chosen on the basis of their valence and arousal ratings (neutral: valence $M = 1.15$, arousal $M = 4.11$; positive: valence $M = 2.09$, arousal $M = 5.95$; negative: valence $M = -2.12$, arousal $M = 6.59$). Negative pictures represented threatening contents associated with withdrawal motivation (e.g., pointing gun, poisonous snake), while positive pictures showed contents related to approach motivation (e.g., erotic couples, food, sports). Within blocks, pictures were presented randomly for 6 s (with no more than three pictures of the same

²IAPS numbers: negative: 1050, 1201, 1300, 2730, 3010, 3170, 6020, 6260, 6350, 9040, 9300; neutral: 5500, 5535, 7000, 7004, 7006, 7010, 7020, 7100, 7140, 7500, 7550; positive: 2208, 2216, 4608, 4660, 4680, 5621, 5626, 8030, 8190, 8500, 8531.

category shown in sequence). The intertrial intervals (ITI) varied randomly between 18 and 20 s. Within the ITIs, participants rated the pictures for valence and arousal using the Self-Assessment Manikin (SAM, Bradley & Lang, 1994). Startle probes were delivered randomly during an interval between the third and fifth second after picture onset. Probes were presented during 14 picture presentations of each valence category and during 12 ITIs.

2.3 | Questionnaires

Because frontal asymmetry is thought to constitute a trait-like vulnerability factor for the development of emotion-related disorders (for a review, see Coan & Allen, 2004b), we assessed anxiety and depression to later control for these factors within the data. Trait anxiety was assessed with the trait form of the State-Trait Anxiety Inventory (STAI-T, Laux, Schaffner, Glanzmann, & Spielberger, 1981) while depression was assessed with the Depression Scale (DS, von Zerssen & Koeller, 1976). For the DS, scores below 10 are considered to be within the normal range (comparative samples, mean: 5.5; depressive samples, mean: 26.3, see von Zerssen & Koeller, 1976). Both the STAI-T as well as the DS showed good internal consistency in the actual sample (STAI-T: Cronbach's α [CR- α] = .85, DS: CR- α = .79).

2.4 | Psychophysiological recordings and response scoring

All psychophysiological data were recorded with a sampling rate of 1000 Hz using Ag/AgCl electrodes, digitized with 16-bit (BrainAmp, Brain Products, Germany) and filtered online with a 50 Hz notch filter. EEG was recorded according to the International 10/20 system from 32 scalp locations (Fp1, Fp2, F7, F3, Fz, F4, F8, Fc5, Fc1, Fc2, Fc6, T7, C3, Cz, C4, T8, Tp9, Cp5, Cp1, Cp2, Cp6, Tp8, P7, P3, Pz, P4, P8, Po9, O1, Oz, O2, Po10) in reference to the left mastoid with impedances below 2 kOhm. Orbicularis oculi electromyogram (EMG) electrodes were placed according to published guidelines (Blumenthal et al., 2005), and electrodermal activity electrodes were attached at the distal phalanges of the nondominant hand's middle and index finger.

Offline, EEG channels were referenced to linked mastoids, high- (0.05 Hz, 24 db/oct) and low-pass filtered (40 Hz, 24 db/oct), and corrected for ocular artifacts (Gratton, Coles, & Donchin, 1983). Periods with excessive noise were excluded (i.e., amplitudes below -150 or above 150 μ V, slopes > 50 μ V/ms). Frontal asymmetry was assessed in accord with published recommendations (cf. Allen, Coan, & Nazarian, 2004). In brief, data were segmented in 2-s intervals for resting frontal asymmetry and in 1-s intervals for asymmetry data during picture viewing (Gable & Poole,

2014; Harmon-Jones et al., 2006; Poole & Gable, 2014; both 50% overlap), and fast Fourier transform was applied using an end-tapered Hamming window. For resting asymmetry, segments were then averaged across eyes closed and eyes open conditions. For state asymmetry during picture viewing, segments were averaged according to the respective valence category (i.e., positive, neutral, negative). Then, power values in the alpha band (8–13 Hz) were extracted separately for each EEG channel, and an asymmetry score was calculated by subtracting right frontal activity from left frontal activity (i.e., $\ln F4 - \ln F3$). For resting data, we averaged across eyes open and eyes closed conditions, because Spearman-Brown corrected reliability was .91 for the eyes open and eyes closed conditions, and averaging yields a more reliable estimate of frontal asymmetry than either condition alone (Hagemann, 2004; Tomarken, Davidson, Wheeler, & Kinney, 1992). In addition, Spearman-Brown corrected split half reliability between the first and last 4 min of measurement was high (.98) thus confirming highly reliable assessment of frontal asymmetry.

To assess the ERPs in response to picture onset, data were segmented (100 ms prior to 1,000 ms following picture onset), baseline-corrected (100 ms prior to stimulus onset), and averaged according to the conditions. Areas of interest were defined based on visual inspection of grand averages (see Figure 1). The general topography of the ERP wave showed a prominent negative-going peak with a latency of about 100 ms (i.e., N1) followed by sustained positive waves, peaking at latencies of approximately 200 and 300 ms, terminating in a sustained positive-going slow wave (i.e., LPP) peaking about 700–1,000 ms after picture onset. For the purpose of the current study, we were interested in early spatial attention processing as well as late motivated attention. Thus, we focused on the N1 and LPP for further processing. Therefore, an area between 90 and 130 ms served to cover the N1 component and a window between 400 and 1,000 ms was used to obtain the LPP.

Startle responses were extracted in accord with published guideline (see Blumenthal et al., 2005). In brief, offline orbicularis oculi EMG was high (20 Hz, 24 db/oct) and low-pass filtered (500 Hz, 24 db/oct). Data were then baseline-corrected (20 ms before probe onset), rectified, and smoothed (10-ms moving average). Startle magnitudes were extracted as the maximum peak in a time window between 30 and 150 ms after startle probe onset and scored as zero if they did not exceed the maximum during the baseline interval by the factor two. Outliers (conditions mean plus 3 *SD*) were excluded, data were *z*-standardized and averaged according to the conditions (i.e., positive, negative, neutral). Spearman-Brown corrected split-half reliability for the startle data was .92.

Electrodermal activity was low-pass filtered (1 Hz, 24 db/oct), baseline-corrected ($-1,000$ – 0 ms before picture

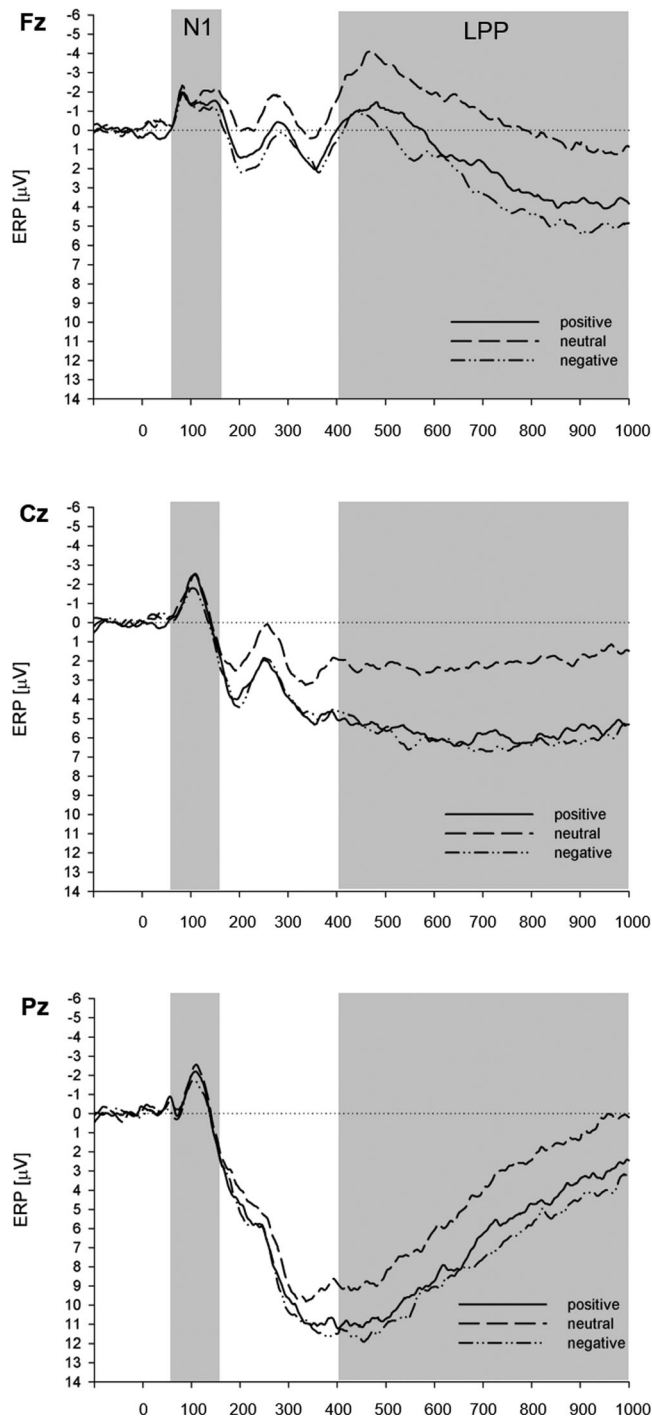


FIGURE 1 ERPs elicited by neutral, positive, and negative pictures at Fz, Cz, and Pz. Positive and negative emotional pictures elicited larger LPPs than neutral pictures

onset), and the SCR was extracted as the maximum deflection in a time window between 1,000 and 8,000 ms following picture onset. SCR below $0.01 \mu\text{S}$ were scored as zero. Prior to averaging according to the conditions, SCR were log-transformed, $\ln(\text{SCR} + 1)$. Spearman-Brown corrected split-half reliability for the SCR data was .99.

2.5 | Data analysis

Because it reduces statistical power and may result in artificial groups that distort the underlying continuous relationships, dichotomizing is not recommended for asymmetry data (see Coan & Allen, 2004). Thus, for all analyses of emotional responses, a continuous between-subjects factor asymmetry was included. For subjective ratings, skin conductance response and startle data mixed general linear models were conducted including the within-subject factor emotion (positive, neutral, negative) and the between-subjects factor asymmetry. Previous research suggests that changes in current states substantially influence frontal asymmetry (Coan & Allen, 2004b; Hagemann, Hewig, Seifert, Naumann, & Bartussek, 2005). It has been argued that, by controlling for current mood, these influences can be substantially reduced (Adolph & Margraf, 2017). Thus, to control for state influences, we performed a linear regression using frontal asymmetry as dependent variable and current mood as a predictor (as assessed with a modified version of the Self-Assessment-Manikin, SAM (for details, see Adolph & Margraf, 2017). Resulting residuals were then free from the influence of state mood and were thereafter used for further analysis.

Confirming previous research (Foti, Hajcak, & Dien, 2009), visual inspection of EEG grand averages showed that N1 waveforms were most prominent around central and parietal electrode sites (C3, Cz, C4, P3, Pz, P4), and LPPs occurred around central and parietal (e.g., Weinberg & Hajcak, 2011), as well as frontal electrode sites (Cunningham, Espinet, DeYoung, & Zelazo, 2005; Diedrich, Naumann, Maier, & Becker, 1997). Therefore, we included central, parietal, and anterior sites in further analysis for the LPP (i.e., P3, Pz, P4, C3, Cz, C4, F3, Fz, F4). Taken together, the factors transversal (N1 and LPP: left, middle, right) and sagittal electrode sites (N1: central, parietal; LPP: frontal, central, parietal) were included in the models. Significant main effects and interactions were followed up with nested effects and simple regression analyses. Cohen's f and R^2 effect sizes, as well as Huynh-Feldt corrected p values are reported. Moreover, to assess the influence of trait cortical activation on emotion discrimination (see Weinberg & Hajcak, 2011), we then calculated emotional discrimination scores by subtracting emotional reactions toward neutral pictures from emotional activation toward emotional pictures (i.e., Δ emotion discrimination scores: positive-neutral, negative-neutral; e.g., Weinberg & Hajcak, 2011). For those dependent variables where significant interaction with frontal asymmetry were found within the mixed-model analyses of variance (ANOVAs), we then calculated correlations between emotion discrimination scores and frontal asymmetry (according to Jackson et al., 2003). Finally, to assess the relationship between emotional responding and state frontal asymmetry

during picture viewing, correlations were conducted between emotional responding (i.e., ERPs, startle, SCR, ratings) toward the respective picture category (i.e., positive, neutral, negative) and state asymmetry assessed during the same picture category (see Gable & Poole, 2014; Harmon-Jones et al., 2006; Poole & Gable, 2014). For correlations effect size R^2 was calculated, and for all statistical tests an alpha level of 5% was used.

2.6 | Procedure

Upon arrival, participants were seated in a recliner in a dimly lit room. Afterward, electrodes were attached, and participants completed the mood questionnaire. Then, participants were instructed to relax with their eyes open (O) and closed (C) in one of two alternating orders of eight 1-min intervals (OCCOCOOC or COOCOCCO) while resting EEG was recorded. After recording ended, participants completed the STAI-T and the DS. Emotional reactivity was then assessed beginning with six startle probes to induce startle habituation. After the assessment of emotional responses ended, electrodes were removed and participants were paid.

3 | RESULTS

3.1 | Associations between resting frontal asymmetry and emotional responses

3.1.1 | Self-reported valence

Self-reported valence was strongly influenced by picture category (main effect for emotion, $F(2, 70) = 168.93$, $p < .001$, $f = 2.19$). In detail, as expected, negative pictures were rated significantly more negatively than neutral pictures, which in turn were rated less positively than positive pictures (all t tests $p < .001$, one-tailed). Furthermore, results show that larger right frontal asymmetry was related to more negative valence ratings (main effect for asymmetry, $F(1, 35) = 6.78$, $p = .013$, $f = 0.44$; $\beta = .403$). However, this effect was independent of emotion category, Emotion \times Asymmetry, $F(2, 70) = 0.05$, ns . Partial correlations revealed that this effect was also independent of trait anxiety and depression, $r_p = .385$, $p = .043$, $R^2 = .148$ (see Table 1).

3.1.2 | Self-reported arousal

Self-reported arousal ratings differed for the three emotion categories (main effect for emotion, $F(2, 70) = 70.81$, $p < .001$, $f = 1.42$). Neutral pictures were rated less arousing than both positive and negative pictures. However, negative

TABLE 1 Means and standard deviations for self-report, skin conductance response, and startle reflex data

| | | <i>M</i> | <i>SD</i> |
|----------------------|----------|----------|-----------|
| Valence ratings | Positive | 1.08 | 0.63 |
| | Neutral | 0.04 | 0.54 |
| | Negative | -1.36 | 0.80 |
| Arousal ratings | Positive | 4.35 | 1.35 |
| | Neutral | 3.30 | 1.26 |
| | Negative | 4.90 | 1.15 |
| EDA (μ S) | Positive | 0.07 | 0.07 |
| | Neutral | 0.05 | 0.07 |
| | Negative | 0.07 | 0.07 |
| Startle (z score) | Positive | -0.12 | 0.24 |
| | Neutral | 0.00 | 0.25 |
| | Negative | 0.12 | 0.25 |

pictures were rated more arousing than positive ones (all $ps < .001$, one-tailed). The interaction Emotion \times Asymmetry, $F(2, 70) = 0.56$, ns , and the main effect for asymmetry, $F(1, 35) = 0.62$, ns , were not significant (see Table 1).

3.1.3 | Startle reflex

Paralleling valence ratings and, as expected, startle responses were largest for negative pictures, intermediate for neutral pictures, and smallest for positive pictures (t tests: positive vs. neutral, $p = .046$; positive vs. negative, $p = .001$; negative vs. neutral, $p = .046$, one-tailed). This finding was substantiated by the significant main effect for emotion, $F(2, 68) = 5.95$, $p = .004$, $f = 0.42$, as well as a significant linear polynomial contrast, $F(1, 34) = 12.18$, $p = .001$, $f = 0.60$. The interaction Emotion \times Asymmetry, $F(2, 68) = 0.22$, ns , as well as the main effect for asymmetry, $F(1, 35) < 0.01$, ns , were not significant³ (see Table 1).

3.1.4 | SCR

Emotional pictures elicited larger SCR than neutral pictures, while responses for positive and negative pictures did not differ (main effect for emotion, $F(2, 66) = 3.59$, $p = .040$, $f = 0.33$, t tests: positive vs. neutral $p = .022$, positive vs. negative, ns , negative vs. neutral: $p = .024$, all one-tailed). This effect was further substantiated by a significant quadratic polynomial contrast, $F(1, 33) = 4.85$, $p = .035$, $f = 0.38$. Both the interaction Emotion \times Asymmetry, $F(2, 68) = 0.60$, ns , and the main effect

³Analysis of nonstandardized startle raw data revealed comparable results.

TABLE 2 GLM results for the N1 and the LPP analysis

| | N1 | | | LPP | | |
|---------------|------------------------|------------------|-----------------|------------------------|------------------|-----------------|
| | <i>F</i> (<i>df</i>) | <i>p</i> | <i>Cohens f</i> | <i>F</i> (<i>df</i>) | <i>p</i> | <i>Cohens f</i> |
| E | 0.41 (2, 56) | <i>ns</i> | – | 31.02 (2, 56) | < .001 | 1.05 |
| E × A | 1.22 (2, 56) | <i>ns</i> | – | 0.76 (2, 56) | <i>ns</i> | – |
| S | 6.51 (2, 56) | .017 | 0.48 | 30.38 (1, 28) | < .001 | 1.04 |
| S × A | 0.42 (2, 56) | <i>ns</i> | – | 1.40 (2, 56) | <i>ns</i> | – |
| T | 10.92 (1, 28) | < .001 | 0.63 | 3.72 (2, 56) | .038 | 0.36 |
| T × A | 3.50 (1, 28) | .037 | 0.35 | 2.57 (1, 28) | <i>ns</i> | – |
| E S | 1.42 (4, 112) | <i>ns</i> | – | 1.03 (4, 112) | <i>ns</i> | – |
| E × S × A | 1.36 (4, 112) | <i>ns</i> | – | 1.46 (2, 56) | <i>ns</i> | – |
| E × T | 1.17 (2, 56) | <i>ns</i> | – | 2.95 (2, 56) | .023 | 0.32 |
| E × T × A | 0.22 (2, 56) | <i>ns</i> | – | 2.62 (4, 112) | .039 | 0.30 |
| S × T | 15.81 (2, 56) | < .001 | 0.75 | 2.25 (2, 56) | <i>ns</i> | – |
| S × T × A | 1.14 (2, 56) | <i>ns</i> | – | 0.13 (2, 56) | <i>ns</i> | – |
| E × S × T | 0.30 (4, 112) | <i>ns</i> | – | 0.70 (4, 112) | <i>ns</i> | – |
| E × S × T × A | 0.31 (4, 112) | <i>ns</i> | – | 1.25 (4, 112) | <i>ns</i> | – |
| A | 1.10 (1, 28) | <i>ns</i> | – | 2.01 (1, 28) | <i>ns</i> | – |

Note: Dashes indicate that effect sizes were omitted for nonsignificant effects. Bold values mark significant main effects or interactions. E = emotion; T = transversal; S = sagittal; A = frontal asymmetry.

for asymmetry, $F(1, 33) = 0.07$, *ns*, failed to reach significance (see Table 1).

3.1.5 | ERPs—N1

Table 2 shows all ANOVA effects for the N1 waveform. The N1 appeared largest at central electrode sites (see Figure 1). This impression was substantiated by a significant interaction of Sagittal × Transversal electrode sites (see Table 2). Planned contrasts revealed that the N1 was largest at midline electrodes (transversal left vs. central, $p < .001$, transversal right vs. central, $p < .001$). While the N1 did not differ at central electrodes (Cz vs. Pz, *ns*), N1 was larger at left and right central electrode sites as compared to left and right parietal sites (C3 vs. P3, $p = .007$; C4 vs. P4, $p = .022$). Results further indicated that asymmetry influenced N1 amplitudes as a function of transversal electrode sites (i.e., interaction Transversal × Asymmetry). Enhanced right frontal asymmetry was related to larger N1 amplitudes at left electrode sites, $\beta = .379$, $t = 2.17$, $p = .039$, but not central, $\beta = .102$, $t = 0.54$, *ns*, or right electrode sites, $\beta = .104$, $t = 0.55$, *ns*. As for valence ratings, this effect was independent of trait anxiety and depression (partial correlation: Asymme-

try × N1 at left electrode sites, $r_p = .362$, $p = .058$, $R^2 = .131$).

3.1.6 | ERPs—LPP

Table 2 shows the ANOVA results. The LPP waveform was largest at parietal electrode sites ($M = 8.75$, $SD = 4.17$, see Figure 1), intermediate at central electrode sites ($M = 4.10$, $SD = 2.63$), and smallest at frontal electrode sites ($M = -1.07$, $SD = 4.60$, main effect for sagittal, all planned contrasts, $p < .001$). Furthermore, the LPP was more positive at midline electrodes ($M = 4.42$, $SD = 2.97$) as compared to left ($M = 3.31$, $SD = 2.59$) electrodes (planned contrast for main effect for transversal: midline vs. left, $p = .001$). While left electrodes tended to show larger LPPs as compared to right ($M = 4.05$, $SD = 2.85$) electrodes ($p = .053$), LPPs at midline and right electrode sites did not differ significantly ($p > .10$). Neutral pictures ($M = 2.27$, $SD = 2.56$) elicited significantly smaller LPPs than positive ($M = 4.59$, $SD = 2.95$) and negative ($M = 4.91$, $SD = 3.18$) pictures (planned contrasts main effect for emotion: positive vs. negative, $p = .374$; negative vs. neutral, $p < .001$, one-tailed; positive vs. neutral, $p < .001$, one-tailed). Results further revealed that asymmetry influenced emotion as a function of

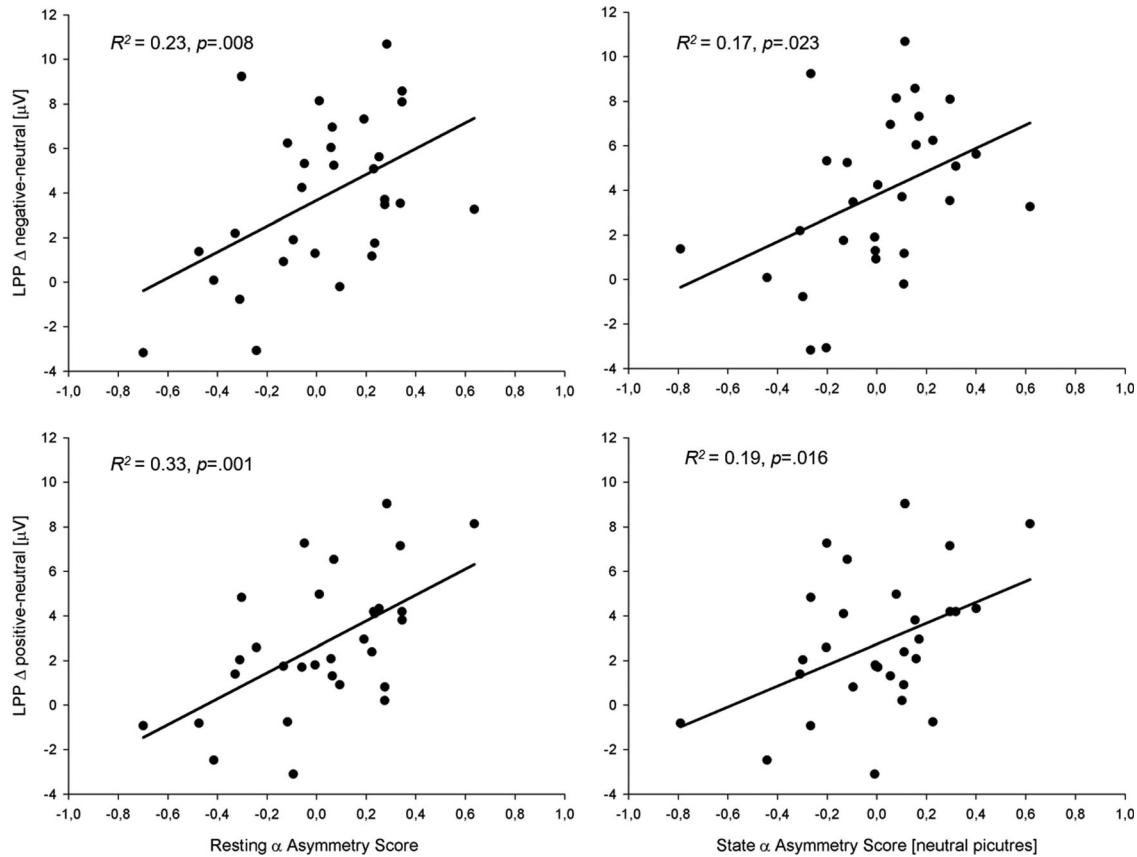


FIGURE 2 Correlations between resting alpha asymmetry scores (left), as well as state alpha asymmetry scores while viewing neutral pictures (right) and LPP Δ discrimination scores at Fz (emotional-neutral). Larger right frontal cortical activation is associated with diminished emotional reactivity scores toward positive (lower) and negative emotional pictures (upper)

transversal electrode sites (see Table 2, significant interaction Emotion \times Asymmetry \times Transversal). Larger right frontal cortical activation was associated with enhanced LPPs at midline electrode sites toward neutral pictures, $\beta = -.490$, $t = 2.98$, $p = .006$, but not toward negative, $\beta = -.157$, $t = -0.84$, *ns*, or positive pictures, $\beta = -.162$, $t = -0.87$, *ns*. Again, this effect was independent of trait anxiety and depression (partial correlation: asymmetry with LPP for neutral pictures at midline electrode sites: $r_p = -.532$, $p = .004$, $R^2 = .283$)

3.2 | Correlations between emotional reactivity scores and resting frontal asymmetry

Because the general linear model analysis revealed significant interactions between asymmetry and emotion for the LPP only, emotion reactivity scores were only reported for the LPP. Results revealed that larger resting right frontal cortical activation is associated with diminished Δ LPP emotion discrimination scores toward positive, $r = .389$, $p = .033$, $R^2 = .151$, and negative pictures, $r = .345$, $p = .062$, $R^2 = .119$, along midline electrodes (Fz, Cz, Pz). For both positive, $r = .572$, $p = .001$, $R^2 = .327$, and negative pictures, $r = .484$, $p = .008$, $R^2 = .234$, this effect was

maximal over Fz (see Figure 2, left panel). To determine whether the relationship between trait frontal cortical activation and Δ LPP emotion discrimination scores is independent of trait anxiety and depression, we calculated partial correlations controlling for these factors. Results indicate that correlations between frontal activity and emotion discrimination toward positive, $r_p = .610$, $p = .001$, $R^2 = .372$, and negative, $r_p = .472$, $p = .011$, $R^2 = .223$, pictures was independent of depression and trait anxiety.

3.3 | Associations between state changes in frontal asymmetry and emotional responses

Consistent with previous studies (Gable & Harmon-Jones, 2008; Harmon-Jones, 2007; Harmon-Jones et al., 2006), state frontal asymmetry within the 6 s of picture viewing did not differ between picture types (for all comparisons $p > .80$). However, based on previous findings (e.g., Poole & Gable, 2014), we examined the hypothesis that individuals' differences in state frontal asymmetry were related to emotional responses for pictures similar in emotional valence. Results revealed that larger right frontal activation while viewing negative pictures was related to more negative subjective valence, $r = .393$, $p = .024$, $R^2 = .154$, and higher arousal

ratings, $r = -.480$, $p = .005$, $R^2 = .230$, toward these pictures. Similarly, larger right frontal activation while viewing neutral pictures was significantly associated with more negative valence ratings, $r = .393$, $p = .024$, $R^2 = .154$, but only marginally significantly with higher arousal ratings, $r = -.298$, $p = .092$, $R^2 = .089$. Paralleling results for resting trait-like asymmetry, we found that larger right frontal activation while viewing neutral pictures was associated with larger LPPs toward neutral pictures at midline electrode sites, $r = -.450$, $p = .013$, $R^2 = .203$. Again, this effect was largest at frontal electrodes: At Fz, larger right frontal activation toward neutral pictures was associated with diminished Δ LPP emotion discrimination scores for positive pictures, $r = .436$, $p = .016$; $R^2 = .190$, and negative pictures, $r = .414$, $p = .023$, $R^2 = .171$ (see Figure 2, right panel). There were no significant correlations for the startle reflex and the skin conductance data.

4 | DISCUSSION

The present study aimed to test whether resting trait-like frontal brain asymmetry is associated with emotional and attentional responses to approach- and withdrawal-related stimuli. Therefore, we used the well-established passive picture viewing paradigm. We found that enhanced right frontal cortical activation is associated with an undifferentiated negativity bias, and enhanced attention toward ambiguous stimuli. Right frontal asymmetry might thus constitute a potential biomarker of deviant attention deployment.

However, the first aim of our study was to induce approach and avoidance motivation using the passive viewing paradigm. In general, as compared to neutral pictures, positive and negative pictures elicited larger motivated attention (i.e., larger LPP for emotional as compared to neutral pictures), larger sympathetic physiological arousal (i.e., the SCR indicating orienting toward a meaningful stimulus), and larger self-reported arousal (SAM arousal ratings; i.e., neutral < positive = negative). In addition, negative pictures elicited larger withdrawal motivation (potentiated startle reflex), while positive pictures elicited larger approach motivation (attenuated startle reflex) as compared to neutral pictures (i.e., positive < neutral < negative). Paralleling these results, negative pictures were rated to elicit more negative and positive pictures to elicit more positive subjective emotions (SAM valence ratings) than neutral pictures. Taken together, we replicated the well-known pattern of emotional responses within the passive viewing paradigm (e.g., Bradley et al., 2001; Cuthbert et al., 2000).

Having proven that our emotional stimulation elicited approach and withdrawal motivation, we looked for associations of emotional and attentional stimulus processing with frontal brain asymmetry. We found evidence for an associa-

tion between resting traitlike frontal asymmetry with early (N1) and late (LPP) attentional stimulus processing, as well as emotional self-report (SAM valence ratings). In detail, persons with larger right frontal brain activation showed enhanced early spatial attention allocation (larger N1) to all stimuli regardless of emotional content. This early spatial attention effect was accompanied by diminished discriminative processing of emotional stimuli in terms of motivated attention (i.e., lower Δ LPP for negative and positive stimuli) and a more negative emotional evaluation of all picture categories in terms of self-reported valence.

In addition, we found that enhanced right frontal cortical activation during the perception of neutral and negative pictures was associated with more negative and more arousing subjective evaluation of these stimuli. Paralleling results for resting frontal asymmetry larger LPPs toward neutral pictures were associated with larger right frontal cortical activation during the perception of these pictures.

4.1 | Early spatial attention and resting frontal brain asymmetry

We found evidence for an association between enhanced N1 amplitudes and larger right frontal cortical activation. This effect was independent of emotional valence, suggesting an undifferentiated enhancement of early attentional stimulus processing. The N1 is sensitive to selective spatial attention allocation, and amplitudes are typically higher for attended stimulus locations (Clark & Hillyard, 1996; Luck, Woodman, & Vogel, 2000; Vogel & Luck, 2000). Thus, the current data suggest a functional association between frontal cortical asymmetry and enhanced spatial attention processing. Interestingly, several previous studies found emotion-unspecific perceptual enhancement of focused stimuli as evidenced by enhanced early ERP amplitudes in highly anxious individuals (Bar-Haim, Lamy, & Glickman, 2005; Dennis & Chen, 2007; Eldar, Yankelevitch, Lamy, & Bar-Haim, 2010; Fisher et al., 2010). Furthermore, emotion-unspecific, tonic enhancement was also found for other physiological variables. For example, people with anxiety disorders show enhanced baseline startle responsivity (review in Grillon, 2002), indicating a generalized, tonic enhancement of withdrawal motivation. In the same vein, people high in trait anxiety show enhanced context conditioning, a procedure testing for tonic anxiety-like, rather than phasic fear responsivity (Grillon, 2002). These findings index uncertainty in light of ambiguous stimuli or contexts (Grupe & Nitschke, 2013). Interestingly, paralleling unspecific enhancement of N1 amplitudes, our data indicate emotion-unspecific elevated negative emotional evaluation in persons with relatively right frontal activation. Previous research has shown that ERPs within early time windows are sensitive to emotional

stimulus significance (reviewed in Olofsson et al., 2008). Thus, the current pattern of results supports and extends previous research and suggests an anxiety-like negativity bias mediated by trait-like resting frontal cortical asymmetry associated with negative emotional self-report and enhanced early attention allocation (for a comparable line of arguments, see Grimshaw et al., 2014).

4.2 | Late motivated attention and resting frontal asymmetry

We found that higher scores of right frontal cortical activation are associated with lower Δ LPP for negative and positive emotional stimuli. The LPP represents flexible and dynamic allocation of attention to emotional content within the visual cortex (Liu, Huang, McGinnis-Deweese, Keil, & Ding, 2012; Sabatinelli, Keil, Frank, & Lang, 2013; Sabatinelli, Lang, Keil, & Bradley, 2007). The current results thus suggest a diminished differential attentional processing of emotional in comparison to neutral stimuli in persons with relatively enhanced right frontal activation. Interestingly, previous research demonstrated that diminished Δ LPP scores are associated with anxiety (Frenkel & Bar-Haim, 2011; Holmes, Nielsen, & Green, 2008; Mühlberger et al., 2009; Weinberg & Hajcak, 2011) and depression (Kayser, Bruder, Tenke, Stewart, & Quitkin, 2000; MacNamara, Kotov, & Hajcak, 2016).

Basically, this pattern of results suggests that in persons with larger right frontal activation emotional and neutral stimuli are perceived as more similar in terms of their motivational significance. This subsequently leads to more uniform attentional processing and infelicitous differentiation between important and unimportant stimuli. Most previous studies have linked diminished Δ LPP (as observed frequently in anxious participants) to cognitive avoidance of threat-related or even positive emotional material. In contrast, our data indicate that in persons with larger right frontal asymmetry this diminished emotion discrimination stems from enhanced processing of neutral stimuli rather than diminished processing of emotional pictures. Interestingly, the current results parallel a variety of findings typically shown in association with heightened anxiety. For example, similarly diminished emotional discrimination of LPPs due to enhanced processing of neutral stimuli has been observed previously in persons with anxiety disorders (Mühlberger et al., 2009; Weinberg & Hajcak, 2011). Moreover, it has been repeatedly demonstrated that people with anxiety disorders show diminished discrimination learning in conditioning experiments due to increased responding toward CSminus cues (Dibbets, van den Broek, & Evers, 2015; Lissek et al., 2009; Sachs, Anderer, Doby, Saletu, & Dantendorfer, 2003). Finally, individuals with generalized anxiety disorder inter-

pret neutral and ambiguous stimuli or situations as more threatening than nonanxious controls (Butler & Mathews, 1983; Hazlett-Stevens & Borkovec, 2004; Mathews, Richards, & Eysenck, 1989). Taken together, the current data suggest a functional association between frontal brain asymmetry and a deficient, anxiety-like pattern of emotion discrimination. Numerous studies have shown a close relationship between frontal asymmetry and depression as well as anxiety, and frontal asymmetry has been labeled a risk factor for these disorders (review in Coan & Allen, 2004a). Interestingly, the current data show that the association between asymmetry and attention processing is independent of current strength of trait anxiety and depressive symptoms. This likely indicates that the association between frontal asymmetry and diminished emotion discrimination might not develop as a secondary cause of the development of anxiety or depressive symptoms. Rather, it further underscores the importance of asymmetry as a biological vulnerability marker for anxietylike attention processing.

In contrast to previous studies linking the modulation of the LPP to centroparietal electrode sites, previous studies (see review in Olofsson et al., 2008), we observed LPP modulation also at anterior electrode sites. This observation is in accord with previous research showing that passively viewed target pictures also elicit prominent positive slow waves in anterior regions, especially when the task was to later do evaluative judgments of the pictures, as was the case in our study (e.g., Cunningham et al., 2005; Diedrich et al., 1997).

4.3 | Frontal brain asymmetry—Functional significance within cortical attention networks?

The current data show an association of frontal asymmetry with deviant processing within motivationally significant attention networks, more specifically with attentional enhancement. While this cognitive enhancement was stimulus unspecific for early ERP components (see N1 results), it was specific for neutral stimuli at later time intervals (see LPP results). The enhanced attentional processing was paralleled by generally elevated negative stimulus evaluation. Interestingly, a distributed network controlling visual attention has been proposed, including the dorsolateral prefrontal cortex (dlPFC) controlling the selective sensory bias in working memory to maintain spatial attention focus (Corbetta & Shulman, 2002). Recent source localization studies (Koslov, Mendes, Pajtas, & Pizzagalli, 2011; Pizzagalli, Sherwood, Henriques, & Davidson, 2005) have shown that the dlPFC is also the neural generator for frontal brain asymmetry (Davidson, 2004). Thus, the current results might indicate that enhanced right frontal cortical activation promotes a generalized negativity bias (see also Grimshaw & Carmel, 2014) associated with negative emotional experience and enhanced

early spatial attention allocation as measured with the N1 component (Hillyard & Anllo-Vento, 1998). This frontal enhancement of early spatial attention deployment extends to later motivated attention for neutral pictures. Source localization studies have mapped the modulation of LPP amplitude to modulations within visual cortical areas. This modulation is accomplished via a distributed network including subcortical emotion-generating areas, as well as higher order prefrontal control structures including medial PFC and dlPFC (Kang, Liu, Miskovic, Keil, & Ding, 2016). Interestingly, this network also guides attention under conditions of uncertainty or “low threat” (Pessoa, 2009). The current data might thus suggest that frontal brain asymmetry, representing alterations in action of the dlPFC, acts to enhance perception and attention in light of ambiguous or low-threat stimuli, rendering frontal asymmetry a potential biological marker of deviant attention deployment.

4.4 | Sympathetic arousal, startle reflex, and frontal asymmetry

The current data indicate that covariance of traitlike resting frontal asymmetry with physiological responding was generally weak. There were no associations between frontal asymmetry and arousal-related sympathetic activity or the affect-modulated startle reflex.⁴ In terms of the biphasic model of emotion, heightened SCRs, as well as the affect modulation of the startle reflex, are thought to represent action dispositions preparing the organism for action in light of emotionally significant stimuli (Bradley et al., 2001; Lang, 2014; Lang & Bradley, 2013). Moreover, several lines of evidence suggest that the amplitude of the affect-modulated startle reflex is a direct readout of the stimulus’ motivational significance (e.g., Bradley et al., 2005; Grillon, 2002). Thus, the lack of a relationship between startle modulation and frontal asymmetry might suggest that affect-modulated startle and frontal asymmetry are not both measuring the same kind of motivational mechanism.⁵ In sum, the current data suggest that the modulating impact of frontal brain asymmetry might be limited at this point of emotion processing. Concerning

⁴We additionally fitted Bayes general linear models for the startle and the SCR data using default priors as suggested for ANOVA models by Rouder, Morey, Speckman, and Province (2012) using R (version 3.1.0) and the BayesFactor package (version 0.9.2). For the startle data, the main effect asymmetry revealed a Bayes factor of $BF_{01} = 0.2$, while the interaction Asymmetry \times Emotion revealed a Bayes factor of $BF_{01} = 0.08$. For the SCR data, the main effect asymmetry revealed a Bayes factor of $BF_{01} = 0.23$, while the interaction Asymmetry \times Emotion revealed a Bayes factor of $BF_{01} = 0.07$. According to Jeffreys (1961), these values give strong to moderate support in favor of the null hypothesis rather than in favor of the alternative hypothesis.

⁵We would like to thank an anonymous reviewer for this valuable comment.

startle, previous studies have shown that frontal brain asymmetry was related to startle responding following picture offset rather than during picture presentations (Goodman et al., 2013; Jackson et al., 2000). This result was interpreted as an index of automatic emotion regulation. Emotion regulation, including automatic emotion regulation, has been shown to recruit prefrontal brain areas including dorsolateral PFC (Ochsner & Gross, 2007), the putative neuronal generator of frontal asymmetry (Koslov et al., 2011; Pizzagalli et al., 2005). Contrary to this, in the present study, we presented startle probes during picture presentation, assessing stimulus-related withdrawal motivation rather than emotion regulation. Thus, the current findings are most likely based on the fact that potentiation of the startle response (Davis, 1992), and also the modulation of the skin conductance response (Critchley, 2002), basically rely on activity of subcortical emotion generation areas centered in the amygdala, rather than prefrontal cortical areas.

We also found no emotional modulation of N1 amplitude. Within the literature, findings for early ERP components revealed mixed results. While several studies found modulation of early ERP components (i.e., N1/P1) due to emotional valence, others did not (Olofsson et al., 2008). Within the current study, we found emotion to modulate ERP responses from around 200 ms after picture onset, a common finding among the ERP literature on emotion processing (Olofsson et al., 2008).

4.5 | State frontal asymmetry versus resting frontal asymmetry

Following the capability model of hemispheric activation, we also assessed state frontal asymmetry during picture viewing for each emotion category and related it to emotional responses toward the same picture categories. Paralleling our results for resting frontal asymmetry, we found state asymmetry to be associated with subjective ratings and motivated attention (i.e., the LPP).

Larger right frontal asymmetry to negative and neutral stimuli was associated with more negative and more arousing emotional evaluation of these picture categories, respectively (i.e., valence and arousal ratings). This finding is in line with the capability model (see Coan et al., 2006). It extends previous research on LPP modulation (Gable & Harmon-Jones, 2008; Gable & Poole, 2014; Poole & Gable, 2014) and shows that subjective ratings of both valence and arousal can also be influenced by state asymmetrical frontal brain activation. This association between emotion-specific enhanced negative evaluations with larger state right frontal asymmetry is in line with the specific predictions of the approach withdrawal model (i.e., larger withdrawal motivation toward negative stimuli). In contrast, the association of enhanced

negative emotion evaluation with resting right frontal activation was emotion unspecific. This finding is at odds with the specific predictions of the approach withdrawal model. Rather, these findings argue toward a broader conceptualization of resting frontal asymmetry. For example, Coan and coworkers (2006) have argued that the approach-withdrawal model aims to assess general individual dispositions. That is, persons react with either enhanced withdrawal or approach motivation regardless of the specific situation (Coan, et al., 2006, p. 198). Coan et al. further stated that the dispositional model would thus predict that persons with larger right frontal asymmetry would react with more withdrawal to threatening but also to other emotional situations, even to positive ones (Coan et al, 2006, p. 199). These data are also paralleled by an undifferentiated N1 enhancement. As outlined above, these measures suggest an undifferentiated negativity bias in perception of ambiguous stimuli. Thus, in conclusion, the current rating data are in line with this broader conceptualization of frontal asymmetry. In addition to the findings for emotion ratings, we found state asymmetry toward neutral pictures to be associated with enhanced LPP to neutral pictures, as well as with diminished Δ LPP emotion-discrimination scores for positive and neutral pictures. Again, these data largely parallel those for resting frontal asymmetry and provide further evidence for a link between enhanced motivated attention and enhanced right frontal activation toward neutral stimuli.

However, in sum, the current LPP findings are at odds with the assumptions from the approach-withdrawal model, which would predict enhanced right frontal activation to be associated with enhanced LPPs toward negative stimuli. Rather, these data are consistent with the conceptualization of enhanced right frontal cortical activation as a risk marker for emotion-related disorders. That is, in the literature, the observed enhanced attentional deployment to neutral stimulus material has been associated with heightened anxiety (see above). It indicates enhanced personal relevance of otherwise neutral materials for persons with elevated right frontal activation. Interestingly, it has been previously shown that frontal alpha asymmetry is sensitive to modulations in personal relevance (Harmon Jones et al., 2006). Thus, the current data may support these findings and underscores the sensitivity of frontal asymmetry toward individual differences in personal relevance detection.

4.6 | Limitations

For the purpose of the current study, we used a linked mastoid reference. This was chosen in favor of other classical reference schemes (i.e., average reference, vertex reference) because (a) it is favorable for the measurement of anterior alpha activity above the other classical schemes (Hagemann,

2004), and (b) it has been widely used in research on frontal asymmetry (Hagemann, 2004). It thus ensures comparability of results with previous literature. However, it was argued that a current source density measure (CSD) might be promising in order to avoid several reference issues such as mirroring of dipoles and others (Hagemann, 2004; Velo, Stewart, Hasler, Towers, & Allen, 2012). Moreover, some research suggests that the CSD transform might be more sensitive to the relationship between resting traitlike frontal asymmetry with depression or anxiety (Stewart, Bismark, Towers, Coan, & Allen, 2010). Thus, although previous research on resting frontal asymmetry in a nonclinical sample showed comparable results for the CSD derivation and the linked mastoids reference (see Adolph & Margraf, 2017), an influence of the current reference scheme on our results cannot be entirely ruled out.

Another limitation might stem from the fact that resting frontal asymmetry was assessed at one occasion only. It has been suggested that frontal asymmetry assessed at rest contains trait and state influences (Hagemann, Naumann, Thayer, & Bartussek, 2002) and that these influences are best controlled by assessing frontal asymmetry at different occasions (Hagemann, 2004). Thus, although we controlled for current mood in the present analyses (a method applied successfully before; Adolph & Margraf, 2017), it cannot be entirely ruled out that some state influences remained in our frontal asymmetry estimates.

Finally, arousal ratings for positive pictures were significantly smaller than those for negative pictures. It is widely accepted, that the level of arousal induced by a stimulus determines the intensity of motivational engagement in response to that stimulus. However, the significant attenuation of the startle response and the equally enhanced skin conductance responses indicate that the positive pictures robustly elicited approach motivation and physiological arousal. Nonetheless, on the basis of current arousal ratings, it cannot be ruled out that the motivational significance of our positive stimuli might have been smaller than those of our negative stimuli.

4.7 | Conclusion

The present study shows that enhanced right frontal cortical activation is associated with an undifferentiated negativity bias, consisting of enhanced early attentional and more negative evaluation of all stimuli in persons with enhanced right frontal cortical activation. This early enhanced spatial attention effect is later followed by diminished differential emotion processing due to sustained attentional enhancement of nonthreatening neutral stimuli. Taken together, we found a pattern of results previously associated with heightened anxiety. At the same time, the current data do not support a link

between enhanced withdrawal motivation for negative, withdrawal-related stimuli, although previous findings of selectively enhanced negative stimulus evaluation could be replicated. Taken together, the current study provides new insights into the relationship between frontal brain asymmetry and the processing of emotion-related stimuli. Although the correlative design of the study does not allow causal statements, our results pose important starting points for future experimental studies.

REFERENCES

- Adolph, D., & Margraf, J. (2017). The differential relationship between trait anxiety, depression, and resting frontal alpha-asymmetry. *Journal of Neural Transmission*, *124*(3), 379–386. doi: 10.1007/s00702-016-1664-9
- Allen, J. J. B., Coan, J. A., & Nazarian, M. (2004). Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. *Biological Psychology*, *67*(1–2), 183–218. doi: 10.1016/j.biopsycho.2004.03.007
- 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. doi: 10.1016/j.ijpsycho.2011.01.010
- Bar-Haim, Y., Lamy, D., & Glickman, S. (2005). Attentional bias in anxiety: A behavioral and ERP study. *Brain and Cognition*, *59*(1), 11–22. doi: 10.1016/j.bandc.2005.03.005
- Blumenthal, T. D., Cuthbert, B. N., Filion, D. L., Hackley, S., Lipp, O. V., & van Boxtel, A. (2005). Committee report: Guidelines for human startle eyeblink electromyographic studies. *Psychophysiology*, *42*(1), 1–15. doi: 10.1111/j.1469-8986.2005.00271.x
- Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: Defensive and appetitive reactions in picture processing. *Emotion*, *1*(3), 276–298. doi: 10.1037/1528-3542.1.3.276
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: the Self-Assessment Manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, *25*(1), 49–59. doi: 10.1016/0005-7916(94)90063-9
- Bradley, M. M., Moulder, B., & Lang, P. J. (2005). When good things go bad: The reflex physiology of defense. *Psychological Science*, *16*, 468–473. doi: 10.1111/j.0956-7976.2005.01558.x
- Butler, G., & Mathews, A. (1983). Cognitive processes in anxiety. *Advances in Behaviour Research and Therapy*, *5*(1), 51–62. doi: 10.1016/0146-6402(83)90015-2
- Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *Journal of Cognitive Neuroscience*, *8*(5), 387–402. doi: 10.1162/jocn.1996.8.5.387
- Coan, J. A., & Allen, J. J. B. (2003). Varieties of emotional experience during voluntary emotional facial expressions. *Annals of the New York Academy of Sciences*, *1000*, 375–379. doi: 10.1196/annals.1280.034
- Coan, J. A., & Allen, J. J. B. (2004a). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology*, *67*(1–2), 7–49. doi: 10.1016/j.biopsycho.2004.03.002
- Coan, J. A., & Allen, J. J. B. (2004b). The state and trait nature of frontal EEG asymmetry in emotion. In K. Hugdahl & R. J. Davidson (Eds.), *The Asymmetrical Brain*. (pp. 565–616). Cambridge, MA: MIT Press.
- Coan, J. A., Allen, J. J., & McKnight, P. E. (2006). A capability model of individual differences in frontal EEG asymmetry. *Biological Psychology*, *72*(2), 198–207. doi: 10.1016/j.biopsycho.2005.10.003
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. doi: 10.1038/nrn755
- Critchley, H. D. (2002). Electrodermal responses: What happens in the brain. *Neuroscientist*, *8*(2), 132–142. doi: 10.1177/107385840200800209
- Cunningham, W. A., Espinet, S. D., DeYoung, C. G., & Zelazo, P. D. (2005). Attitudes to the right- and left: Frontal ERP asymmetries associated with stimulus valence and processing goals. *NeuroImage*, *28*(4), 827–834. doi: 10.1016/j.neuroimage.2005.04.044
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology*, *52*(2), 95–111. doi: 10.1016/S0301-0511(99)00044-7
- Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, *20*(1), 125–151. doi: 10.1016/0278-2626(92)90065-T
- Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition and Emotion*, *12*(3), 307–330. doi: 10.1080/026999398379628
- Davidson, R. J. (2004). What does the prefrontal cortex “do” in affect: Perspectives on frontal EEG asymmetry research. *Biological Psychology*, *67*, 219–233. doi: 10.1016/j.biopsycho.2004.03.008
- Davidson, R. J., Jackson, D. C., & Kalin, N. H. (2000). Emotion, plasticity, context, and regulation: Perspectives from affective neuroscience. *Psychological Bulletin*, *126*(6), 890–909. doi: 10.1037/0033-2909.126.6.890
- Davis, M. (1992). The role of the amygdala in fear-potentiated startle: implications for animal models of anxiety. *Trends in Pharmacological Sciences*, *13*(1), 35–41. doi: 10.1016/0165-6147(92)90014-W
- Davis, M. (2006). Neural systems involved in fear and anxiety measured with fear-potentiated startle. *American Psychologist*, *61*(8), 741–756. doi: 10.1037/0003-066X.61.8.741
- Dennis, T. A., & Chen, C.-C. (2007). Emotional face processing and attention performance in three domains: Neurophysiological mechanisms and moderating effects of trait anxiety. *International Journal of Psychophysiology*, *65*(1), 10–19. doi: 10.1016/j.ijpsycho.2007.02.006
- Dibbets, P., van den Broek, A., & Evers, E. A. T. (2015). Fear conditioning and extinction in anxiety- and depression-prone persons. *Memory*, *23*(3), 350–364. doi: 10.1080/09658211.2014.886704
- Diedrich, O., Naumann, E., Maier, S., & Becker, G. (1997). A frontal positive slow wave in the ERP associated with emotional slides. *Journal of Psychophysiology*, *11*(1), 71–84.

- Ekman, P. (1992). An argument for basic emotions. *Cognition & Emotion*, 6(3), 169–200. doi: 10.1080/02699939208411068
- Eldar, S., Yankelevitch, R., Lamy, D., & Bar-Haim, Y. (2010). Enhanced neural reactivity and selective attention to threat in anxiety. *Biological Psychology*, 85(2), 252–257. doi: 10.1016/j.biopsycho.2010.07.010
- Fabiani, M. (2015). The embodied brain. *Psychophysiology*, 52(1), 1–5. doi: 10.1111/psyp.12381
- Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin and Review*, 1(4), 429–438. doi: 10.3758/BF03210947
- Fisher, J. E., Sass, S. M., Heller, W., Siltan, R. L., Edgar, J. C., Stewart, J. L., & Miller, G. A. (2010). Time course of processing emotional stimuli as a function of perceived emotional intelligence, anxiety, and depression. *Emotion*, 10(4), 486–497. doi: 10.1037/a0018691
- Foti, D., Hajcak, G., & Dien, J. (2009). Differentiating neural responses to emotional pictures: Evidence from temporal-spatial PCA. *Psychophysiology*, 46(3), 521–530. doi: 10.1111/j.1469-8986.2009.00796.x
- Frenkel, T. I., & Bar-Haim, Y. (2011). Neural activation during the processing of ambiguous fearful facial expressions: An ERP study in anxious and nonanxious individuals. *Biological Psychology*, 88, 188–195. doi: 10.1016/j.biopsycho.2011.08.001
- Gable, P. A., & Poole, B. D. (2014). Influence of trait behavioral inhibition and behavioral approach motivation systems on the LPP and frontal asymmetry to anger pictures. *Social Cognitive and Affective Neuroscience*, 9(2), 182–190. doi: 10.1093/scan/nss130
- Gable, P., & Harmon-Jones, E. (2008). Relative left frontal activation to appetitive stimuli: Considering the role of individual differences. *Psychophysiology*, 45(2), 275–278. doi: 10.1111/j.1469-8986.2007.00627.x
- Goodman, R. N., Rietschel, J. C., Lo, L.-C., Costanzo, M. E., & Hatfield, B. D. (2013). Stress, emotion regulation and cognitive performance: The predictive contributions of trait and state relative frontal EEG alpha asymmetry. *International Journal of Psychophysiology*, 87(2), 115–123. doi: 10.1016/j.ijpsycho.2012.09.008
- Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4), 468–484. doi: 10.1016/0013-4694(83)90135-9
- Grillon, C. (2002). Startle reactivity and anxiety disorders: Aversive conditioning, context, and neurobiology. *Biological Psychiatry*, 52(10), 958–975. doi: 10.1016/S0006-3223(02)01665-7
- Grillon, C. & Baas, J. (2003). A review of the modulation of the startle reflex by affective states and its application in psychiatry. *Clinical Neurophysiology*, 114, 1557–1579. doi: 10.1016/S1388-2457(03)00202-5.
- Grimm, S., Schmidt, C. F., Bermpohl, F., Heinzl, A., Dahlem, Y., Wyss, M., . . . Northoff, G. (2006). Segregated neural representation of distinct emotion dimensions in the prefrontal cortex—An fMRI study. *NeuroImage*, 30(1), 325–340. doi: 10.1016/j.neuroimage.2005.09.006
- Grimshaw, G. M., & Carmel, D. (2014). An asymmetric inhibition model of hemispheric differences in emotional processing. *Frontiers in Psychology*, 5, 489. doi: 10.3389/fpsyg.2014.00489
- Grimshaw, G. M., Foster, J. J., & Corballis, P. M. (2014). Frontal and parietal EEG asymmetries interact to predict attentional bias to threat. *Brain and Cognition*, 90, 76–86. doi: 10.1016/j.bandc.2014.06.008
- Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, 14(7), 488–501. doi: 10.1038/nrn3524
- Hagemann, D. (2004). Individual differences in anterior EEG asymmetry: Methodological problems and solutions. *Biological Psychology*, 67, 157–182. doi: 10.1016/j.biopsycho.2004.03.006
- Hagemann, D., Hewig, J., Seifert, J., Naumann, E. and Bartussek, D. (2005). The latent state-trait structure of resting EEG asymmetry: Replication and extension. *Psychophysiology*, 42, 740–752. doi: 10.1111/j.1469-8986.2005.00367.x
- Hagemann, D., Naumann, E., Becker, G., Maier, S., & Bartussek, D. (1998). Frontal brain asymmetry and affective style: A conceptual replication. *Psychophysiology*, 35(04), 372–388. doi: 10.1111/1469-8986.3540372
- Hagemann, D., Naumann, E., Thayer, J. F., & Bartussek, D. (2002). Does resting electroencephalograph asymmetry reflect a trait? An application of latent state-trait theory. *Journal of Personality and Social Psychology*, 82(4), 619–641. doi: 10.1037/0022-3514.82.4.619
- Hamann, S., & Canli, T. (2004). Individual differences in emotion processing. *Current Opinion in Neurobiology*, 14, 233–238. doi: 10.1016/j.conb.2004.03.010
- Harmon-Jones, E. (2007). Trait anger predicts relative left frontal cortical activation to anger-inducing stimuli. *International Journal of Psychophysiology*, 66, 154–160. doi: 10.1016/j.ijpsycho.2007.03.020
- Harmon-Jones, E., & Allen, J. J. B. (1998). Anger and frontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. *Journal of Personality and Social Psychology*, 74, 1310–1316. doi: 10.1037/0022-3514.74.5.1310
- 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. doi: 10.1016/j.biopsycho.2009.08.010
- Harmon-Jones, E., Lueck, L., Fearn, M., & Harmon-Jones, C. (2006). The effect of personal relevance and approach-related action expectation on relative left frontal cortical activity. *Psychological Science*, 17(5), 434–440. doi: 10.1111/j.1467-9280.2006.01724.x
- Hazlett-Stevens, H., & Borkovec, T. D. (2004). Interpretive cues and ambiguity in generalized anxiety disorder. *Behaviour Research and Therapy*, 42(8), 881–892. doi: 10.1016/S0005-7967(03)00204-3
- Heller, W. (1993). Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology*, 7, 476–489. doi: 10.1037/0894-4105.7.4.476
- Heller, W., Nitschke, J. B., Etienne, M. A., & Miller, G. A. (1997). Patterns of regional brain activity differentiate types of anxiety. *Journal of Abnormal Psychology*, 106(3), 376–385. doi: 10.1037/0021-843X.106.3.376
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, 95(3), 781–787.

- Holmes, A., Nielsen, M. K., & Green, S. (2008). Effects of anxiety on the processing of fearful and happy faces: An event-related potential study. *Biological Psychology*, *77*(2), 159–173. doi: 10.1016/j.biopsycho.2007.10.003
- Izard, C. (1977). *Human emotions*. New York, NY: Plenum Press.
- Jackson, D. C., Malmstadt, J. R., Larson, C. L., & Davidson, R. J. (2000). Suppression and enhancement of emotional responses to unpleasant pictures. *Psychophysiology*, *37*(4), 515–522. doi: 10.1111/1469-8986.3740515
- Jackson, D. C., Mueller, C. J., Dolski, I., Dalton, K. M., Nitschke, J. B., Urry, H. L., . . . Davidson, R. J. (2003). Now you feel it, now you don't: Frontal brain electrical asymmetry and individual differences in emotion regulation. *Psychological Science*, *14*(6), 612–617. doi: 10.1046/j.0956-7976.2003.psci_1473.x
- Jeffreys, H. (1961) *The theory of probability* (3rd ed.). New York, NY: Oxford University Press.
- Kang, D., Liu, Y., Miskovic, V., Keil, A., & Ding, M. (2016). Large-scale functional brain connectivity during emotional engagement as revealed by beta-series correlation analysis. *Psychophysiology*, *53*, 1627–1638. doi: 10.1111/psyp.12731
- Kayser, J., Bruder, G. E., Tenke, C. E., Stewart, J. E., & Quitkin, F. M. (2000). Event-related potentials (ERPs) to hemifield presentations of emotional stimuli: Differences between depressed patients and healthy adults in P3 amplitude and asymmetry. *International Journal of Psychophysiology*, *36*(3), 211–236. doi: 10.1016/S0167-8760(00)00078-7
- Koslov, K., Mendes, W. B., Pajtas, P. E., & Pizzagalli, D. A. (2011). Asymmetry in resting intracortical activity as a buffer to social threat. *Psychological Science*, *22*(5), 641–649. doi: 10.1177/0956797611403156
- Lang, P. J. (1988). What are the data of emotion? In V. Hamilton, G. H. Bower, & N. H. Frijda (Eds.), *Cognitive perspectives on emotion and motivation* (pp. 173–191). Dordrecht, Netherlands: Springer.
- Lang, P. J. (2014). Emotion's response patterns: The brain and the autonomic nervous system. *Emotion Review*, *6*(2), 93–99. doi: 10.1177/1754073913512004
- Lang, P. J., & Bradley, M. M. (2013). Appetitive and defensive motivation: Goal-directed or goal-determined? *Emotion Review*, *5*(3), 230–234. doi: 10.1177/1754073913477511
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes*. (pp. 97–135). Mahwah, NJ: Erlbaum.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1998a). Emotion and motivation: Measuring affective perception. *Journal of Clinical Neurophysiology*, *15*(5), 397–408.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. (1998b). Emotion, motivation, and anxiety: Brain mechanisms and psychophysiology. *Biological Psychiatry*, *44*, 1248–1263. doi: 10.1016/S0006-3223(98)00275-3
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1998). Emotion and motivation: Measuring affective perception. *Journal of Clinical Neurophysiology*, *15*(5), 397–408.
- Laux, L., Schaffner, P., Glanzmann, P., & Spielberger, C. D. (1981). *Das State-Trait Angst Angstinventar (STAI) [State-Trait Anxiety Inventory]*. Weinheim, Germany: Beltz Testgesellschaft.
- Leventhal, H., & Tomarken, A. J. (1986). Emotion: Today's problems. *Annual Review of Psychology*, *37*, 565–610. doi: 10.1146/annurev.ps.37.020186.003025
- Lissek, S., Rabin, S. J., McDowell, D. J., Dvir, S., Bradford, D. E., Geraci, M., . . . Grillon, C. (2009). Impaired discriminative fear-conditioning resulting from elevated fear responding to learned safety cues among individuals with panic disorder. *Behaviour Research and Therapy*, *47*(2), 111–118. doi: 10.1016/j.brat.2008.10.017
- Liu, Y., Huang, H., McGinnis-Deweese, M., Keil, A., & Ding, M. (2012). Neural substrate of the late positive potential in emotional processing. *Journal of Neuroscience*, *32*(42), 14563–14572. doi: 10.1523/jneurosci.3109-12.2012
- Löw, A., Lang, P. J., Carson Smith, J., & Bradley, M. M. (2008). Both predator and prey: Emotional arousal in threat and reward. *Psychological Science*, *19*, 865–873. doi: 10.1111/j.1467-9280.2008.02170.x
- Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*(11), 432–440. doi: 10.1016/S1364-6613(00)01545-X
- MacNamara, A., Kotov, R., & Hajcak, G. (2016). Diagnostic and symptom-based predictors of emotional processing in generalized anxiety disorder and major depressive disorder: An event-related potential study. *Cognitive Therapy and Research*, *40*(3), 275–289. doi: 10.1007/s10608-015-9717-1
- Mathews, A., Richards, A., & Eysenck, M. (1989). Interpretation of homophones related to threat in anxiety states. *Journal of Abnormal Psychology*, *98*(1), 31–34. doi: 10.1037/0021-843X.98.1.31
- Mauss, I. B., Levenson, R. W., McCarter, L., Wilhelm, F. H., & Gross, J. J. (2005). The tie that binds? Coherence among emotion experience, behavior, and physiology. *Emotion*, *5*(2), 175–190. doi: 10.1037/1528-3542.5.2.175
- McRae, K., Misra, S., Prasad, A. K., Pereira, S. C., & Gross, J. J. (2012). Bottom-up and top-down emotion generation: Implications for emotion regulation. *Social Cognitive and Affective Neuroscience*, *7*(3), 253–262. doi: 10.1093/scan/nsq103
- Miltner, W., Matjak, M., Braun, C., Diekmann, H., & Brody, S. (1994). Emotional qualities of odors and their influence on the startle reflex in humans. *Psychophysiology*, *31*(1), 107–110. doi: 10.1111/j.1469-8986.1994.tb01030.x
- Miskovic, V., & Schmidt, L. A. (2010). Frontal brain electrical asymmetry and cardiac vagal tone predict biased attention to social threat. *International Journal of Psychophysiology*, *75*(3), 332–338. doi: 10.1016/j.ijpsycho.2009.12.015
- Mühlberger, A., Wieser, M. J., Herrmann, M. J., Weyers, P., Troger, C., & Pauli, P. (2009). Early cortical processing of natural and artificial emotional faces differs between lower and higher socially anxious persons. *Journal of Neural Transmission*, *116*(6), 735–746. doi: 10.1007/s00702-008-0108-6
- Ochsner, K. N., & Gross, J. J. (2007). The neural architecture of emotion regulation. In J. J. Gross & R. Buck (Eds.), *The Handbook of Emotion Regulation* (pp. 87–109). New York, NY: Guilford Press.
- Ochsner, K. N., Ray, R. R., Hughes, B., McRae, K., Cooper, J. C., Weber, J., . . . Gross, J. J. (2009). Bottom-up and top-down processes in emotion generation: Common and distinct neural

- mechanisms. *Psychological Science*, 20(11), 1322–1331. doi: 10.1111/j.1467-9280.2009.02459.x
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology*, 77(3), 247–265. doi: 10.1016/j.biopsycho.2007.11.006
- Pérez-Edgar, K., Kujawa, A., Nelson, S. K., Cole, C., & Zapp, D. J. (2013). The relation between electroencephalogram asymmetry and attention biases to threat at baseline and under stress. *Brain and Cognition*, 82(3), 337–343. doi: 10.1016/j.bandc.2013.05.009
- Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences*, 13(4), 160–166. doi: 10.1016/j.tics.2009.01.006
- Pizzagalli, D. A., Sherwood, R. J., Henriques, J. B., & Davidson, R. J. (2005). Frontal brain asymmetry and reward responsiveness: A source-localization study. *Psychological Science*, 16(10), 805–813. doi: 10.1111/j.1467-9280.2005.01618.x
- Poole, B. D., & Gable, P. A. (2014). Affective motivational direction drives asymmetric frontal hemisphere activation. *Experimental Brain Research*, 232(7), 2121–2130. doi: 10.1007/s00221-014-3902-4
- Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, 56(5), 356–374. doi: 10.1016/j.jmp.2012.08.001
- Sabatinelli, D., Keil, A., Frank, D. W., & Lang, P. J. (2013). Emotional perception: Correspondence of early and late event-related potentials with cortical and subcortical functional MRI. *Biological Psychology*, 92(3), 513–519. doi: 10.1016/j.biopsycho.2012.04.005
- Sabatinelli, D., Lang, P. J., Keil, A., & Bradley, M. M. (2007). Emotional perception: Correlation of functional MRI and event-related potentials. *Cerebral Cortex*, 17, 1085–1091. doi: 10.1093/cercor/bhl017
- Sachs, G., Anderer, P., Doby, D., Saletu, B., & Dantendorfer, K. (2003). Impaired conditional discrimination learning in social phobia. *Neuropsychobiology*, 47(2), 66–72. doi: 10.1159/000070011
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology*, 37(2), 257–261. doi: 10.1111/1469-8986.3720257
- Silberman, E. K., & Weingartner, H. (1986). Hemispheric lateralization of functions related to emotion. *Brain and Cognition*, 5(3), 322–353. doi: 10.1016/0278-2626(86)90035-7
- Stewart, J. L., Bismark, A. W., Towers, D. N., Coan, J. A., & Allen, J. J. (2010). Resting frontal EEG asymmetry as an endophenotype for depression risk: Sex-specific patterns of frontal brain asymmetry. *Journal of Abnormal Psychology*, 119(3), 502–512. doi: 10.1037/a0019196
- Taylor, S. F., Phan, K. L., Decker, L. R., & Liberzon, I. (2003). Subjective rating of emotionally salient stimuli modulates neural activity. *NeuroImage*, 18(3), 650–659. doi: 10.1016/S1053-8119(02)00051-4
- Tomarken, A. J., Davidson, R. J., & Henriques, J. B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology*, 59(4), 791–801. doi: 10.1037/0022-3514.59.4.791
- Tomarken, A. J., Davidson, R. J., Wheeler, R. E., & Kinney, L. (1992). Psychometric properties of resting anterior EEG asymmetry: Temporal stability and internal consistency. *Psychophysiology*, 29(5), 576–592. doi: 10.1111/j.1469-8986.1992.tb02034.x
- Velo, J. R., Stewart, J. L., Hasler, B. P., Towers, D. N., & Allen, J. J. B. (2012). Should it matter when we record? Time of year and time of day as factors influencing frontal EEG asymmetry. *Biological Psychology*, 91(2), 283–291. doi: 10.1016/j.biopsycho.2012.06.010
- Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, 37(2), 190–203. doi: 10.1111/1469-8986.3720190
- von Zerssen, D., & Koeller, D.-M. (1976). *Paranoid-Depressivitäts-Skala/PD-S [Paranoid-Depression Scale]*. Göttingen, Germany: Hogrefe.
- Vrana, S. R., Spence, E. L., & Lang, P. J. (1988). The startle probe response: A new measure of emotion? *Journal of Abnormal Psychology*, 97(4), 487–491. doi: 10.1037/0021-843X.97.4.487
- Weinberg, A., & Hajcak, G. (2011). Electro cortical evidence for vigilance-avoidance in generalized anxiety disorder. *Psychophysiology*, 48(6), 842–851. doi: 10.1111/j.1469-8986.2010.01149.x
- Wheeler, R. E., Davidson, R. J., & Tomarken, A. J. (1993). Frontal brain asymmetry and emotional reactivity: A biological substrate of affective style. *Psychophysiology*, 30(1), 82–89. doi: 10.1111/j.1469-8986.1993.tb03207.x

How to cite this article: Adolph D, von Glischinski M, Wannemüller A, Margraf J. The influence of frontal alpha-asymmetry on the processing of approach- and withdrawal-related stimuli—A multichannel psychophysiology study. *Psychophysiology*. 2017;54:1295–1310. <https://doi.org/10.1111/psyp.12878>