



Subjective ratings of fear are associated with frontal late positive potential asymmetry, but not with early brain activity over the occipital and centro-parietal cortices

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Abstract

The human frontal cortex is asymmetrically involved in motivational and affective processing. Several studies have shown that the left-frontal hemisphere is related to positive and approach-related affect, whereas the right-frontal hemisphere is related to negative and withdrawal-related affect. The present study aimed to investigate whether evolutionarily threatening stimuli modulate asymmetrical frontal activity. We examined hemispheric differences in frontal late positive potentials (f-LPP asymmetry) and frontal alpha power activation (frontal alpha asymmetry, FAA) in response to images depicting snakes, spiders, butterflies, and birds. Results showed that the late component of f-LPP asymmetry, but not FAA, was modulated by the category of stimuli. Specifically, threatening stimuli (snakes and spiders) evoked a relatively large late f-LPP over the right-frontal hemisphere than non-threatening stimuli (birds and butterflies). Moreover, this relatively great right-frontal activity was positively associated with the subjective ratings of fear. Importantly, the subjective ratings of fear were not associated with early brain activity over the occipital or centro-parietal cortices. These results suggest that late f-LPP asymmetry may reflect higher order affective processes, specifically the subjective appraisal of threatening stimuli and the subjective experience of fear, that are independent of the fast and automatic processing of evolutionarily significant and affectively arousing stimuli.

1 | INTRODUCTION

1.1 | Snakes and evolutionary priorities in visual perception

Humans and other primates are very efficient in detecting snakes (Öhman, Flykt, & Esteves, 2001; Shibasaki & Kawai, 2009). The “Snake Detection Theory” (Isbell, 2006, 2009) states that the ancestral selection pressure posed by dangerous snakes may have been one major

factor in the changes and enlargement of the primates' visual system. A study (Van Le et al., 2013) in macaque monkeys (*Macaca fuscata*) showed that pictures of snakes selectively enhanced the activity of a specific group of neurons in the (medial and dorsolateral) pulvinar of the thalamus. These neurons form part of a neural pathway that processes visual information from the retina via the superior colliculus, allowing for fast detection of threatening stimuli (Morris, Öhman, & Dolan, 1999; Tamietto & de Gelder, 2010).

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Several electroencephalographic (EEG) studies on humans have provided evidence in support of the Snake Detection Theory (He, Kubo, & Kawai, 2014; Grassini et al., 2019; Grassini, Holm, Railo, & Koivisto, 2016; Grassini, Railo, Valli, Revonsuo, & Koivisto, 2018; Langeslag & van Strien, 2017; Van Strien, Christiaans, Franken, & Huijding, 2016; Van Strien, Eijlers, Franken, & Huijding, 2014a; Van Strien, Franken, & Huijding, 2014b; Van Strien & Isbell, 2017). These have shown that images of snakes specifically modulate an early/intermediate event-related potential (ERP) component—the Early Posterior Negativity (EPN, a negative deflection around 225–300 from stimulus onset). The EPN component reflects the visual processing of emotional stimuli (for reviews, see Luck & Kappenman, 2011; Olofsson, Nordin, Sequeira, & Polich, 2008) and has been argued to reflect the modulation of the visual cortex by the amygdala (Dolan, 2002; Tamietto & de Gelder, 2010). Additionally, the EPN is modulated by evolutionarily relevant stimuli (e.g., erotic contents, mutilations, and threats; Schupp, Junghöfer, Weike, & Hamm, 2003). Previous investigations have not found any correlations between the subjective ratings of fear elicited by snakes and the amplitude of the EPN (e.g., Grassini et al., 2016, 2018; Van Strien et al., 2016). This has been interpreted as support for the suggestion that the EPN reflects the automatic processing of visual stimuli, which is independent of the subjective evaluation of fear. Furthermore, although most studies have not controlled for low-level visual features of the images (e.g., luminance, contrast, colors, and spatial frequency), it has been shown that snake images selectively enhance the amplitude of the EPN component irrespective of those features (Grassini et al., 2016, 2018; He et al., 2014).

Although the fear of spiders is prevalent in the healthy population (see, e.g., Agras, Sylvester, & Oliveau, 1969; Davey, 1994), the visual processing of spider images, as compared to snake images, seems to have a lower early attentional priority. This is demonstrated by a smaller EPN elicited by spider, as compared to snake, images (He et al., 2014; Van Strien et al., 2016; Van Strien, Eijlers, et al., 2014; Van Strien, Franken, et al., 2014). However, the EPN elicited by spider images is still higher than that evoked by the images of other animals, such as birds, butterflies, beetles, or slugs (cf. He et al., 2014). On the one hand, differences in the processing of snake and spider images have been suggested to reflect differences in the underlying reasons as to why snakes and spiders are perceived as threatening (Langeslag & Van Strien, 2018). Snakes constituted a predatory threat for primates and probably also for early mammals for millions of years (see, e.g., Isbell, 2006), while spiders have been associated with illness, disease, and infection from the Middle Ages (Davey, 1994). Therefore, the fear of spiders may be driven by the feeling of disgust (learned or automatically developed), rather than by the perception of actual threat or danger

(De Jong & Muris, 2002). Thus, according to this perspective, whereas the fear of snakes has an evolutionary origin, the fear of spiders is more related to social/learned fear (Van Strien, Eijlers, et al., 2014).

On the other hand, the findings that both snake and spider images are processed differently from the images of other animals can be taken to suggest that not only snakes, but also spiders represent evolutionarily significant stimuli for humans. The evolutionary argument is that, although spiders do not pose much threat to humans currently, humans and their primate ancestors were at perennial, unpredictable, and significant risk of encountering highly venomous and harmful spiders in their ancestral environments (New & German, 2015). The experimental evidence comes from studies showing that spiders and spider-like stimuli capture human attention much more efficiently than other stimuli depicting modern threats or depicting harmless insects, and this happens even when spiders are presented unexpectedly, very briefly, and peripherally (New & German, 2015). Furthermore, spiders capture attention more than other stimuli already in 5- and 6-month-old infants (Hoehl et al., 2017; Rakison & Derringer, 2008), suggesting very early preparedness for spider detection that is independent of prior learning opportunities.

In sum, whereas snakes are considered evolutionarily threatening stimuli, the evolutionary nature of spider-induced fear is more debatable.

1.2 | Hemispheric asymmetry and human affective processes

A long line of research has explored the role of hemispheric asymmetry of the human brain, specifically of the frontal cortical areas, in affective and motivational processes. Many EEG studies have shown that the activity of the left and right frontal hemispheres is differentially associated with affective traits and states: the left hemisphere is related to positive and approach-related affect, whereas the right hemisphere is related to negative and withdrawal-related affect (for reviews, see Harmon-Jones & Gable, 2018; Reznik & Allen, 2018).

1.2.1 | Frontal alpha asymmetry

A large number of studies have explored the involvement of hemispheric asymmetry in affective processes by analyzing alpha oscillations (typically 8–12/13 Hz) over the frontal cortical regions. This so-called frontal alpha asymmetry (FAA) is calculated as a difference in alpha power between the right and left homologous frontal electrodes (e.g., F4-F3; Reznik & Allen, 2018). Because alpha frequency band power is assumed to reflect

functional inhibition of underlying brain areas (Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch, Sauseng, & Hanslmayr, 2007), and due to interhemispheric inhibitory connections (Grimshaw & Carmel, 2014; Schutter & Harmon-Jones, 2013), higher FAA scores (i.e., more alpha power in the right hemisphere) are assumed to reflect a relatively high level of left-frontal (or relatively low level of right-frontal) activity. Hereinafter, in the present article with “alpha” we refer to the 8–13-Hz activity range.

Although originally relatively great left-frontal activity was associated with positive affect, and relatively great right-frontal activity with negative affect, more recently it has been suggested that motivational direction, rather than affective valence, underlies FAA (for reviews, see Angus & Harmon-Jones, 2016; Harmon-Jones & Gable, 2018; Reznik & Allen, 2018). As such, relatively great left-frontal activity is related to approach motivation and approach-related affect (e.g., elation, anger), whereas relatively great right-frontal activity is linked to withdrawal motivation and withdrawal-related affect (e.g., fear, anxiety) (Harmon-Jones & Gable, 2018; Schutter, de Weijer, Meuwese, Morgan, & van Honk, 2008). FAA has also been related to affect regulation and related psychopathology (e.g., anxiety disorders) (see Reznik & Allen, 2018 for a review).

FAA has been mostly investigated during the resting state with frontal EEG activity recorded over an extended period (often over several minutes). Few studies have explored EEG activation causally triggered by stimuli, such as affective images. Moreover, results regarding the stimulus-evoked FAA have remained inconsistent. Whereas some studies have reported FAA (specifically, greater relative left-sided) activation in response to images with high approach positive affect (dessert images in Gable & Harmon-Jones, 2008; erotic images in Schöne, Schomberg, Gruber, & Quirin., 2016), others have failed to find significant relationships between FAA and affective images (e.g., Gable & Poole, 2014; Poole & Gable, 2014; Uusberg, Thiruchselvam, & Gross, 2014). It has been suggested that one reason for these inconsistencies may be that the images used do not evoke strong affective or motivational tendencies for all individuals (Gable & Harmon-Jones, 2008; Harmon-Jones & Gable, 2009). Along similar lines, it can be argued that some images may induce not only stronger but categorically different, affective, and motivational tendencies (e.g., erotic images and positive approach states; Schöne et al., 2016). Also, the fact that in previous studies different images were grouped together (e.g., those assumed to evoke negative withdrawal states) may explain the null results obtained. Because stimuli of evolutionary relevance evoke stronger affective and motivational states than non-evolutionary stimuli (Schupp, Flaisch, Stockburger, & Junghöfer, 2006), it may well be that FAA is more strongly related to the former than to the latter. However, to our knowledge, no study to date has explored stimulus-evoked FAA

specifically in response to evolutionarily threatening stimuli (e.g., snakes), as compared to non-threatening stimuli.

1.2.2 | Late positive potential asymmetry

The late positive potential (LPP) is a broad positive deflection that becomes visible around 400 ms from stimulus onset and can be sustained for several seconds. It shifts spatially over time, with the early portion of the LPP (400–1,000 ms) being centered over the centro-parietal cortex and the later portion of the LPP (>1,000 ms) being more frontally distributed (Foti, Hajcak, & Dien, 2009; Hajcak, Weinberg, MacNamara, & Foti, 2012; MacNamara, Foti, & Hajcak, 2009).

The centro-parietal LPP component (cp-LPP), usually measured over the midline regions, is enhanced in response to affective (e.g., Hajcak & Olvet, 2008; Schupp et al., 2006) and arousing (e.g., Ito, Cacioppo, & Lang, 1998; Schupp, Cuthbert, et al., 2004), as compared to neutral, stimuli. Importantly, the cp-LPP is enhanced in response to certain evolutionarily relevant stimuli, such as erotic images or mutilations (Briggs & Martin, 2009; Schupp, Junghöfer, Weike, & Hamm, 2004a; Weinberg & Hajcak, 2010). Moreover, Van Strien, Eijlers, et al. (2014), as well as Langeslag and Van Strien (2018), showed that the images of both snakes and spiders elicited a larger cp-LPP than the images of birds.

Whereas there is considerable evidence that the cp-LPP is related to the processing of affective stimuli, only a few studies have investigated the involvement of frontal LPP (f-LPP), and specifically hemispheric lateralization of frontal late positive potentials (f-LPP asymmetry), in affective and motivational processes. In an experiment in which words describing “good” and “bad” concepts were shown, it was found that positively valenced words elicited a greater left f-LPP, whereas negatively valenced words evoked a greater right f-LPP (Cunningham, Espinet, DeYoung, & Zelazo, 2005). In the study of Van de Laar, Licht, Franken, and Hendriks (2004), photographs depicting drugs evoked greater f-LPPs over the left hemisphere in recovering drug addicts, as compared to a control group. Furthermore, Graham and Cabeza (2001) found that happy faces evoked greater f-LPPs over the left than the right hemisphere.

The sustained nature of the LPP and the different spatial distribution of the early and late portions of the LPP have been taken to suggest that cp-LPP and f-LPP reflect distinct, albeit overlapping, components (Hajcak et al., 2012). Therefore, the modulation of cp-LPP and f-LPP asymmetry may have different neural substrates. While cp-LPP has been linked to the activity of the visual cortex and the amygdala (Sabatinelli, Keil, Frank, & Lang, 2013), f-LPP asymmetry may originate from the activity of the prefrontal cortex (Moratti, Saugar, & Strange, 2011). Therefore, these ERP components may reflect different cognitive

processes: cp-LPP lower level (e.g., attention allocation to motivationally salient stimuli), but f-LPP asymmetry more elaborate higher level processes (e.g., appraisal of stimuli) (Foti et al., 2009; MacNamara et al., 2009). Moreover, there is evidence that cp-LPP and f-LPP are differentially modulated by affect regulation (e.g., Bernat, Cadwallader, Seo, Vizueta, & Patrick, 2011; Moser, Hartwig, Moran, Jendrusina, & Kross, 2014; Shafir, Schwartz, Blechert, & Sheppes, 2015). The findings that more effortful regulation strategies preferentially engage f-LPP (e.g., Moser et al., 2014; Shafir et al., 2015) further suggest the involvement of f-LPP in higher level processes.

In sum, both FAA and f-LPP asymmetry have been related to affective–motivational processes and affect regulation (Bernat et al., 2011; Moser et al., 2014; Reznik & Allen, 2018; Shafir et al., 2015). As such, both indices may reflect similar (higher order) processes involved in affective reactivity (see, e.g., Hajcak, MacNamara, & Olvet, 2010). To our knowledge, only one study has investigated both the FAA and f-LPP asymmetry in the framework of the same experiment. Poole and Gable (2014) found that affective images evoked f-LPP asymmetry (within the time window 400–1,000 ms) but not FAA. However, whereas approach-related (both positively and negatively valenced) stimuli evoked greater f-LPPs in the left-frontal (as compared to right-frontal) hemisphere, withdrawal-related negative stimuli did not evoke any hemispheric differences in f-LPPs. Null results regarding f-LPP asymmetry and stimulus-evoked FAA for withdrawal-related negative stimuli may have resulted from the stimuli having low (or not enough) evolutionary significance.

1.3 | The present study

The present study aimed to investigate whether evolutionarily threatening stimuli modulate asymmetrical brain activity over the frontal cortex, as indexed by f-LPP asymmetry and FAA. To this end, we first dissociated early activity over the visual cortex associated with an evolutionary threat (as indexed by the EPN) from slower ERP components related to affective and motivational processes (as indexed by cp-LPP and f-LPP asymmetry). For this, we needed to replicate the EPN modulation of evolutionarily threatening stimuli with longer stimulus presentation durations, as compared to the rapid serial visual presentation (RSVP) used in previous investigations (see, e.g., Grassini et al., 2016; Van Strien, Eijlers, et al., 2014). Longer stimulus duration was necessary for studying the later occurring cp-LPP and f-LPP asymmetry.

In the present study, we used images of four different animal types: snakes, spiders, birds, and butterflies (similarly to Grassini et al., 2016). To understand the

neurophysiological dynamics specific to stimuli of evolutionary relevance, we used images of snakes (evolutionarily threatening) and images of spiders (purportedly evolutionarily threatening). Additionally, we used images of birds and butterflies (non-threatening) as control stimuli for the threatening stimuli (snakes and spiders).

2 | METHOD

2.1 | Participants

Participants were 34 university students (28 women) with normal or corrected-to-normal vision. All participants self-assessed to be right-handed. Participants' age ranged from 19 to 32 years (mean = 23.97; *SD* = 3.43). All the participants received credits for an introductory psychology course as compensation. The study was conducted with the understanding and written consent of each participant and in accordance with the Declaration of Helsinki. The study was approved by the Ethics Committee of the University of Turku.

2.2 | Stimuli

Visual stimuli were presented using E-prime 2.0 software on a 19-in. CRT monitor with a resolution of 1,024 × 768 pixels and 85-Hz screen refresh rate (1 refresh ≈ 12 ms). The stimuli included images of snakes, spiders, birds, and butterflies (examples of the stimuli are shown in Figure 1). The size of the images was 600 × 450 pixels, 9.8 × 7.4 degrees when viewed from the participants' eyes (1.5 m). Thirty images per stimulus category were selected from free-to-use stock images on the Internet. The same images were used in a previous study (Grassini et al., 2016), in which a different experimental paradigm was employed. As in earlier studies (Grassini et al., 2016, 2018), the luminance histogram of the images was equalized using Matlab (The MathWorks, Natick, MA) and the SHINE toolbox (Willenbockel et al., 2010). After luminance equalization, 20 images per category were selected, excluding those spoiled after the algorithmic equalization procedure.

2.3 | Procedure

Participants were asked to attend to a continuous presentation stream of a total of 320 trials, divided into two blocks of 160 trials each. The pictures were presented in a random order in both blocks. Each picture was presented four times to each participant (2 times per experimental block). During each trial, a picture from one of the four stimulus categories

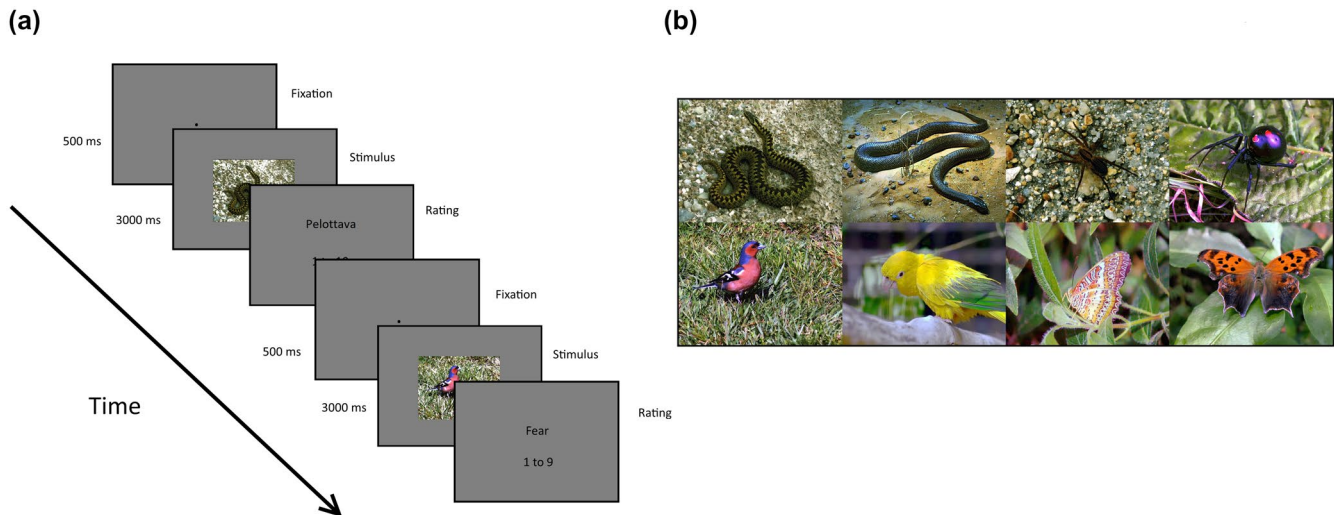


FIGURE 1 Panel (a) shows a section of the experimental procedure. After a 500-ms fixation point, an image from one of the four stimulus categories (snakes, spiders, birds, butterflies) was shown in the center of the screen on a gray background for 3,000 ms. Next, the word “pelottava” (frightening) was shown in the center of the screen, and the participants were instructed to rate their fear of the stimulus from 1 to 9. Panel (b) shows examples of the four stimulus categories. From top left to bottom right: snakes, spiders, birds, and butterflies

was shown: snake (threatening, evolutionary), spider (threatening, purportedly evolutionary), bird (non-threatening, control), and butterfly (non-threatening, control).

Each picture was preceded by a 500-ms fixation point and remained on the screen for 3 s. After each picture, a question was shown in the center of the screen, and the participants were instructed to report how frightening the stimulus picture was (the text was presented in Finnish, using the word “pelottava”) on a scale from 1 to 9 (1: not at all, 9: very much, see Figure 1).

2.4 | EEG recording and pre-processing

EEG was recorded with Ag/AgCl sintered ring electrodes connected to an EEG cap (EASYCAP GmbH, Germany) using the international 10/20 system placement: Fp1, Fp2, F3, F4, F7, F8, Fz, P3, P4, Pz, C3, C4, Cz, T3, T4, T5, T6, O1, O2. The reference electrode was located on the nose tip, and the ground electrode was positioned in front of Fz. Eye movements and blinks were recorded using an electrode below the left eye and an electrode 1.5 cm from the corner of the left eye. EEG was amplified (SynAmps) using a band pass of 0.05–100 Hz, with a sampling rate of 500 Hz. All the electrode impedances were kept below 5 k Ω . The EEG data were then pre-processed offline using Matlab (The MathWorks, Natick, MA) and the EEGLAB toolbox version 14.1.1 (Delorme & Makeig, 2004). The reference was not modified offline: all the analyses (except for the cp-LPP analyses, see Section 2.5 below) used a nose-tip reference scheme. Offline, a high-pass Hamming windowed-sinc FIR filter was

applied at 0.1 Hz (EEGLAB function *pop_eegfiltnew.m*). For the ERP analysis, data were epoched (200 from stimulus onset until 3,000 ms after stimulus onset) and baseline corrected from –200 to 0 ms before the onset of the stimulus. Eye movements were corrected using the Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983). Finally, data epochs containing artifacts were rejected (EEGLAB function *pop_rejkm.m*). ERPs were obtained by averaging the waveforms separately for each of the four stimulus categories. Scalp map topographies were computed using Brain Vision Analyzer 2.2 (Brain Products GmbH, Gilching, Germany).

2.5 | Data analysis and statistics

Statistics were computed using IBM SPSS v. 24 and Matlab (R2014b).

We tested the differences in fear ratings between the four categories of stimuli using a repeated measures ANOVA with stimulus category as a factor (4: snakes, spiders, birds, butterflies).

For the ERP analysis, we first validated our data considering prior published results (e.g., Grassini et al., 2016, 2018, 2019; Van Strien et al., 2017; Van Strien, Eijlers, et al., 2014) that investigated differences in EEG activation in response to threatening stimuli (snakes, spiders) and control stimuli (birds, butterflies). This was necessary as our experimental paradigm was different from previous studies that have typically presented visual stimuli for only a few milliseconds in an RSVP (e.g., Van Strien, Eijlers, et al., 2014). Therefore, we analyzed EEG activation over the occipital cortex, expecting

the snake pictures to selectively enhance the EPN component (225–300 ms from stimulus onset). A repeated measures ANOVA was conducted on the average activation over the occipital electrodes (O1 and O2) with the stimulus category as a factor (4: snakes, spiders, birds, butterflies).

For the assessment of f-LPP asymmetry, following Poole and Gable (2014), we averaged the ERP waveforms of electrodes F4, F8 (right hemisphere, Figure 3a), and F3 and F7 (left hemisphere, Figure 3b) for each of the stimulus categories. Then, we subtracted the obtained left-frontal activity from the right-frontal activity (right-left; Figure 3c). Based on the visual inspection of the obtained waveforms, we individuated two different hemispheric asymmetry trends for all the four stimulus categories: (a) the first negative trend (left hemisphere producing larger LPP activity compared with the right), starting from around 400 ms and lasting until 1,000 ms from stimulus onset—early frontal LPP asymmetry (ef-LPP asymmetry); (b) a second positive trend, starting roughly at 1,200 ms and lasting until 2,500 ms from stimulus onset—late frontal LPP asymmetry (lf-LPP asymmetry). The ef-LPP asymmetry corresponds to that analyzed in previous studies (Hajcak, Dunning, & Foti, 2007; Poole & Gable, 2014). To provide further support for our selected time windows, we used a mass-univariate approach to individuate the time windows in which the stimulus categories showed the most pronounced relative asymmetry. We computed ANOVAs, comparing the amplitude scores for each time point (1,600) for the whole f-LPP asymmetry waveform. The results of the analysis (data points showing $ps < .05$ in the ANOVAs are highlighted in blue in Figure 3c) confirmed the presence of at least two distinct sub-components within the LPP time window, approximately corresponding to the ones we previously individuated using visual inspection. Therefore, two different f-LPP asymmetry indices were analyzed: the mean EEG activity within the time windows of 400–1,000 ms (ef-LPP asymmetry) and 1,200–2,500 ms (lf-LPP asymmetry).

To explore whether the observed differences between stimulus categories in f-LPP asymmetry were specific to frontal, but not to posterior, cortical areas, parieto-temporal LPP asymmetry was calculated for the same time windows as for ef-LPP asymmetry and lf-LPP asymmetry. In this case, the time windows were labeled as early and late parieto-temporal LPP (ept-LPP and lpt-LPP, respectively). The electrodes (P3 and T5 for the left hemisphere, and P4 and T6 for the right hemisphere) were selected post hoc since they showed a peak of potentially asymmetrical activities according to the scalp topographic maps. ERP waves were obtained by subtracting the left-hemisphere parieto-temporal activity (average of P3, T5) from that of the right hemisphere (average of P4, T6).

To enable better comparison with previous studies (e.g., Poole & Gable, 2014), we analyzed the cp-LPP. For this, ERPs were re-referenced offline to the average of all electrodes. Because

we used a low-density EEG (19 electrodes on the scalp), average referencing is not always recommended because it may cause significant distortion of the data (see, e.g., Hajcak et al., 2007). However, preliminary analyses using both nose-tip and average referencing schemes for the cp-LPP showed that analyses using the average reference scheme yielded results more in line with those published in the literature. The cp-LPP was obtained by clustering together the ERPs obtained for Cz and Pz electrodes for each stimulus category (see, e.g., Olofsson et al., 2008; Poole & Gable, 2014). As with the frontal and posterior LPP asymmetries, the cp-LPP was divided into two sub-components: an early (ecp-LPP, 400–1,000 ms) and a late component (lcp-LPP, 1,200–2,500 ms).

We then analyzed FAA (8–13 Hz) by calculating the power spectra density (EEGLAB function *newtimef()*), using Fast Fourier Transformation, Hanning window tapering, and a sliding-windows length of 500 data-points [1 s] with 50% overlap) event-related oscillations (EROs), using the same electrodes as for the f-LPP asymmetry analyses (F3 and F7 for the left hemisphere, and F4 and F8 for the right hemisphere). To have a long-enough (around 200 ms) baseline for baseline correction (*newtimef()* analyzes the data using a sliding windows method, starting from the time-series data center, therefore, data edges that cannot be estimated were removed), the waveforms for this analysis were epoched from –500 to 3,000 ms relative to the stimulus onset. FAA scores were obtained by averaging the power spectra density estimated from the stimulus onset until the end of the epoch and subtracting the resulting left hemisphere power from that of the right hemisphere. This procedure was repeated for each of the four stimulus categories.

For all the asymmetry indices (i.e., ef-LPP asymmetry, lf-LPP asymmetry, ept-LPP asymmetry, lpt-LPP asymmetry, FAA) one-sample *t* tests were performed to compare the scores for each stimulus category against “0” (0 = no hemispheric asymmetry). Regarding the asymmetry and cp-LPP (i.e., ecp-LPP, lcp-LPP) indices, differences between stimulus categories were tested using repeated measures ANOVAs with stimulus category (4) as a factor.

When the sphericity assumption was violated in ANOVAs, the Greenhouse–Geisser correction was applied for *p*-values. Post hoc multiple comparisons were Bonferroni corrected.

Finally, to study the possible association between the subjective fear ratings and the EEG data, we computed correlation analyses (Pearson's *r*) between the fear ratings and the ef-LPP asymmetry, lf-LPP asymmetry, cp-LPP, and FAA for each stimulus category. Additionally, to control for false positives due to outliers, we computed robust correlation analyses using the Robust Correlation Matlab toolbox (function *skipped_correlation.m* as described in Pernet, Wilcox, & Rousselet, 2013) for those correlations that were statistically significant. The skipped correlation function computed

robust correlations using Pearson correlation on the data after bivariate outliers were removed. Such analysis is based on the data distribution central point (mid-covariance determinant) and on the orthogonal distances of every data point from the center of the data distribution. Data points located outside the orthogonal limits (calculated using the *idealf* estimator of the interquartile range; see Pernet et al., 2013; Wilcox & Keselman, 2012) were removed and Pearson's r calculated. The significance level was estimated based on CIs (95% confidence interval computed by bootstrapping the data without outliers).

In all the analyses, the significance level of $p < .05$ and two-tailed tests were used.

3 | RESULTS

3.1 | Fear ratings

Fear ratings (1–9) of the images were separately averaged for each image category (snakes, spiders, birds, butterflies). Average fear scores were 4.96 ($SD = 1.74$) for snakes, 5.83 ($SD = 1.81$) for spiders, 1.52 ($SD = 0.71$) for birds, and 1.31 ($SD = 0.45$) for butterflies. A repeated measures ANOVA revealed a significant difference in fear ratings between the four stimulus categories, $F(3,99) = 160.85$, $p < .001$, $\eta_p^2 = 0.83$. Post hoc t tests showed that spiders were rated as the most frightening ($p < .019$ vs. snakes, and $ps < .001$ vs. birds and butterflies), followed by snakes ($ps < .001$ vs. birds and butterflies), while the ratings of birds and butterflies did not differ ($p = .257$).

3.2 | Data validation (EPN)

EEG epochs corresponding to the four stimulus categories (snakes, spiders, birds, and butterflies) were compared. The mean ERP amplitudes for each category were calculated in the 225–300-ms time window for each participant ($N = 34$), and for the electrodes O1 and O2. The activities registered in O1 and O2 were averaged to form the occipital cluster.

A repeated measures ANOVA revealed a significant effect of stimulus category, $F(3,99) = 34.19$, $p < .001$, $\eta_p^2 = 0.51$.

Post hoc t tests showed that snakes elicited the most prominent EPN ($p = .047$ vs. spiders, and $ps < .001$ vs. birds and butterflies), followed by spiders ($ps < .001$ vs. birds and butterflies), whereas the EPN elicited by butterflies and birds did not differ ($p = .12$) (see Figure 2). Thus, as expected, snake images evoked an enhanced EPN compared with the other threatening (spiders) and non-threatening stimuli (birds and butterflies). See Figure S1 for EPN values separately for each participant.

3.3 | f-LPP asymmetries

To investigate hemispheric asymmetry, ef-LPP asymmetry (400–1,000 ms) and lf-LPP asymmetry (1,200–2,500 ms) for each stimulus category (see Figure 3c) were compared against 0 (i.e., no difference in activation between the hemispheres). For ef-LPP asymmetry, one-sample t tests revealed

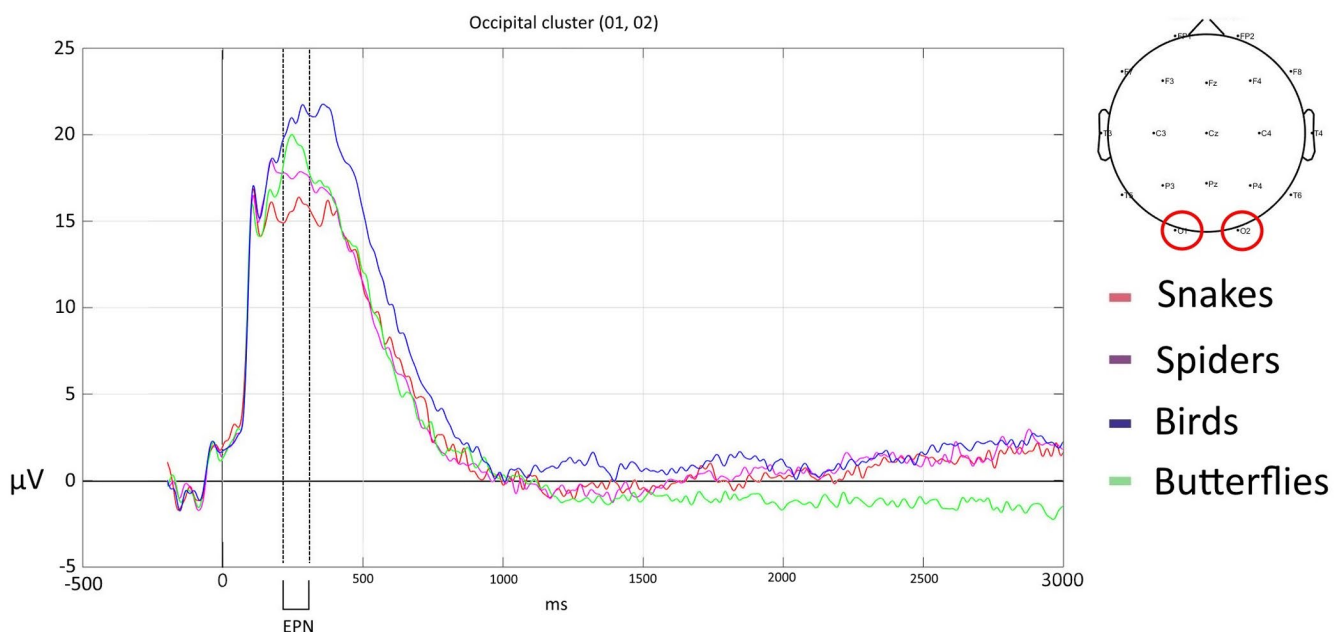


FIGURE 2 Waveforms obtained for each stimulus category for the occipital cluster (average activity in electrodes O1 and O2). Early Posterior Negativity (EPN) time window (225–300 ms) is shown with vertical dotted lines. The red line represents the activity for snake images, the violet line for spiders, the blue line for birds, and the green line for butterflies. The y-axis shows amplitude (microvolts), while the x-axis shows time (milliseconds)

an asymmetry for birds ($p = .013$) but not for butterflies ($p = .076$), snakes ($p = .93$), or spiders ($p = .625$). Specifically, birds evoked a greater relative activation in the left-frontal hemisphere. For lf-LPP asymmetry, one-sample t tests

revealed an asymmetry for snakes and spiders ($ps < .001$), and birds ($p = .014$) but not for butterflies ($p = .189$). Snakes, spiders, and birds evoked greater relative activity in the right-frontal hemisphere.

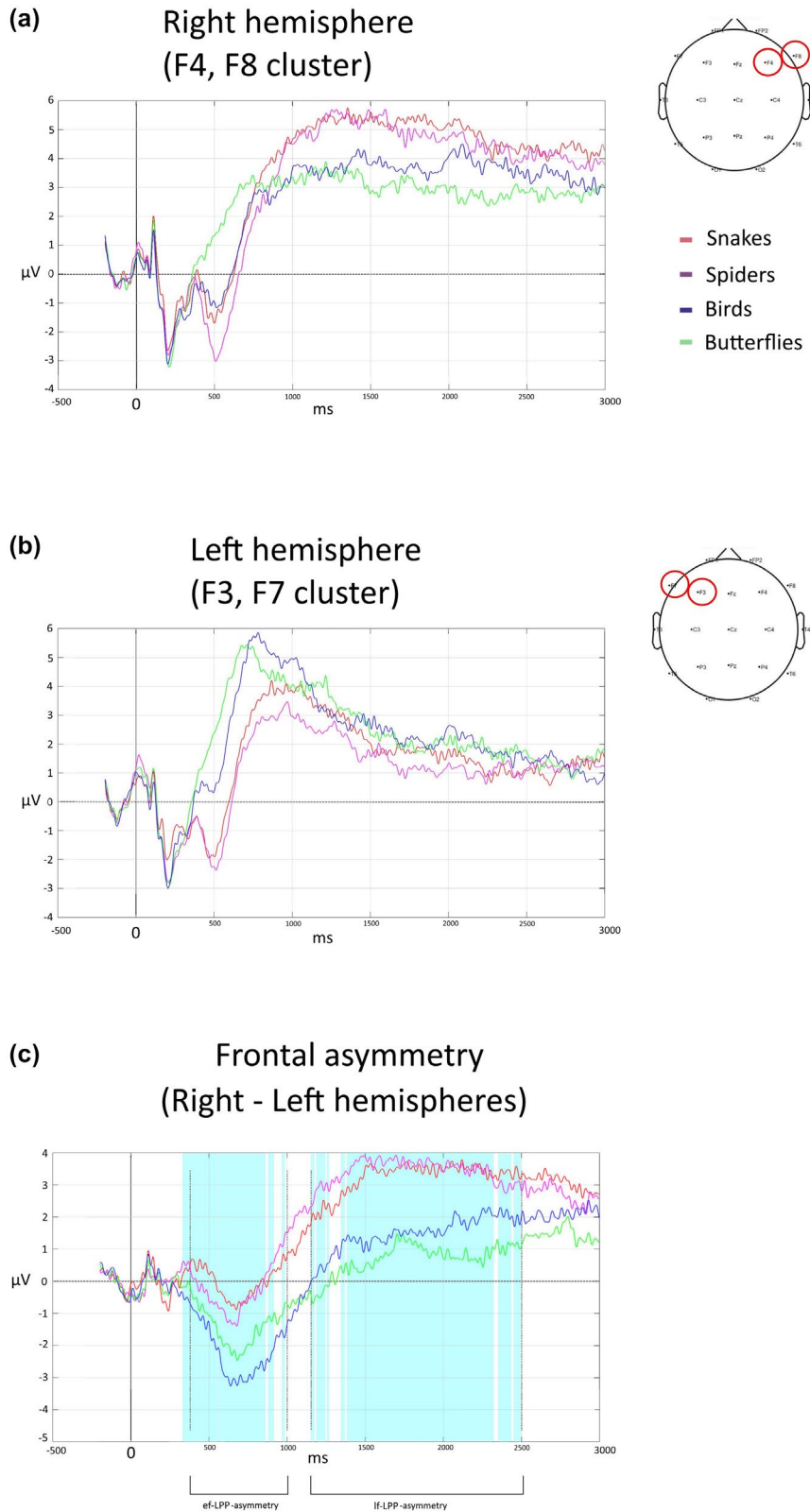


FIGURE 3 Panel (a) shows the waveforms obtained from the average of the activity in electrodes F4 and F8 (right hemisphere). Panel (b) shows those obtained from the average of the activity in F3 and F7 (left hemisphere). Panel (c) shows the difference between the right and the left frontal activity. Red lines represent the activity for snake images, violet lines for spiders, blue lines for birds, and green lines for butterflies. The y-axis shows amplitude (microvolts), while the x-axis shows time (milliseconds). Blue shade in panel (c) represents the area where the ANOVA with stimulus category (4) as factor showed statistically significant differences between the categories ($ps < .05$). Panel (c) displays the time windows corresponding to ef-LPP asymmetry and lf-LPP asymmetry

To investigate differences in hemispheric asymmetry between the stimulus categories, ef-LPP asymmetry and lf-LPP asymmetry indices for each stimulus category were compared against each other using repeated measures ANOVAs. For ef-LPP asymmetry, ANOVA revealed a significant effect of stimulus category, $F(3,99) = 5.65$, $p = .001$, $\eta_p^2 = 0.15$. Following t tests showed that birds induced the most asymmetric activity (more activity in the left, as compared with the right, hemisphere; see Figure 3c) and differed from the two threatening stimulus categories (i.e., snakes and spiders; $ps < .040$) but not from butterflies ($p = 1$). Butterflies induced the second most asymmetric activity but did not differ from any of the other categories ($ps > .122$). Activity induced by spiders did not differ from that of snakes and butterflies ($ps > .608$), but it did differ from birds ($p = .040$). Snakes induced the least asymmetric activity in ef-LPP, and differed from birds ($p = .005$) but not from the other two categories ($ps > .122$).

For lf-LPP asymmetry, ANOVA revealed a main effect of stimulus category $F(3,99) = 9.35$, $p < .001$, $\eta_p^2 = 0.22$. Following t tests revealed that snakes induced the most asymmetric activity (more activity in the right, as compared with the left, hemisphere; see Figure 3c) and differed from the two non-threatening animal categories (i.e., birds and butterflies; $ps < .04$) but not from spiders ($p = 1$). Spiders induced the second most enhanced asymmetry, and similarly to snakes, differed from the two non-threatening categories ($ps < .021$). Birds and butterflies induced the least asymmetrical activity and did not differ from each other ($p = .497$). See Figure S2 for ef-LPP-asymmetry and lf-LPP-asymmetry values separately for each participant.

The topographic maps of ef-LPP and lf-LPP are presented in Figure 4.

3.4 | LPP asymmetry over the posterior cortical regions

First, ept-LPP asymmetry (400–1,000 ms) and lpt-LPP asymmetry (1,200–2,500 ms) for each stimulus category were compared against “0.” For ept-LPP asymmetry, one-sample t tests revealed an asymmetry for butterflies ($p = .046$) but not for birds ($p = .836$), snakes ($p = .254$), or spiders ($p = .877$). Butterflies evoked a greater relative activation over the right parieto-temporal hemisphere. For lpt-LPP asymmetry, one-sample t tests revealed an asymmetry for birds and butterflies ($ps < .046$) but not for snakes and spiders ($ps > .254$). Birds and butterflies evoked greater relative activity over the left parieto-temporal brain area.

The posterior LPP asymmetries (see Figure 5) evoked by different stimulus categories were compared to each other using repeated measures ANOVAs. For ept-LPP asymmetry, the analyses showed a statistically significant main effect $F(3,99) = 5.59$, $p = .001$, $\eta_p^2 = 0.15$. The following t tests showed that the most pronounced asymmetry (right hemisphere more active than the left) was evoked by butterflies, which differed from spiders ($p = .05$), and birds ($p = .025$) but not from snakes ($p = .664$). The second most pronounced asymmetrical activity was evoked by snakes, but it did not differ from any of the other stimulus categories ($ps > .187$). The third largest asymmetry was the one elicited by the bird stimuli, differing only from butterflies ($p = .025$) but not from the other stimuli ($ps > .553$). The least pronounced asymmetry was evoked by spiders, that differed only from butterflies ($p = .005$) but not from the other animal categories ($ps > .187$).

For lpt-LPP asymmetry, comparison of stimulus categories showed a statistically significant main effect $F(3,99) =$

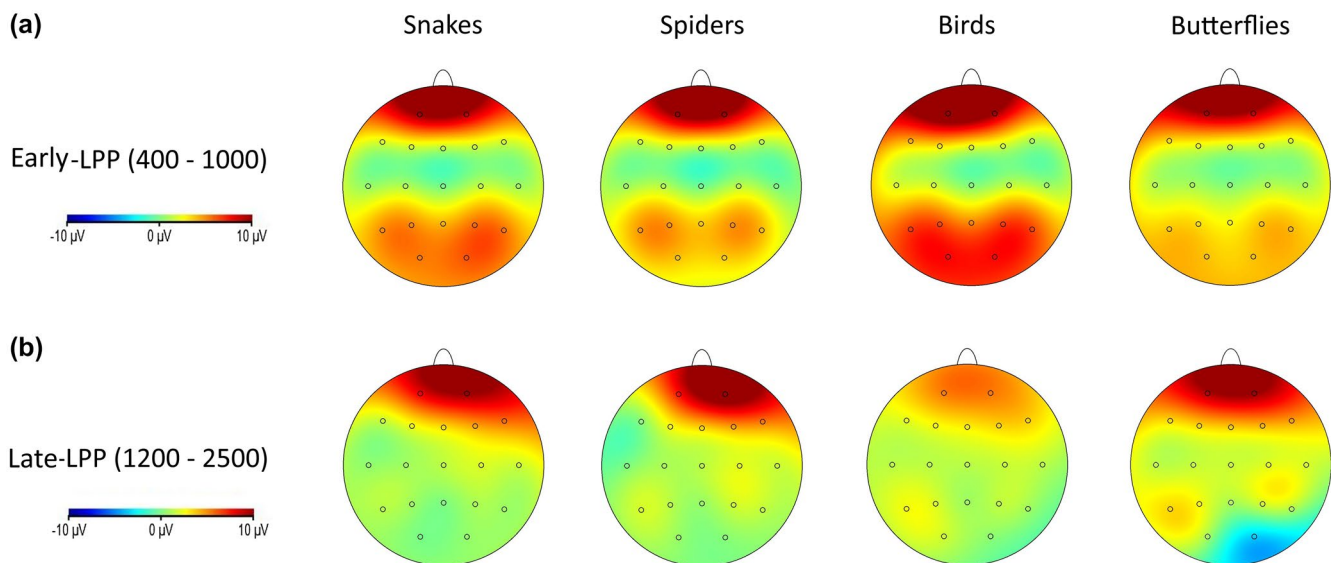


FIGURE 4 Panel (a) shows the scalp topography of brain activity for the stimulus categories in the ef-LPP time window (400 to 1,000 ms). Panel (b) shows the scalp topography of brain activity for the stimulus categories in the lf-LPP time window (1,200–2,500 ms)

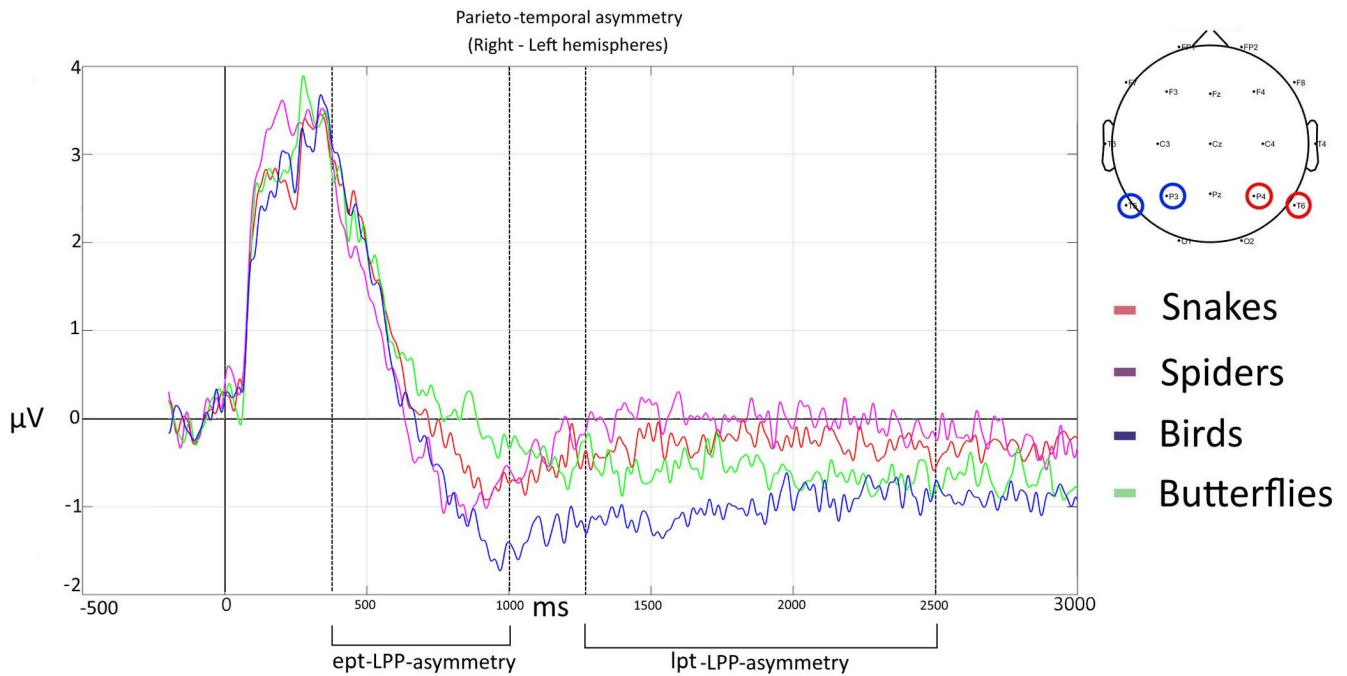


FIGURE 5 The figure shows the difference between the right and the left parieto-temporal activity, calculated using the channels P3 and T5 for the left hemisphere and P4 and T6 for the right hemisphere (P4/T6–P3/T5). The red line represents the activity for snake images, the violet line for spiders, blue line for birds, and green line for butterflies. The y-axis shows amplitude (microvolts), while the x-axis shows time (milliseconds)

8.32, $p = .001$, $\eta_p^2 = 0.20$. The following t tests showed that

birds induced the most asymmetric activity (more activity in the left compared to the right hemisphere), differing from snakes ($p = .003$), and spiders ($p = .001$) but not from butterflies ($p = .506$). Butterflies produced the second most asymmetric activity, differing only from spiders ($p = .023$) but not from the other categories ($ps > .506$). Snakes produced the third most asymmetric activity, differing from birds ($p = .003$) but not from the other animal categories ($ps = 1$). The least pronounced asymmetry was produced by spiders, that differed from birds ($p = .001$) and butterflies ($p = .023$) but not from snakes ($p = 1$). See Figure S3 for ept-LPP asymmetry and lpt-LPP-asymmetry values separately for each participant.

3.5 | cp-LPP

To explore the effect of the stimuli on non-asymmetric brain activity and to compare our results with previous investigations, early and late cp-LPPs (see Figure 6) were analyzed. A repeated measures ANOVA for ecp-LPP revealed a main effect of stimulus category $F(3,99) = 6.82$, $p < .001$, $\eta_p^2 = 0.17$. The following t tests revealed that spi-

ders elicited the highest positivity in LPP and differed from butterflies ($p = .003$) but not from birds and snakes ($ps > .171$). Snakes elicited the second highest positivity,

differing from butterflies ($p = .001$) but not from birds and spiders ($ps > .432$). The ecp-LPP evoked by birds did not differ from the cp-LPP evoked by any of the other animal categories ($ps > .171$). Butterflies evoked the least positive ecp-LPP, differing from snakes ($p = .001$) and spiders ($p = .003$) but not from birds ($p = .765$). Thus, images of threatening animals evoked a larger ecp-LPP than images of non-threatening animals.

For lcp-LPP, a repeated measures ANOVA showed a significant main effect of stimulus category $F(3,99) = 4.64$, $p = .004$, $\eta_p^2 = 0.12$. The following t tests showed that butterflies elicited

a more positive lcp-LPP, compared to spiders ($p = .029$) but did not differ from the other stimuli ($ps > .79$). All the other stimuli did not differ from each other ($ps > .236$). See Figure S4 for ecp-LPP and lcp-LPP values separately for each participant.

3.6 | Frontal alpha asymmetry

Mean stimulus-evoked (log) alpha power (measured in db of difference from baseline) asymmetry for each of the image category were -0.065 ($SD = 1.751$) for snakes, -0.301 ($SD = 0.672$) for spiders, 0.095 ($SD = 0.737$) for birds, and -0.234 ($SD = 0.811$) for butterflies. One-sample t tests against “0” showed that no image category evoked an FAA ($ps < .130$). A repeated measures ANOVA comparing the FAA between the four image categories did not result in any significant main effects ($p = .520$). Thus, the images did not elicit a clear

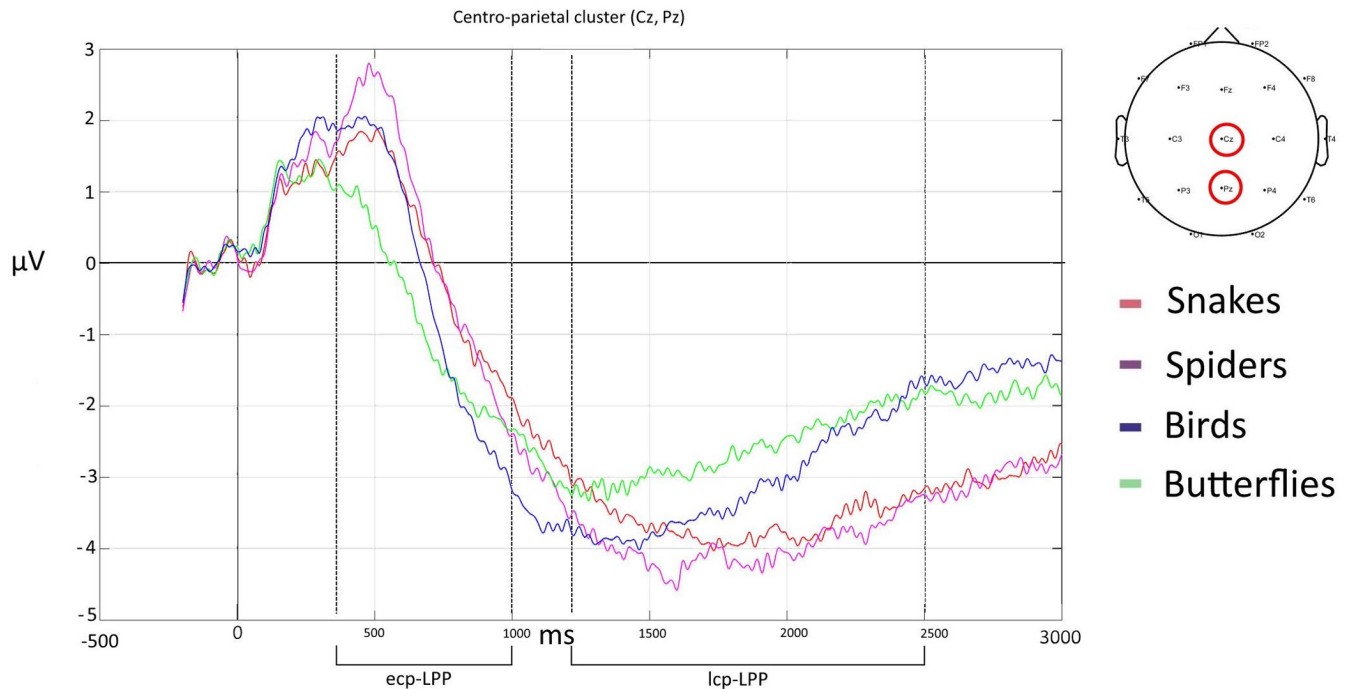


FIGURE 6 The figure shows the waveforms obtained from the average of the activity in electrodes Cz and Pz. The red line represents the activity for snake images, the violet line for spiders, blue line for birds, and the green line for butterflies. The y-axis shows amplitude (microvolts), while the x-axis shows time (milliseconds)

different asymmetric brain activity in frontal alpha waves. See Figure S5 for FAA values separately for each participant.

3.7 | Correlation analyses

Correlation analyses between the EPN amplitude and subjective fear ratings did not yield significant results for any of the stimulus categories ($ps > .294$).

Similarly, the subjective ratings of fear did not correlate with the ef-LPP asymmetry ($ps > .083$) or FAA ($ps > .079$).

Correlation analyses between the lf-LPP asymmetry and fear ratings showed a positive association between the lf-LPP asymmetry of snakes and snake-related fear ($r = .355$, $p = .039$) and between the lf-LPP asymmetry of spiders and spider-related fear ($r = .492$, $p = .003$). No associations were found for the non-threatening stimulus categories and the respective fear ratings ($ps > .834$). Analyses using the Robust Correlations method confirmed these significant associations (see Figure 7: for snakes $r = .393$, 95% CI = [.092 0.639], and for spiders $r = .420$, 95% CI = [.084 0.705]).

For the parieto-temporal area, no associations between the subjective ratings of fear and the ept-LPP asymmetry ($ps > .189$) or the lpt-LPP asymmetry ($ps > .280$) were found.

Subjective fear ratings of the different stimulus categories did not correlate with ecp-LPP ($ps > .619$). The lcp-LPP was negatively correlated with the subjective ratings of fear for butterflies only ($r = -.443$, $p = .009$), while for all the other categories no

associations were found ($ps > .196$). However, subsequent analyses using Robust Correlations showed that the association between the lcp-LPP of butterflies and butterfly-related fear was due to the presence of an outlier, and after the correction, no association was found ($r = -.18$, 95% CI = [-0.593 0.165]).

4 | DISCUSSION

In the present study, we investigated whether evolutionarily threatening stimuli modulate late indices of brain activation related to affective and motivational processing. Specifically, we focused on asymmetrical activity over the frontal cortical regions—f-LPP asymmetry and FAA—that is associated with approach/avoidance motivation and the affective valence of stimuli.

Our experimental paradigm differed from earlier studies exploring brain activity in response to evolutionarily threatening stimuli. Therefore, we first validated our data by investigating fast brain activation in response to snake stimuli (see, e.g., Grassini et al., 2018; Van Strien, Eijlers, et al., 2014). The results were in line with previous findings in showing that the threatening stimuli (i.e., snakes and spiders) selectively elicited the EPN, with snakes eliciting the largest EPN.

Behavioral data showed that spiders were rated as the most frightening, followed by snakes, and the other stimulus categories (i.e., birds and butterflies). These behavioral results corroborate previous studies in which spiders have

Snakes: subjective fear ratings and lf-LPP-asymmetry

Spiders: subjective fear ratings and lf-LPP-asymmetry

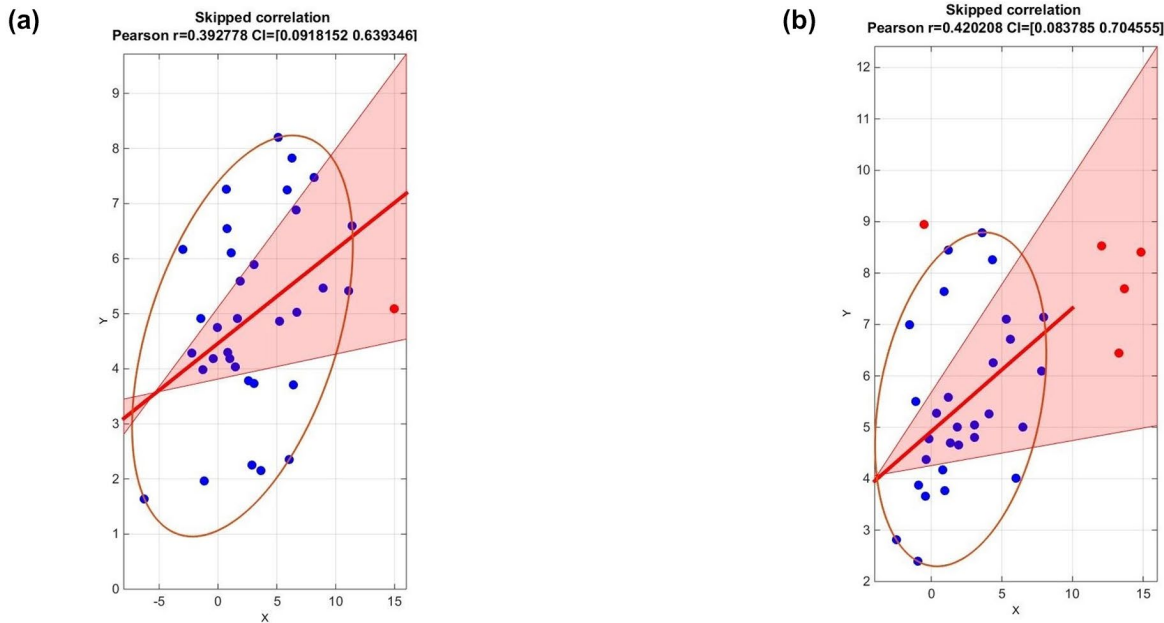


FIGURE 7 Panel (a) shows robust (skipped) correlation between the fear ratings of snakes and snake-induced lf-LPP asymmetry, while panel (b) shows the robust (skipped) correlation between the fear ratings of spiders and spider-evoked lf-LPP asymmetry. Pearson's r coefficients, as well as 95% CIs obtained by bootstrapping, are shown on top of the panels. The y-axis shows the average fear rating, while the x-axis shows the average lf-LPP asymmetry score. In the figures, the red line represents the regression line, whereas the orange circle represents the accepted distances (outlier evaluation) from the orthogonal center of the data. Red dots represent data points considered outliers and eliminated before the correlation analysis, while blue dots represent data points considered non-outliers. The 95% bootstrapped CIs are shown as pink-shaded areas. For detailed information regarding robust correlation analysis, see Pernet et al. (2013)

also been rated as the most frightening or unpleasant, albeit not always significantly more than snakes (see Langeslag & van Strien, 2018; Van Strien et al., 2016; Van Strien, Eijlers, et al., 2014; Van Strien, Franken, et al., 2014; cf. Grassini et al., 2016). One explanation for spiders, rather than snakes, being rated as the most frightening may be that in Northern Europe people are not very likely to encounter snakes in real life and, therefore, their ratings are based not on real-life but imagined encounters (Van Strien, Eijlers, et al., 2014).

The ef-LPP asymmetry (400–1,000 ms) for the non-threatening visual stimuli (birds and butterflies) revealed a tendency for enhanced brain activity in the left-frontal, compared to the right-frontal, hemisphere (however, statistically significant only for birds), while no asymmetry was observed in response to the threatening visual stimuli (snakes and spiders). Moreover, ef-LPP asymmetry was not associated with the subjective ratings of the stimuli. Similarly, Poole and Gable (2014) did not observe ef-LPP asymmetry in response to withdrawal-negative stimuli nor find any correlations between subjective ratings of the stimuli and ef-LPP asymmetry.

The lf-LPP asymmetry (1,200–2,500 ms) showed an inverse trend: the threatening stimuli (snakes and spiders), as well as birds, evoked significantly larger relative activity in the right-frontal (as compared to left-frontal) hemisphere. However, the threatening stimuli (snakes and spiders) evoked

significantly larger relative right-frontal activation than the non-threatening stimuli (birds). Importantly, only the lf-LPP asymmetry for the threatening stimuli (snakes and spiders) was positively correlated with subjective fear ratings. Thus, the more frightening the threatening stimuli, the larger the relative right-sided lf-LPP. This association applied to both snake- and spider-related fear. These findings imply that right-sided lf-LPP may reflect the subjective appraisal of threatening stimuli, irrespective of whether these appraisals are based on real (in case of spiders) or imaginary (in case of snakes) encounters.

To control for the spatial specificity of the observed findings, we conducted post hoc analyses of posterior LPP asymmetry over the parieto-temporal cortices. Results showed that only non-threatening animals evoked both ept-LPP asymmetry (butterflies right-sided asymmetry) and lpt-LPP asymmetry (birds and butterflies left-sided asymmetry). The posterior LPP asymmetries were not associated with subjective fear ratings. Thus, the findings regarding right-sided asymmetry for threatening animals and its association with subjective ratings applied to frontal LPP asymmetry only.

These results show that snakes and spiders are processed similarly. Both modulate the early visual cortical activity (indexed by the EPN)—albeit spiders less strongly than snakes—which is not associated with the subjective ratings

of fear. Brain activity related to evolutionary threat responses should be associated with fast, automatic, and unaware (i.e., not associated with the subjective perception of fear) processes, as it is mediated by the superior-colliculus-amygdala-pulvinar neural network (Morris et al., 1999; Tamietto & de Gelder, 2010). Hence, the EPN reflects a hard-wired response to evolutionarily relevant stimuli. Both snakes and spiders induced relatively large later occurring right-frontal cortical activity (indexed by lf-LPP asymmetry), which was associated with the subjective ratings of fear. Thus, lf-LPP asymmetry may reflect higher order affective processes, specifically the subjective appraisal of threatening stimuli and the subjective experience of fear.

According to our results, specifically the later portion of the f-LPP asymmetry (i.e., lf-LPP asymmetry) is a measure associated with subjective fear. This can be explained by the motivational direction and affective valence of the visual stimuli because snakes and spiders are both related to withdrawal motivation and have a negative valence. As such, these findings are in line with theoretical models according to which greater relative right-sided frontal activity is associated with withdrawal motivation and withdrawal-related affect (Harmon-Jones & Gable, 2018; Reznik & Allen, 2018; Schutter et al., 2008).

To compare our findings with previous studies, we explored cp-LPP. Previous investigations have specifically focused on the ecp-LPP showing that it is modulated by arousing and affective stimuli (e.g., Hajcak & Olvet, 2008; Ito et al., 1998; Schupp, Cuthbert, et al., 2004; Schupp et al., 2006). In line with these findings, our analyses revealed that snakes and spiders evoked the strongest positive deflection. Yet, only butterflies differed significantly from snakes and spiders, with birds provoking a comparable positive ecp-LPP to all the other stimulus categories. Thus, the affective (i.e., threatening) stimuli did indeed evoke a larger ecp-LPP than the non-affective (i.e., non-threatening) stimuli. However, it remains unclear why birds evoked a relatively large ecp-LPP, a finding that stands in contrast to previous studies (Langeslag & van Strien, 2018; Van Strien, Christiaans, Franken, & Huijding, 2016). Arousal ratings were not obtained in the present study but may provide more information regarding this. Perhaps bird images elicited arousal, irrespective of not having elicited fear. Future studies including arousal measures can shed more light on this issue.

As with frontal and posterior LPP analyses, we also explored lcp-LPP. Results showed that only butterflies evoked a more positive lcp-LPP (as compared to spiders), with no other stimulus categories differing from each other. Importantly, neither ecp-LPP nor lcp-LPP was associated with subjective ratings of fear. This provides further support for our findings being specific to frontal regions only.

The analyses regarding the FAA did not yield any significant results. This is in line with previous studies that have failed to find FAA in response to affective pictures (Poole & Gable, 2014; Uusberg et al., 2014). One possible explanation for these null findings is that data sampling for stimulus-evoked FAA may be too short. If the participants were presented with a sequence of images for a longer duration, a longer data sample could be obtained, and then the stimulus-evoked FAA could be calculated from a longer window, reducing data noise in the computation of spectral power density. A second explanation could be that stimulus-evoked FAA may be significantly moderated by individual differences. It has been argued that about 60% of the variance in the FAA is due to trait and 40% due to state factors (Hagemann, Naumann, Thayer, & Bartussek, 2002). Therefore, it may be that the stimulus-evoked FAA can only be observed for people who are, for example, high in anxiety. For example, Gable and Poole (2014) showed that the trait Behavioral Activation System predicted higher left FAA to anger pictures. Future studies should thus include individual difference measures to explore the possible trait effects on stimulus-evoked FAA.

Moreover, whereas the relationship between the FAA and approach-related motivation and affect is well established, the relationship between the FAA and withdrawal-related motivational and affective processes has remained more controversial. Therefore, it has recently been suggested that FAA (especially the right-frontal activity) may reflect more general supervisory control rather than withdrawal-related processes as such. Importantly, this supervisory control system may be activated only when there is a conflict between the approach and avoidance systems (Gable, Mechin, Hicks, & Adams, 2015; Gable, Neal, & Threadgill, 2018). As such, it may well be that lf-LPP asymmetry and FAA reflect different processes, with the former being related to withdrawal-related affective and motivational processes but the latter to regulatory control. This may thus explain the different results obtained with the two frontal asymmetry indices.

It is important to point out some limitations of the present study. Most studies investigating LPP have used linked mastoids as a reference (see the review in Luck & Kappenman, 2011), compared to that used for online (nose) and offline recording (average for cp-LPP components) in this study. This has been shown to be crucial for the magnitude and direction of the LPP (Hajcak et al., 2012). While for f-LPP asymmetry the possible effect of the reference system may remain rather small (LPP asymmetry is a difference calculated from two waveforms recorded in the same subject, and these waveforms should be similarly modulated by a change in the reference system), for cp-LPP the effect of the reference system may be important. The online reference used (nose tip) may also have contributed to non-significant

findings for FAA (see Reznik & Allen, 2018; Smith, Reznik, Stewart, & Allen, 2017).

In studies investigating brain activation induced by affective images, one of the intrinsic confounds is the different arousal levels evoked by these images. Generally, stimuli used to induce affect have also been reported to evoke high levels of arousal (see, e.g., Gable and Harmon Jones 2008a, 2008b, 2009, 2010, 2011; Gable & Poole, 2012). This may be a possible confounding factor in our study, as the images of snakes and spiders may be perceived as more arousing compared to the more neutral images of birds and butterflies. However, past studies have ruled out that asymmetrical frontal brain activity could be directly induced by physiological arousal (Gable & Harmon-Jones, 2013; Poole & Gable, 2014).

As pointed out by Cunningham, Raye, and Johnson (2004), Cunningham et al. (2005), explicit evaluation of valenced stimuli (in the present study participants were asked to provide fear ratings after each stimulus) may involve different brain areas and processes than implicit (or automatic) response to the same stimuli. This possibility should be assessed in future studies utilizing a different experimental design, for example, by asking participants to rate the stimuli only after the EEG recordings.

Future studies should investigate the relationship between the stimulus-evoked f-LPP asymmetry and FAA following the suggestions for data acquisition and data pre-processing put forward by Smith et al. (2017). These authors showed that the detection of the FAA is sensitive to several methodological variables in data acquisition and pre-processing, such as the choice of online and offline reference systems, data artifact cleaning methods, etc. However, some of these methodologies can be reliably applied only to data from high-density EEG equipment and were, therefore, outside the technical possibilities of the present study. Furthermore, future studies should measure variables that may have modulated the results of the present study, such as the subjective ratings of approach avoidance and arousal of the stimuli and investigate the impact of individual differences (e.g., affect-related traits) and state factors (e.g., level of psychological distress). Future studies should aim to use stimuli that induce stronger affective and motivational states, since in the present study even the spider and snake images were rated at (snakes) or just slightly above the midpoint (spiders) of the rating scale.

In conclusion, we showed that the late component of f-LPP asymmetry, but not the early component of f-LPP asymmetry nor FAA, is modulated by the category of visual stimuli and the subjective ratings of fear. First, threatening stimuli (snakes and spiders) evoked a relatively great lf-LPP over the right-frontal hemisphere than non-threatening stimuli (birds and butterflies). Second, this relatively great right-frontal activity of threatening stimuli (snakes and spiders) was positively associated with the subjective ratings of

fear. Third, the subjective ratings of fear were not associated with early brain activity over the occipital (as indexed by the EPN), centro-parietal (as indexed by the cp-LPP), or parieto-temporal (as indexed by the pt-LPP asymmetry) cortices. Taken together, these results suggest that lf-LPP asymmetry may reflect higher order affective processes, specifically the subjective appraisal of threatening stimuli and subjective experience of fear, which are independent from the fast and automatic processing of evolutionarily significant and affectively arousing stimuli. Future studies are needed to replicate these findings and further clarify the association between lf-LPP asymmetry and subjective fear. Nevertheless, lf-LPP asymmetry may prove to be useful as an objective index of experienced fear, for example, in clinical and interventional studies evaluating the efficacy of treatments for phobias.

AUTHORS' CONTRIBUTIONS

S. Grassini conceptualized the study, created the experimental paradigm, tested the participants, ran the analysis, and had the responsibility to write the present manuscript.

P. Sikka gave a highly valuable contribution to the study idea and highly contributed to the writing of the manuscript, extensively commenting on earlier manuscript drafts.

A. Revonsuo provided funding for the present research and had a valuable role in elaborating on the theoretical framework of the study. He extensively commented and corrected the earlier drafts of the present work.

M. Koivisto supervised the present research work, gave his inputs on data analysis and interpretations, as well as giving valuable feedback at all phases of research.

All the authors contributed to the latest version of the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Fig S1

Fig S2

Fig S3

Fig S4

Fig S5

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