Both low and high spatial frequencies drive the early posterior negativity in response to snake stimuli

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A B S T R A C T

Previous event-related potential (ERP) studies have shown that snake pictures elicit greater early posterior negativity (EPN) compared to other animal pictures. The EPN reflects early selective visual processing of emotionally significant stimuli. Evidence for the role that high and low spatial frequencies play in the early detection of snakes is still inconsistent. The current study aims to clarify this by studying the effect of high and low spatial frequencies on the elevated EPN for snakes separately. Using a rapid serial visual presentation paradigm, participants viewed images of snakes, spiders and birds in three different conditions of filtered spatial frequencies: high spatial frequency, low spatial frequency, and full spatial frequency (the original image). P1 and mean EPN activity in a time window of 225–300 ms after stimulus onset were measured at the occipital cluster (O1, O2, Oz). The results show smaller P1 amplitudes and shorter P1 latencies in response to full-spectrum snake pictures compared to full-spectrum spider and bird pictures, and an increased EPN in response to snake pictures compared to spider and bird pictures in all three filtering conditions. The EPN in response to full-spectrum snake pictures was larger than the EPN in response to filtered snake images. No difference in EPN was found between the snake pictures in the high and low spatial frequency conditions. The results suggest that the roles of high and low spatial frequencies in early automatic attention to snakes are equally important.

1. Introduction

Humans exhibit a selective attention bias towards potential danger, a bias believed to be of survival value and being present in everyone (Koster et al., 2004). Since the distant past, snakes have posed a potential threat to human beings. Research has consistently shown that humans detect snakes faster compared to other animals and that snake stimuli trigger rapid attentional capture at an early stage (Isbell, 2006; Van Strien, Franken and Huijding, 2014; Kawai and He, 2016). This rapid attentional capture elicited by snakes, serves as an automatic mechanism to increase the chance of survival and could be culture related (Van Strien et al., 2014a, b). Numerous Event-Related Potential (ERP) studies have found evidence for the early visual attentional capture of snake pictures (He et al., 2014; Grassini et al., 2016; Van Strien, Eijlers, Franken and Huijding, 2014; Van Strien, Franken and Huijding, 2014; Van Strien and Isbell, 2017). This attentional capture is reflected by an elevated Early Posterior Negativity (EPN) in particular. The EPN is an electrophysiological response that occurs mainly at the parietal-occipital cluster, in the 225–330 ms time frame upon stimulus onset (Schupp et al., 2006). The EPN has been argued to be elevated in response to evolutionary-relevant stimuli (Schupp et al., 2003). One paradigm that is frequently employed when measuring the EPN is the Rapid Serial Visual Presentation (RSVP). The RSVP procedure presents randomized stimuli typically at a rate of 3 pictures per second and is thought to be an effective technique to measure attentional processing, since it requires fast processing of emotionally-relevant stimuli while high processing loads occur (Junghofer et al., 2001).

Several ERP RSVP studies have focused on identifying the distinct visual snake characteristics that trigger the elevated EPN amplitudes in

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response to snake stimuli. One of these characteristics is the partial exposure of the snake. Van Strien and Isbell (2017), investigated whether the scales and patterns on the snake skin are a relevant characteristic for the EPN snake effect. They showed participants close-up pictures of snake skin, lizard skin and bird plumage in their first task, and pictures of partially exposed snakes, spiders and birds in their second task. They reported that pictures of close-up snake skin and pictures of partially exposed snakes triggered significantly higher EPN amplitudes compared to all other animal conditions. This outcome supports the SDT and suggests that snakeskin scales and patterns may trigger early attentional capture.

Another characteristic that may modulate the EPN snake effect, is the curvilinear shape of snake bodies. Van Strien et al. (2016) compared the EPN in response to snakes to the EPN in response to animals with (e.g., worms) and without curvilinear body shapes (e.g., beetles). They found that snakes elicited significantly higher EPN amplitudes. Interestingly, worms (i.e., creatures with curvilinear body) triggered a significantly higher EPN compared to beetles. This suggests that the curvilinear body shape might be a relevant feature modulating the snake EPN effect and triggering early attentional capture.

The proximity of the snake appearing in the picture might likewise be a relevant characteristic explaining the early attentional capture of snakes. Beligiannis and van Strien (2020), presented participants with close-up (heads, high proximity) and medium-shot (full body exposure, low proximity) pictures of snakes, spiders and birds and measured the EPN in response to these pictures. In line with previous research, snakes elicited the highest EPN amplitudes across both proximity conditions. Interestingly, they further reported that medium-shot (low proximity) snake pictures elicited a higher EPN component compared to close-up (high proximity) snake pictures, suggesting that proximity could indeed be a modulating factor for the snake EPN effect. Additionally, they conducted a spatial frequency analysis that indicated that medium-shot (low proximity) snake pictures possessed more power in the high spatial frequency bands, suggesting that spatial frequency (SF) may play a role in triggering early attentional capture.

Thus, the SF of local (e.g., snakeskin patterns and scales) and global (e.g., curvilinear shape of snakes) features is an attribute that is likely to modulate the EPN snake effect. When it comes to visual processing, the incoming visual information is split up and processed by different encoding techniques based on the SFs of the stimuli. More specifically, there are two specialized parallel neural pathways responsible for the differential encoding of visual information: the upper magnocellular and the lower parvocellular pathways. The magnocellular neurons are sensitive to low spatial frequencies (LSFs) and allow rapid transfer of information. The parvocellular neurons are sensitive to high spatial frequencies (HSFs) and are slower in the transferring of information (Pourtois et al., 2005). The global characteristics of a stimulus (e.g., curvilinear shape) represent LSF encoding, since they contain a broad and holistic view of the incoming information. On the other hand, the local characteristics (e.g., snakeskin patterns and scales) represent HSF encoding and focus on individual detailed elements of the stimulus (Tian et al., 2002). In should be noted that other research has suggested that the functional dissociation between parvo and magno-cellular pathways are luminance and color specific and therefore difficult to distinguish based on frequency filtering (Skottun and Skoyles, 2008). Nonetheless, the roles of HSF and LSF have been found important in threat detection. The distinction between HSF and LSF in visual processing, has led to contradictory interpretations of their roles in early threat detection. David Navon (1977) in his classic global precedence paradigm, argued that global information (LSF attributes) processing is faster, and consequently earlier, than local information processing. LSFs could thus play an important role particularly to threat detection. Vuilleumier, Armony, Driver and Dolan (2003) presented subjects with pictures of fearful faces and reported that LSF global information was sufficient to activate the amygdala, which holds a critical role in the activation of threat detection relevant neural circuits. In a study that compared snake and bird stimuli in both HSF and LSF conditions by employing breaking continuous flash suppression (b-CSF), Gomes et al. (2018) explored how global and local visual information separately contribute to rapid snake detection. They reported that snakes are detected faster when viewing images in the original and LSF condition, but not in the HSF condition. This suggests that rapid snake detection is mainly driven by LSF attributes, which in snakes would be represented by global attributes such as the curvilinear shape of the animal. Electrophysiological evidence from ERP research on the EPN snake effect (van Strien, Christiaans, Franken and Huiding, 2016) supports the role the curvilinear shape in snake detection. However, when snakes are compared to other curvilinear creatures, snakes still elicit higher EPN amplitudes (van Strien, Christiaans, Franken and Huiding, 2016). This suggests that LSF global features such as the curvilinear shape, cannot fully explain the snake EPN effect.

It has been argued that HSF characteristics might also contribute to rapid snake detection. In a recent study, Beligiannis and van Strien (2019), presented participants with blurred (i.e., not containing high visual frequencies) and non-blurred (i.e., full spectrum) snake, spider and bird pictures and compared the EPN amplitudes in response to these pictures. In support with the SDT, the authors reported that snakes elicited significantly higher EPN amplitudes compared to spider and birds, in both blurred and non-blurred conditions. Interestingly, they also reported that even though the EPN was significantly higher in both conditions, the EPN snake effect was weakened in blurred pictures, compared to the full-spectrum original pictures. This suggests that local, HSF, snake characteristics might play a role in snake detection, since in a natural setting with vegetation the typical snakeskin is more striking than just the shape of the animal (Isbell and Etting, 2017). This is in line with previous research where partial exposure of snakeskin elicited significantly higher EPN amplitudes compared to lizard skin and bird plumage, further highlighting the importance of local HSF features in snake detection (van Strien and Isbell, 2017).

The primary aim of this study is to investigate the unique contribution of HSFs vs LSFs on the well-established snake EPN effect. In the present RSVP study, we employed snake, spider and bird pictures in three different conditions: one HSF condition where LSFs were filtered out, one LSF condition where HSFs were filtered out and one original SF condition (original full-spectrum pictures) containing both HSFs and LSFs. We expect snake pictures to elicit significantly higher EPN amplitudes across all conditions compared to spider and bird pictures. Additionally, we expect that the snake EPN effect will be significantly weaker in the HSF and LSF conditions compared to the original condition, since the original condition contains both types of SF and both their individual effects will be observable.

Given the time-course of the ERP response to snake and spider pictures, it is worthwhile to explore an earlier attention related component, the P1, as well. The P1, typically peaking around 100–120 ms after stimulus onset at occipital sites, is sensitive to attentional manipulations and physical stimulus characteristics. The outcomes regarding the emotional modulation of the P1 have been mixed because of differences in stimulus and task characteristics (Hajcak et al., 2012). Van Strien et al. (2012), employing a RSVP with neutral, negative, and spider pictures, found no emotional modulation of the P1 amplitude. In a RSVP study that included snake pictures, Van Strien, Eijlers, Franken, and Huiding (2014) found smaller P1 amplitudes and shorter P1 latencies at Oz in response to the snake pictures than in response to spider and bird pictures. The shorter P1 latency in response to snake pictures might support the snake detection theory.

As the P1 is sensitive to physical stimulus characteristics, it may be modulated by spatial frequency. There is evidence that for HSF and LSF neutral pictures (natural scenes) P1 amplitudes are more pronounced at midline occipital sites, whereas P1 amplitudes for FS pictures are more pronounced at lateral occipital sites (De Cesarei, Mastria and Codispoti, 2013). In a RSVP task with spatially filtered happy, fearful, and neutral faces, Tian et al. (2018) found larger P1 amplitudes for LSF pictures than...
for HSF pictures, suggesting that the P1 reflects more coarse processing.

2. Method

2.1. Participants

Twenty-nine participants (17 males, 12 females, mean age = 20.21, range = 18–28 years) were recruited for the purpose of this study. Participants were undergraduate students and participated in the experiment in exchange for course credits. Most of them were right-handed (n = 24) and everyone had normal or corrected to normal vision. The experimental design was approved by the local ethics committee. The participants provided written informed consent and received course credits for participation.

2.2. Stimuli and procedure

Participants watched a RSVP of 600 snake, 600 spider and 600 bird grey-toned pictures (3 conditions, 10 pictures per category, 20 repetitions per picture). The pictures were obtained from a previous RSVP study (Van Strien et al., 2014a,b). Each picture showed a complete specimen against a natural unobtrusive background. The SF conditions (HSF, LSF and full frequency spectrum) were blocked and counterbalanced across participants by creating two versions of the procedure where the order of the SF conditions differed (i.e., HSF, full spectrum, LSF; and LSF, full spectrum, HSF). The snake, spider and bird animal pictures were presented randomly within each block. All pictures were converted to grayscale, filtered and brightness equated after filtering. The different SF conditions were accomplished using Matlab routines, by transforming each image to the Fourier domain and applying high- and low-pass filtering, respectively. For the HSF condition, we employed a high-pass filter with a 6 cycle/degree cut-off. For the LSF condition, a low-pass filter with a 2 cycles/degree was employed (see Fig. 1, for example stimuli). These cut-off frequencies were based on previous research (Stein et al., 2014; Vlamings et al., 2009). All images were 600 × 480 pixels in size and were displayed at a distance of 120 cm on a 20-inch monitor with a resolution of 1024 × 768 pixels, which resulted in a visual angle of 11.40° × 8.55°.

2.3. EEG recording

A BioSemi Active-Two system was used to record brain activity during the RSVP task. The system used 32 pin type active Ag/AgCL electrodes on an elastic cap, following the rules of the international 10–20 system. Flat type active electrodes were used to record the Electro-ocular activity (EOG). For this purpose, two electrodes were placed above and below the left eye and another set of two electrodes on the outer corners of both eyes.

2.4. Self-report measures

After the RSVP task, participants rated the pictures in the RSVP task on valence and arousal, on a scale from 1 to 9. This task was a computerized version of the Self-Assessment Manikin (SAM) questionnaire (Bradley and Lang, 1994). Pictures were displayed in random order. Additionally, after the RSVP task, participants were asked about their subjective fear of snakes, spiders and birds. They indicated to what extent they would be afraid when confronted with each of the three animals in daily life. This was measured on a seven-point scale where 1 = not at all afraid and 7 = very afraid.

Fig. 1. Example stimuli. Pictures of a snake, spider, and bird in the original (full frequency spectrum) condition (left), HSF condition (center), and LSF condition (right).
2.5. ERP data analysis

ERP data were analyzed off-line with Brain Vision Analyzer 2.0 (Brainproducts, Gilching, Germany). We re-referenced all signals by using an average reference. Data were filtered phase-shift-free with a 0.10–30 Hz band pass (24dB/Oct). We corrected for existing ocular artifacts using the Gratton, Coles & Donchin algorithm (Gratton et al., 1983). We set the ERP time window at 50 ms before and 330 after the stimulus onset. We baseline corrected ERP signals according to the 50 ms pre-stimulus period mean. We computed averaged ERPs for each combination of stimulus category (snakes, spiders, birds) and condition (original, HSF and LSF). We omitted epochs with amplitudes exceeding ±100 μV.

All time frames (100%) were valid at the electrodes of interest for all stimulus categories. P1 peak amplitudes and latencies were scored within the 70–170 ms time window after stimulus onset (Van Strien et al., 2014a,b), and pooled at a cluster of occipital electrodes (O1, Oz, O2). As in our previous studies (Van Strien, Eijlers, Franken and Huijding, 2014; Van Strien, Franken and Huijding, 2014; Van Strien, Christians, Franken, and Huijding, 2016; Van Strien and Isbell, 2017), we defined the EPN as the mean activity in the 225–330 ms time window after stimulus onset at the occipital cluster (O1, Oz, O2).

2.6. Statistical analyses

For the fear scores, a repeated measures ANOVA was employed with stimulus category (snake, spider and bird) as factor. For the valence and arousal ratings, separate repeated measures ANOVAs were conducted with stimulus category (snake, spider, birds) as factor. For the P1 peaks and latencies and for the EPN area measures, separate repeated measures analyses of variance (ANOVAs) were conducted with stimulus category (snake, spider, bird) and SF condition (original, HSF and LSF) as factors. We employed Greenhouse-Geisser corrections when applicable.

3. Results

3.1. EEG measures

Fig. 2 displays the P1 and EPN in response to snake, spider, and bird pictures at the occipital cluster for the three different SF conditions. The P1 amplitude at the occipital cluster was maximal approximately 120 ms after stimulus onset. Fig. 2A shows the P1 and EPN response to pictures in the normal SF condition (full spectrum). Fig. 2B shows the P1 and EPN response to pictures in the HSF condition and Fig. 2C shows the P1 and EPN response to pictures in the LSF condition. Snake pictures elicited the highest EPN amplitudes across all conditions compared to the spider and bird pictures.

3.2. P1 amplitudes

There were significant main effects of stimulus category, $F(2,56) = 5.47, \, \epsilon = 0.779, \, p = .012$, and SF condition, $F(2,56) = 4.21, \, \epsilon = 0.950, \, p = .022$. Pairwise comparisons using Bonferroni correction showed that across SF conditions, P1 amplitudes were significantly smaller for snake pictures ($M = 5.08 \, \mu V$) than for spider pictures ($M = 5.40 \, \mu V, \, p = .022$) and for snake pictures than for bird pictures ($M = 5.55 \, \mu V, \, p = .040$). Across stimulus categories, P1 amplitudes were significantly higher for LSF pictures ($M = 5.65 \, \mu V$) than for HSF pictures ($M = 5.02 \, \mu V, \, p = .009$). P1 amplitudes in response to LSF and HSF pictures did not differ from P1 amplitudes in response to FS pictures ($M = 5.37 \, \mu V, \, both \, p$-values $\geq .465$).

The main effects were qualified by a significant interaction of stimulus category and SF condition, $F(4,112) = 4.48, \, \epsilon = 0.813, \, p = .004$. Fig. 3A displays this interaction. Subsequent analyses per SF condition revealed a significant stimulus category effect in the FS condition ($p <$...
but not in the HSF ($p = .780$) and LSF ($p = .080$) condition. Bonferroni pairwise comparisons showed that in the FS condition the P1 amplitudes were significantly smaller for snake pictures than for spider pictures ($p = .001$) and for snake pictures than for bird pictures ($p = .005$). P1 amplitudes did not differ in response to FS spider versus FS bird pictures ($p = 1$).

### 3.3. P1 latencies

There were significant main effects of stimulus category, $F(2,56) = 4.51, \epsilon = 0.916, p = .018$, and SF condition, $F(2,56) = 3.77, \epsilon = 0.761, p = .042$. Bonferroni pairwise comparisons showed that across SF conditions, P1 latencies were significantly shorter for snake pictures ($M = 122$ ms) than for spider pictures ($M = 126$ ms, $p = .013$) and near significantly shorter for snake pictures than for bird pictures ($M = 126$ ms, $p = .081$). Across stimulus categories, P1 latencies were significantly shorter for FS pictures ($M = 122$ ms) than for HSF pictures ($M = 127$ ms, $p = .009$). P1 amplitudes in response to LSF ($M = 125$ ms) did not differ from P1 amplitudes in response to FS and HSF pictures (both $p$-values $\geq .238$).

The main effects were qualified by a significant interaction of stimulus category and SF condition, $F(4,112) = 3.01, \epsilon = 0.767, p = .033$. Subsequent analyses per SF condition revealed a significant stimulus category effect in the FS condition ($p = .006$), but not in the HSF ($p = .105$) and LSF ($p = .521$) condition. Bonferroni pairwise comparisons showed that in the FS condition, the P1 latencies were significantly shorter for snake pictures than for FS bird pictures ($p = .034$) and for snake pictures than for FS bird pictures ($p = .004$). P1 latencies did not differ in response to FS spider versus FS bird pictures ($p = 1$).

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**Fig. 3.** (A) P1 amplitudes and (B) P1 latencies as a function of spatial frequency condition and stimulus category. Error bars represent standard error of the mean.
3.4. EPN area measures

We found an overall significant main effect for category, $F(2,56) = 49.78, \epsilon = 0.926, p < .001$. Bonferroni pairwise comparisons showed that snake pictures generated a significantly more negative EPN than spider ($p < .001$) and bird pictures ($p < .001$). No significant differences were found in EPN amplitudes between spider and bird pictures ($p > .001$). The ANOVA also indicated a significant main effect for SF condition, $F(2,56) = 15.13, \epsilon = 0.843, p < .001$. Bonferroni pairwise comparisons indicated that the images with normal SF (full spectrum) differed significantly from both the HSF ($p = .001$) and the LSF images ($p < .001$). No significant differences were found between the HSF and LSF conditions ($p = 1.00$). These main effects were qualified by a significant interaction of category and condition, $F(4,112) = 7.84, \epsilon = 0.863, p < .001$. This interaction is displayed in Fig. 4.

Separate ANOVAs were performed for the category effect per SF condition. For all three SF conditions, we found a significant main effect for category; for the normal SF condition, $F(2,56) = 43.13, \epsilon = 0.909, p < .001$; for the HSF condition, $F(2,56) = 24.56, \epsilon = 0.995, p < .001$; for the LSF condition, $F(2,56) = 22.24, \epsilon = 0.986, p < .001$. Pairwise comparisons using Bonferroni correction showed that snake pictures generated a significantly more negative EPN than spider (all $p's < 0.001$) and bird pictures (all $p's < 0.001$) in all three SF conditions.

No significant differences were found in EPN amplitudes between spider and bird pictures in any of the SF conditions (all $p's > 0.149$).

In addition, separate ANOVAs were performed for the SF effect per stimulus category. Neither the ANOVA for the spider pictures, $F(2,56) = 2.42, \epsilon = 0.754, p = .114$, nor the ANOVA for the bird pictures, $F(2,56) = 0.044, \epsilon = 0.879, p = .941$, produced significant SF effects. The ANOVA for the snake pictures revealed a significant SF effect, $F(2,56) = 24.22, \epsilon = 0.993, p < .001$. Bonferroni pairwise comparisons showed that the snake EPN component in the normal SF condition (full spectrum) was significantly larger compared to the snake EPN components of both the HSF and LSF condition (both $p-values < .001$). No significant differences were found between the HSF and LSF conditions ($p = .691$). Fig. 5 displays the EPN amplitudes of snake pictures for each SF condition. Fig. 6A displays the topographical differences for snake pictures between the normal (original) and HSF conditions, Fig. 6B displays the topographical differences for snake pictures between the normal (original) and LSF conditions, and Fig. 6C displays the typical EPN snake effect for full-spectrum pictures.

3.5. Fear measures

Snakes were scored as being more fearful ($M = 5.59, SD = 1.30$, range 2–7) than spiders ($M = 4.59, SD = 1.21$, range 2–7) and birds ($M = 1.45, SD = 0.87$, range 1–4). Bonferroni-corrected comparisons indicated that both snakes and spiders yielded significantly higher fear scores than birds (both $p-values < .001$). Snake fear was also significantly higher than spider fear ($p = .006$).

3.6. Valence and arousal ratings

The mean valence and arousal ratings for snake, spider and bird pictures are shown in Table 1. There were significant main effects of category for both arousal, $F(2,56) = 44.22, \epsilon = 0.712$ $p < .001$, and valence ratings, $F(2,56) = 60.66, \epsilon = 0.672, p < .001$. Snake and spider pictures yielded lower valence ratings compared to bird pictures (both $p-values < .001$) suggesting they are less pleasing to look at. Additionally, snake and spider pictures yielded higher arousal ratings compared to birds, suggesting that they are more exciting to look at (both $p-values < .001$). No significant differences were found between snakes and spiders for valence and arousal ratings.

3.7. Correlational analysis

To see whether the scores on the Snake and Spider Fear questionnaires were related to the EPN amplitudes, we calculated Pearson’s correlations between the EPN difference measures for snake and spider pictures for each SF condition on the one hand, and the corresponding fear scores on the other hand. The EPN difference measures were obtained by subtraction the EPN in response to bird pictures from the corresponding EPN in response to snake and spider pictures, respectively. We employed difference measures to reduce the possible unexplained variance in ERP amplitudes. The correlations are given in Table 2.

There was a significant correlation ($r = -0.39$) between the EPN difference measure for FS snake pictures and the snake fear score. Participants with greater self-reported fear of snakes displayed larger EPN responses to snake pictures, compared to participants with less snake fear. For HSF and LSF snake pictures, and for spider pictures, no significant correlations were found between the EPN difference measures and fear scores.

None of the correlations between the EPN difference measures and the corresponding valence and arousal ratings were significant, all
In this study, we explored the contribution of high and low SFs to the automatic allocation of early attention to snake and spider pictures by means of early attention related brain potentials (P1 and EPN). To achieve that, we presented participants with a RSVP procedure of FS, HSF and LSF filtered pictures while registering their EEG responses. We specifically hypothesized that more early attention is allocated to snakes than to spiders, as reflected in the EPN snake effect. The EPN has been considered to reflect early attentional activation by evolutionary relevant stimuli (Schupp et al., 2003). We expected that snake pictures would elicit higher EPN amplitudes compared to spider and bird pictures and that the snake EPN-effect would be larger for normal FS pictures compared to HSF and LSF pictures.

Regarding the P1, we found smaller P1 amplitudes and shorter P1 latency in response to high SFs compared to low SFs. This suggests that high SFs may be processed more quickly and with less resource allocation compared to low SFs. However, further research is needed to confirm these findings and to understand the underlying mechanisms.

**Table 1**

Participants’ mean arousal and valence ratings (and standard deviations).

| Stimulus Category | Valence (SD) | Arousal (SD) |
|-------------------|--------------|--------------|
| snake             | 3.53 (1.24)  | 4.63 (2.08)  |
| spider            | 3.22 (1.11)  | 4.66 (1.67)  |
| bird              | 6.28 (1.32)  | 1.85 (1.49)  |

Note. Valence and arousal ratings are based on a rating scale from 1 to 9.

**Table 2**

Pearson’s correlations (and p-values) between fear scores on the snake and spider questionnaire and EPN difference measures (snake minus bird and spider minus bird pictures, respectively) at the occipital cluster (O1, O2, O3).

| Stimulus Category | FS       | HSF      | LSF      |
|-------------------|----------|----------|----------|
| snake             | –.389 (p = .037) | –.122 (p = .529) | –.156 (p = .420) |
| spider            | .062 (p = .748)  | .127 (p = .511)  | .149 (p = .440)  |

The results of the correlation analysis indicate that there is a moderate negative correlation between fear scores on the snake and spider questionnaire and EPN difference measures for snake pictures, while no significant correlation was found for spider pictures. This suggests that the snake EPN-effect is related to fear and anxiety, whereas the spider EPN-effect is not.

The findings of this study have implications for understanding the role of SFs in early attention allocation and the processing of evolutionary relevant stimuli. Further research is needed to extend these findings to different populations and to understand the underlying mechanisms.
pathway) has been questioned (De Cesarei and Codispoti, 2013; Stein exclusive role of LSFs in threat detection (supposedly by a subcortical HSFs contribute equally to the EPN snake effect. In general, empirical main effects revealed that only snake pictures elicited a significantly displayed the global (LSF) or local (HSF) features of the snake. The current findings suggest that the LSFs also play a role and that LSFs and animal categories. The effect of SF on the EPN to snake pictures suggests compared to the HSF and LSF conditions. This appeared to be not the specific relationship between the P1 and the EPN for snake and spider stimuli needs further research.

Across stimulus categories, the P1 amplitudes were significantly larger for LSF pictures than for HSF pictures, with the P1 amplitudes for FS pictures falling in between. The larger P1 amplitudes for LSF versus HSF pictures are in line with the research of Tian et al. (2018) in which LSF neutral and emotional faces yielded larger P1 amplitudes than HSF faces. The larger P1 for LSF pictures suggests that the P1 might reflect more coarse (magnocellular) processing of emotionally relevant stimuli such as pictures of faces or snakes and spiders. Furthermore, P1 latencies were significantly shorter for FS than for HSF pictures and nonsignificantly shorter for FS than for LSF pictures, which could indicate faster processing of the FS pictures in general. It should be noted that these temporal effects are very small, with mean latencies varying just a few milliseconds.

Regarding the EPN, we found that snake pictures produced the highest EPN amplitudes compared to spider and bird pictures across all three SF conditions (normal, HSF, LSF). This finding is in line with previous research on the topic and acts as further support for the SDT (Beligiannis and van Strien, 2020; Grassini et al., 2016; He et al., 2014; Van Strien et al., 2014a,b; Van Strien and Isbell, 2017). This also suggests that regardless of the degradation of each picture by spatial filtering, snakes still may be recognized anyway. The main SF effect indicated that the EPN amplitudes across categories were significantly higher in the normal SF condition (full spectrum) compared to the HSF and LSF conditions. However, the significant interaction of these main effects revealed that only snake pictures elicited a significantly higher EPN amplitude in the normal (full-spectrum) SF condition, compared to the HSF and LSF conditions. This appeared to be not the case for spiders and birds, as no SF effects were found within these two animal categories. The effect of SF on the EPN to snake pictures suggests that the original representation of snakes will trigger automatic attentional capture more efficiently compared to representations that only display the global (LSF) or local (HSF) features of the snake.

No significant differences in EPN amplitudes in response to snake pictures were found between the HSF and LSF conditions. This indicates that individual LSF global attributes (e.g., curvilinear shape) and HSF local attributes (snakeskin patterns and scales) contribute equally to the EPN snake effect.

Previous EPN research already demonstrated a distinct role for HSFs in the snake EPN effect (Beligiannis & Van Strien, 2019, 2020). The current findings suggest that the LSFs also play a role and that LSFs and HSFs contribute equally to the EPN snake effect. In general, empirical evidence from detection paradigms has emphasized the importance of LSFs in snake detection. For instance, in their b-CSF study, Gomes et al. (2018) reported that when examining the distinct contribution of HSFs and LSFs, snakes were detected faster in the LSF and original conditions. Likewise, Gao et al. (2017), found that LSFs contain sufficient information to detect threat-relevant stimuli in their visual search paradigm, showing pictures of threatening and non-threatening animals (including snakes) with different levels of HSF and LSF information. However, an exclusive role of LSFs in threat detection (supposedly by a subcortical pathway) has been questioned (De Cesarei and Codispoti, 2013; Stein et al., 2014).

Here, we designed and employed distinct, isolated SF conditions (i.e., HSF and LSF conditions) while comparing the different animal categories. The independence of these mutually exclusive SF conditions could explain the different findings compared to the detection paradigms. Based on the two distinct SF-sensitive visual encoding pathways (e.g., Pourtois et al., 2005) and on the above empirical evidence, it can be argued that the LSF and HSF processing streams can be distinguished.

Based on our current findings, both streams are necessary for early attentional capture and do not exclusively contribute to the EPN as they both are indispensable. Therefore, it could be the case that even though global characteristics are processed faster, they make a significant contribution to automatic snake detection only when local attributes are available.

In the present study, snakes elicited the highest fear scores, followed by spiders. When we correlated the snake fear and spider fear scores with the EPN difference scores (i.e., EPN for snakes minus EPN for birds; EPN for spiders minus EPN for birds) we found a significant correlation between snake fear and the EPN difference measure for snakes (r = −0.399). Participants who reported more fear of snakes displayed larger EPN responses to snake pictures. Whereas the EPN snake effect has been highly consistent across our previous studies, the relationship between this effect and self-reported snake fear remains ambiguous. In most studies, we have not found an association between psychophysiological and self-report measures related to snake stimuli (Beligiannis and Van Strien, 2019, 2019; Van Strien, Eijlers, et al., 2014; Van Strien, Franken and Huijding, 2014; Van Strien et al., 2016). Van Strien and Isbell found a correlation of −.45 between snake fear scores and the EPN in response to pictures of snake skins. However, they found no association between snake fear scores and the EPN in response to pictures of partially exposed snakes (r = −0.07). The latter result of that study is in agreement with the studies in which pictures of completely exposed snakes were shown. The inconsistent results regarding the association of snake fear and the EPN snake effect may be partly due to the relatively moderate snake fear scores reported by the participants (in this study M = 5.59, range 2–7 on a 9-point scale).

Additionally, snake and spider pictures elicited significantly lower valence and higher arousal ratings compared to birds, suggesting that both snakes and spiders are perceived as more unpleasant and more exciting compared to birds. This is in line with their fear relevant nature. We found no significant correlations between valence and arousal ratings on the one hand and EPN difference measures on the other hand in any of the SF conditions. The comparable valence and arousal ratings for snake and spider pictures suggest that the conscious participants’ ratings cannot explain the EPN differences between these two animal categories. A dissociation of psychophysiological and self-report measures is in line with the premise that the EPN reflects an instinct based, non-conscious processing mechanism as displayed in previous research.

In conclusion, we found significantly larger EPN amplitudes in response to snake pictures, compared to spider and bird pictures. The specific snake EPN effect was found to be significantly larger for the original full spectrum condition (containing both high and low SFs) compared to the HSF and LSF conditions. This suggests that both global LSFs and local HSF snake attributes are equally important to trigger early rapid attentional capture in response to snakes, making the availability of both HSFs and LSFs related snake attributes a possible contributing factor to the snake EPN effect.

Credit author statement

Nick Beligiannis: Conceptualization, Methodology, Writing – original draft preparation, Writing - Reviewing and Editing. Jan W. van Strien: Data curation, Methodology, Software, Writing- Reviewing and Editing, Visualization & Supervision Merel Hermus: Conceptualization, Writing – original draft preparation, Methodology, Visualization, Lise-lotte Gootjes: Supervision.
Data availability

Data will be made available on request.

References

Beligiannis, N., Van Strien, J.W., 2019. Blurring attenuates the early posterior negativity in response to snake stimuli. Int. J. Psychophysiol. 146, 201–207. https://doi.org/10.1016/j.ijpsycho.2019.09.002.

Beligiannis, N., Van Strien, J.W., 2020. Early posterior negativity in humans to pictures of snakes and spiders: effects of proximity. Exp. Brain Res. 238, 2795–2804. https://doi.org/10.1007/s00221-020-06925-5.

De Cesarei, A., Mastrini, S., Codispoti, M., 2013. Early spatial frequency processing of natural images: an ERP study. PloS One 8 (5). https://doi.org/10.1371/journal. pnas.0956103.

Bradley, M.M., Lang, P.J., 1994. Measuring emotion: the self-assessment Manikin and the semantic differential. J. Behav. Ther. Exp. Psychiatry 25 (1), 49–59. https://doi.org/10.1016/0021-9975(94)90063-9.

De Cesarei, A., Codispoti, M., 2013. Spatial frequencies and emotional perception. Rev. Neurosci. 24 (1), 89–104. https://doi.org/10.1515/revneuro-2012-0053.

Gao, X., LoBue, V., Irving, J., Harvey, T., 2017. The effect of spatial frequency information and visual similarity in threat detection. Cognit. Emot. 31 (5), 912–922. https://doi.org/10.1080/02699931.2016.1180280.

Gomes, N., Soares, S.C., Silva, S., Silva, C.F., 2018. Mind the snake: fear detection relies on low spatial frequencies. Emotion 18 (6), 886–895. https://doi.org/10.1037/emo0000391.

Grassini, S., Holm, S.K., Raits, H., Koivisto, M., 2016. Who is afraid of the invisible snake? subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. Biol. Psychol. Part A 121, 53–61. https://doi.org/10.1016/j.biopsycho.2016.10.007.

Gratton, G., Coles, M.G., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.

Hajcak, G., Weinberg, A., MacNamara, A., Foti, D., 2012. ERPs and the study of emotion. In: Luck, S.J., Kappenman, E.S. (Eds.), The Oxford Handbook of Event-Related Potentials. Oxford University Press, New York, pp. 441–472.

Han, S., Weaver, J.A., Murray, S.O., Kang, X., Yund, E.W., Woods, D.L., 2002. Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. Neuroimage 17, 1290–1299.

He, H., Kubo, K., Kawai, N., 2014. Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. Neuroreport 25, 1049–1053.

Ishell, L.A., 2006. Snakes as agents of evolutionary change in primate brains. J. Hum. Evol. 51, 1–35.

Ishell, L.A., Etting, S.F., 2017. Snake scales, partial exposure, and the Snake Detection Hypothesis: an ERP study. Psychophysiology 53, 252–257.

Navon, D., 1977. Forest before trees: the precedence of global features in visual perception. Cognit. Psychol. 9 (3), 353–383. https://doi.org/10.1016/0010-0285(77)90012-3.

Pourtois, G., Dan, E.S., Grandjean, D., Sander, D., Vuilleumier, P., 2005. Enhanced extrastriate visual response to bandpass spatial frequency filtered fearful faces: time course and topographic evoked-potentials mapping. Hum. Brain Mapp. 26 (1), 65–79.

Schupp, H.T., Flaisch, T., Stockburger, J., Junghöfer, M., 2006. Emotion and attention: event-related brain potential differences. Prog. Brain Res. 156, 31–51.

Schupp, H.T., Junghöfer, M., Weike, A.J., Hamm, A.O., 2003. Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. Neuroreport 14, 1107–1110.

Skottun, B.C., Skoyles, J.R., 2008. Visual search: magneto- and parvocellular systems or color and luminance processes? Int. J. Neurosci. 118 (9), 1259–1267. https://doi.org/10.1080/00207450701239434.

Stein, T., Seymour, K., Hebart, M.N., Sterzer, P., 2014. Rapid fear detection relies on high spatial frequencies. Psychol. Sci. 25 (2), 566–574. https://doi.org/10.1177/0956797613512509.

Tian, J., Wang, J., Xia, T., Zhao, W., Xu, Q., He, W., 2018. The influence of spatial frequency content on facial expression processing: an ERP study using rapid serial visual presentation. Sci. Rep. 8 (1), 1–8. https://doi.org/10.1038/s41598-018-20467-1.

Van Strien, J.W., Christiansen, G., Franken, L.H., Huijding, J., 2016. Curvilinear shapes and the snake detection hypothesis: an ERP study. Psychophysiology 53, 252–257.

Van Strien, J.W., Eijlers, R., Franken, L.H.A., Huijding, J., 2014a. Snake pictures draw more early attention than spider pictures in non-phobic women: evidence from event-related brain potentials. Biol. Psychol. 96, 150–157.

Van Strien, J.W., Franken, L.H., Huijding, J., 2012. Early posterior negativity is larger for snake pictures than for spider pictures in non-phobic women. Poster session presented at 16th World Congress of Psychophysiology, Pisa Italy, International Journal of Psychophysiology 85, 374.

Van Strien, J.W., Franken, L.H., Huijding, J., 2014b. Testing the snake detection hypothesis: larger early posterior negativity in humans to pictures of snakes than to pictures of other reptiles, spiders and slugs. Front. Hum. Neurosci. 8, 691.

Van Strien, J.W., Ishell, L.A., 2017. Snake scales, partial exposure, and the Snake Detection Theory: a human event-related potentials study. Sci. Rep. 7, 46231.

Vlaming, P.H.J.M., Goffaux, V., Kemner, C., 2009. Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? J. Vis. 9 (5) https://doi.org/10.1167/9.5.12.

Vuilleumier, P., Armony, J.I., Driver, J., Dolan, R.J., 2003. Distinct spatial frequency sensitivities or processing faces and emotional expressions. Nat. Neurosci. 6, 624.