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Snake pictures draw more early attention than spider pictures in non-phobic women: Evidence from event-related brain potentials

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Abstract

Snakes were probably the first predators of mammals and may have been important agents of evolutionary changes in the primate visual system allowing rapid visual detection of fearful stimuli (Isbell, 2006). By means of early and late attention-related brain potentials, we examined the hypothesis that more early visual attention is automatically allocated to snakes than to spiders. To measure the early posterior negativity (EPN), 24 healthy, non-phobic women watched the random rapid serial presentation of 600 snake pictures, 600 spider pictures, and 600 bird pictures (three pictures per second). To measure the late positive potential (LPP), they also watched similar pictures (30 pictures per stimulus category) in a non-speeded presentation. The EPN amplitude was largest for snake pictures, intermediate for spider pictures and smallest for bird pictures. The LPP was significantly larger for both snake and spider pictures when compared to bird pictures. Interestingly, spider fear (as measured by a questionnaire) was associated with EPN amplitude for spider pictures, whereas snake fear was not associated with EPN amplitude for snake pictures. The results suggest that ancestral priorities modulate the early capture of visual attention and that early attention to snakes is more innate and independent of reported fear.

Keywords

Early posterior negativity (EPN)

Late positive potential (LPP)

Snake fear

Spider fear

Evolution

1. Introduction

For our ancestors, the rapid visual detection of animals was a matter of life and death. Some animals were predators, other animals represented food. According to the animate monitoring hypothesis, the human attention system possesses a visual monitoring system equipped with ancestrally derived animal specific election criteria (New, Cosmides, & Tooby, 2007). This system causes a stronger spontaneous allocation of attention to animals than to objects. Research with the visual change-detection paradigm for instance, has demonstrated that humans are faster and more accurate at detecting changes in animals than at detecting changes in inanimate objects, even if these inanimate objects (e.g., vehicles) can pose life-or-death importance (New et al., 2007).

Within the animate category however, some species might have been more life-threatening, and hence more fear relevant, to our ancestors than other species. From an evolutionary perspective, a specialized visual monitoring system that was focused on animals posing deadly threat, rather than on animals in general, would enable the fast mobilization of defense and would be highly adaptive (Öhman, 2007). Mineka and Öhman (2002) proposed an evolved fear module that is automatically activated by phylogenetically fear-relevant stimuli, and is largely independent of conscious cognition. The amygdala is supposedly the central brain area dedicated to this fear module. Although fear of potentially dangerous animals such as snakes or spiders is, at least in many modern societies, no longer relevant for survival, the fear module in the human brain still responds strikingly to stimuli representing these animals. The studies of Öhman and colleagues have demonstrated that fear-relevant stimuli such as snakes or spiders are more readily associated with aversive unconditioned stimuli than are fear-irrelevant stimuli such as flowers or mushrooms (e.g., Öhman & Soares, 1998; see for review, Öhman & Mineka, 2001). The superior aversive conditioning to snakes or spiders has been explained in terms of evolutionary “preparedness” (Mineka & Öhman, 2002; Seligman, 1970).

Snakes and spiders are typically bracketed together as it comes to superior Pavlovian conditioning to fear-evoking animal stimuli and facilitated attentional capture (Öhman, Flykt, & Esteves, 2001). For our evolutionary ancestors however, snakes were probably more life-threatening than spiders. According to Isbell (2006) snakes in particular provided predatory

pressure on primate evolution. Snakes have a long evolutionary coexistence with primates and their predecessors and may have been their first predators. Old world monkeys, who experienced continuous predatory pressure from snakes, show fear of snakes and have a highly advanced visual system to perceive these hardly detectable animals. As Isbell suggested, the descendants from primates that left Africa and thus escaped predatory pressure from snakes show less fear of snake and have a less advanced visual system. In contrast to fear of snakes, fear of spiders could stem from a cultural origin rather than an evolutionary one. According to Davey (1994), the pervasive spider fear that is found in many Western societies, is the consequence of the disgust-relevant status of spiders. This status resulted from the spiders' association with illness, disease, and infection in European societies from the Middle Ages onward. In this era, the spider was a suitable displaced target for the anxieties caused by many devastating and incomprehensible epidemics. Irrespective of a possible cultural origin, spiders can be considered as fear-relevant, but low predator animals (Davey, Cavanagh, & Lamb, 2003), with spider fear driven by disgust rather than physical harm (De Jong & Muris, 2002; see also, Soares, Esteves, Lundqvist, & Öhman, 2009).

As snakes in particular caused evolutionary change in primate brains by predatory pressure (Isbell, 2006), it can be expected that in humans snakes activate the evolved specific neural circuitry of the fear module more strongly than spiders. As yet, fMRI studies have not demonstrated larger amygdala activation for snakes than for spiders, but it should be noted that these studies have not tested the explicit hypothesis of larger amygdala activation in response to snakes compared to spiders in non-phobic participants. Dilger et al. (2003) found higher left-sided amygdala activation for spiders than for snakes in spider phobics and no differential amygdala activation in controls (for both the spider > snake contrast and the snake > spider contrast). Goossens, Schruers, Peeters, Griez, and Sunaert (2007) found higher left amygdala activation in spider phobic participants than in control participants in response to spider vs. neutral pictures. In Goossens et al.'s study, no specific contrasts for larger activation in response to snakes vs. spiders were examined. Neurophysiological evidence for the animate monitoring hypothesis itself has been provided by an fMRI study with non-phobic individuals (Yang, Bellgowan, & Martin, 2012), which demonstrated that the amygdala responds to

threatening animals such as snakes or spiders but not to weapons, although both animate and inanimate stimuli were rated as negative and high arousing by the participants. Again, no direct comparisons were made between the amygdala activation in response to snakes and the amygdala activation in response to spiders.

In a behavioral study employing a visual search paradigm, participants with high snake fear detected snakes faster than spiders, while participants with high spider fear detected spiders faster than snakes (Öhman et al., 2001). In another study with this visual search paradigm (Soares et al., 2009), the detection of spiders was highly selective for spider fearful participants. The results were ambiguous for snake fearful participants, who exhibited no differences in detection speed between snakes and spiders. The influence of increasing numbers of distractors was less for snakes than for spiders, indicating more efficient search for snake targets than for spider targets. Soares et al. concluded that the detection of snakes may be primarily dependent on bottom-up processes whereas the detection of spiders may more dependent on top-down processes.

The evidence that snakes draw more early attention than spiders is sparse. The focus of previous research on spider phobic or snake phobic individuals renders these studies suboptimal for drawing conclusions about possible differences between the early visual processing of snakes and spiders in the general population. To test the hypothesis that more early visual attention is automatically allocated to snakes relative to spiders, the present event-related potential (ERP) study was done in a sample of non-phobic women.

The ERP technique allows the examination of the time-course of the neural response to snake and spider pictures. Given the automatic attentional capture of fear-relevant stimuli, it can be hypothesized that early visual activity as reflected in early ERPs is modulated by phylogenetic fear. In the present study, the early automatic attentional capture of emotionally relevant stimuli is represented by the P1 response and the early posterior negativity (EPN). We investigated these early ERP components by showing snake, spider and small-bird pictures in a rapid serial visual presentation (RSVP) paradigm. With the RSVP paradigm, a continuous stream of emotional and neutral pictures is presented at a rate of several (typically three) pictures per second, while participants are passively viewing. The RSVP paradigm requires the rapid

processing of emotional stimuli under a high processing load, which makes good evolutionary sense (Junghöfer, Bradley, Elbert, & Lang, 2001).

The P1, peaking between 80 and 130 ms post stimulus onset at occipital sites, reflects early visual processing and is sensitive to attentional manipulations and physical stimulus characteristics. It can be expected that enhanced attention to negative stimuli modulates the P1 component. Results concerning the emotional modulation of the P1 however, have been mixed, probably because of task differences and differences in sensory features of the emotional stimuli (Hajcak, Weinberg, MacNamara, & Foti, 2012). A number of studies indeed have found larger P1 amplitudes in response to negative than in response to positive or neutral pictures (see for review, Olofsson, Nordin, Sequeira, & Polich, 2008), but other studies have found larger P1 amplitudes in response to positive pictures than in response to negative pictures (Alorda, Serrano-Pedraza, Campos-Bueno, Sierra-Vázquez, & Montoya, 2007; Van Strien, Langeslag, Strekalova, Gootjes, & Franken, 2009). With the RSVP paradigm, neither Junghöfer et al. (2001) nor Van Strien, Franken, and Huijding (2009) found emotional modulation of the P1 amplitude at lateral occipital sites.

The EPN is a component that reflects early selective visual processing of emotionally significant information. The EPN is most pronounced between 225 and 300 ms post stimulus onset, at lateral occipital electrodes (Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Junghöfer et al. (2001) employed the RSVP of emotional pictures while recording ERPs. With a 3 Hz presentation rate, they found the largest differences between low and high arousing pictures at the N260 (EPN) component over lateral occipital cortices. The EPN is associated with the functioning of the motivational systems of approach and avoidance and is augmented particularly by stimuli of evolutionary significance (Schupp, Junghöfer, Weike, & Hamm, 2003). The EPN emotion effect is not sensitive to stimulusrepetition (Schupp, Stockburger, et al., 2006).

Van Strien, Franken, and Huijding (2009) investigated the EPN in response to the RSVP of neutral, negatively valenced emotional, and spider pictures in a non-phobic sample. They found that pictures of spiders yielded higher (i.e., more negative going) EPN amplitudes than neutral and negative pictures. Furthermore, they found that this early automatic response to

spider pictures was modulated by the extent of fear of spiders, as indicated by the participants' scores on a spider phobia questionnaire.

The early and automatic attentional capturing of fear-relevant stimuli is followed by sustained processing to assure that these stimuli gain access to capacity-limited processes associated with focused attention and conscious recognition. ERP studies show that the early negative-going potential over occipital regions, is followed by an increased late positive potential (LPP) over centroparietal regions (Schupp, Flaisch, et al., 2006). The LPP starts about 300 ms after stimulus onset and may last for hundreds of milliseconds to seconds, depending on the duration of the emotional stimuli (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). The LPP is more positive-going when people watch emotionally intense and arousing pictures.

In response to spider pictures, spider phobic persons show more enhanced LPP components than non-phobic persons (Kolassa, Musial, Mohr, Trippe, & Miltner, 2005; Leutgeb, Schäfer, & Schienle, 2009). Michalowski et al. (2009) also found enhanced LPP amplitudes to spider pictures in spider phobic participants. Because these authors did not find any LPP differences between phobic and non-phobic participants for standard emotional materials, they concluded that the LPP enhancement was spider-fear-specific, probably reflecting enhanced attention to spiders in preparation of a defensive action (i.e., active escape behavior).

Pictures with high evolutionary significance (e.g., sexual content, threat, mutilations) are found to be associated with increased LPP amplitudes compared to pictures of the same valence, but with less evolutionary significance (Schupp, Flaisch, et al., 2006). If snakes have higher evolutionary significance, it thus could be expected that snake pictures will result in larger LPP amplitudes than spider pictures. A study with non-phobic participants by Mallan and Lipp (2011) does not support this notion. These authors found larger LPP amplitudes to both snake and spider pictures than to pictures of non-fear-relevant animals. However, the LPP amplitudes for snakes and spiders were comparable, which indicates that, in a non-phobic sample, snakes and spiders equally draw more attention at later stages of visual processing. It can be argued that the preferential processing of snakes vs. spiders at earlier stages not necessarily lasts for later processing stages. The later stages of attentional processing of fear relevant stimuli may be linked to the preparation of a defensive action (Michalowski et al.,

2009), and the defensive actions to snakes and spiders may be comparable. In addition, the later stages are more top down and subject to cognitive control.

Differences in visual attention to snake and spider pictures as reflected in the early (P1, EPN) and late (LPP) attention-related ERPs would support the notion of differences in evolutionary relevance between snakes and spiders. To measure the P1 and EPN, we had women watch the RSVP of snake, spider and small-bird pictures. To measure the LPP, we had them watch similar pictures, but at a slower rate. As snakes may have been more important agents of evolutionary changes that allowed rapid visual detection of fearful stimuli (Isbell, 2006), we expected a larger (i.e., more negative going) EPN in response to snakes than to spiders. The smallest EPN was expected in response to bird pictures. Given the mixed results for the emotional modulation of the P1, we had no specific hypothesis regarding this component. Because snakes and spiders are clearly more fear-relevant (and potentially triggering more defensive action) than small birds, the LPP in response to snake and spider pictures will be larger than the LPP in response to bird pictures. Although snakes may phylogenetically be more fear-relevant than spiders, we expected no or only small differences between LPP amplitudes in response to snake and spider stimuli, because previous research suggested a comparable LPP modulation by snake and spider stimuli (Mallan & Lipp, 2011) and because the effects of attention may be comparable for snakes and spiders at later stages of processing.

Participants also filled out fear questionnaires for snakes, spiders and birds. For our sample, we had no particular hypothesis regarding the difference in the degree of fear toward snakes and spiders. Mallan and Lipp (2011) found slightly higher fear scores for snakes than for spiders in their non-phobic sample. Based on our previous research, we expected an association between fear of spiders and EPN amplitude for spider pictures (Van Strien, Franken, & Huijding, 2009). This association with EPN amplitude suggested that greater fear of spiders is accompanied by more automatic early attentional capture of visual spider stimuli. As participants with high snake fear are faster to detect snake targets than non-fearful participants (Öhman et al., 2001), it can be expected that in the present research snake fear is associated with EPN amplitude for snake pictures. We also expected an association between fear and LPP amplitude. For instance, in the study of Scharmüller, Leutgeb, Schäfer, Köchel, and Schienle

(2011), spider phobics showed enhanced LPP amplitudes in response to spider pictures relative to low spider-fearful individuals.

2. Methods

2.1. Participants

Participants were 24 university students with normal or corrected-to-normal vision. To control for sex differences in emotional picture processing (Stevens & Hamann, 2012), only female participants were recruited. Two of them were left-handed, the others were right-handed by self-report. Ages ranged from 18 to 31 years, with a mean age of 21.96 years. They were volunteers, or they participated for course credits. The study complied with departmental ethics committee regulations. All participants provided written informed consent.

2.2. Psychological measures

Before the experimental runs, participants completed three questionnaires regarding fear of spiders, snakes, and birds, respectively. The questionnaires were adapted versions of the Spider Phobia Questionnaire (SPQ; Klorman, Weerts, Hastings, Melamed, & Lang, 1974; Muris & Merckelbach, 1996). Each questionnaire contained 15 statements regarding fear the specific species. With the statements rated on a 4-point scale, scores on each questionnaire could range from 0 (no fear) to 45 (very high fear). Half of the participants completed the spider questionnaire first and the snake questionnaire last, the other half completed the questionnaires in opposite order.

2.3. Stimuli and procedure

Participants attended two passive viewing experiments, one designed to measure the EPN and one to measure the LPP. For the EPN, participants watched the rapid serial presentation of 600 snake pictures, 600 spider pictures, and 600 pictures of small birds. There were 10 different color pictures in each category. Each picture showed a complete specimen against a natural background. The pictures were presented in random order, at a rate of three pictures per second (Schupp, Stockburger, et al., 2006). For the LPP, participants watched 30 different snake, 30 different spider, and 30 different bird pictures. These pictures were different from the pictures in the EPN task, and were presented in random order with a duration of 1000 ms and at random interstimulus intervals (1750–2250 ms).

In both experiments, pictures had a size of approximately 600 × 450 pixels, and were presented on a 20-in. PC monitor with a resolution of 1024 × 768 pixels. Pictures were displayed on a medium gray background, at a distance of approximately 135 cm in front of the participants, resulting in a visual angle of about 10.0° × 7.5°.

Participants were seated in a dimly-lit, and sound-attenuated room. The EPN sequence always preceded the LPP sequence. The EEG was recorded during both sequences. To determine the valence and arousal properties of our picture categories, participants performed, after the EEG measurement, a computerized Self-Assessment Manikin (SAM) questionnaire (Bradley & Lang, 1994) regarding valence and arousal ratings of all pictures on a 9-point scale.

2.4. EEG recording

EEG activity was recorded using a BioSemi Active-Two system from 32 pin type active Ag/AgCl electrodes mounted in an elastic cap. Electrodes were Fz, Cz, Pz, Oz, FP1/2, AF3/4, F3/4, F7/8, FC1/2, FC5/6, C3/4, T7/8, CP1/2, CP5/6, P3/4, P7/8, PO3/4, and O1/2. Flat-type active electrodes were attached to the left and right mastoids. Electro-oculogram (EOG) activity was recorded from flat-type active electrodes placed above and beneath the left eye, and from

electrodes at the outer canthus of each eye. An additional pin-type active electrode (common mode sense) and a pin-type passive electrode (driven right leg) were used to comprise a feedback loop for amplifier reference. The EEG and EOG data were digitized with a sampling rate of 512 Hz, a low-pass filter of 134 Hz, and 24-bit A/D conversion.

2.5. ERP data analysis

For the EPN sequence, the EEG signals were referenced to an average reference, and phase-shift-free filtered with a band pass of .10–30 Hz (24 dB/Oct). Correction for ocular artifacts was done using the Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983). ERP epochs were extracted lasting from 50 ms before stimulus onset to 330 ms after stimulus onset. The ERP signals were defined relative to the mean amplitude of the prestimulus period. For each participant and each stimulus category (snake, spider, bird), average ERPs were computed. All epochs with a baseline-to-peak amplitude difference larger than 100 μ V or smaller than -100 μ V on any channel were excluded from further analysis. The mean percentage of valid epochs was about 99% for each stimulus category. For the P1, peak amplitudes and latencies at the occipital electrodes (O1, Oz, O2, PO3, and PO4; see Fig. 1 for the electrode positions) were scored within the 70–170 ms time window. The EPN was scored at lateral occipital electrodes (O1, O2, PO3, and PO4) and was measured as the mean activity in the 225–300 ms time window after stimulus onset (e.g. Van Strien, Franken, & Huijding, 2009).

For the LPP sequence, the EEG signals were referenced to the averaged mastoids (see for EPN and LPP reference selection, Hajcak et al., 2012). The settings for filtering, eye movement correction, and artifact rejection were identical to the settings for the EPN task. ERP epochs for the LPP were extracted with a 1100-ms duration, beginning 100 ms before stimulus onset. The ERP signals were defined relative to the mean amplitude of this pre-stimulus baseline period, and were averaged for each participant and each stimulus category. The mean number of valid epochs was 93.0% for the snake pictures, 92.0% for the spider pictures, and 95.3% for the bird pictures (the total range was 24–30 valid epochs per stimulus category). The

LPP was scored at parietal electrodes (Pz, P3, P4, CP1, and CP2). Visual inspection of the grand average waveforms revealed that the 500–900-ms time window after stimulus onset best represented the LPP. This time window is consistent with previous studies using passive viewing of emotional pictures (e.g., Brown, Goodman, & Inzlicht, 2013).

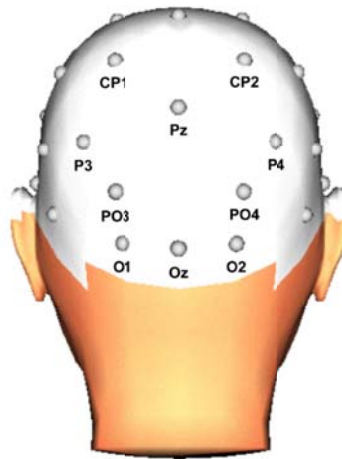


Fig. 1. Diagram of the EEG electrodes included in the statistical analyses. The P1 was scored at Oz, O1, O2, PO3, and PO4; the EPN was scored at O1, O2, PO3, and PO4; the LPP was scored at Pz, P3, P4, CP1, and CP2.

2.6. Statistical analyses

For the fear, valence, and arousal ratings, we conducted repeated measures analyses of variance (ANOVAs) with stimulus category (snakes, spiders, and small birds) as factor. For the ERP components we conducted separate repeated-measures ANOVAs with stimulus category (snakes, spiders, and birds) and electrode as factors. The electrode factor comprised O1, Oz, O2, PO3, and PO4 for the P1 component; O1, O2, PO3, and PO4 for the EPN component; and P3, Pz, P4, CP1, and CP2 for the LPP component. When appropriate, Greenhouse–Geisser correction was applied. To explore the relationship between reported fear and the ERP

amplitudes, we performed correlational analyses between EPN and LPP amplitudes on the one hand, and scores for fear of spiders, snakes, or birds on the other hand. To reduce the total number of correlations, we employed one occipital cluster (comprising O1, O2, PO3, and PO4) for the EPN amplitude and one parietal cluster (comprising P3, Pz, P4, CP1, and CP2) for the LPP amplitude.

3. Results

3.1. Fear measures

Scores on the spider questionnaire ranged from 7 to 25, with a mean of 16.29 (SD = 5.90). Scores on the snake questionnaire ranged from 2 to 27, with a mean of 12.17 (SD = 7.37). On the bird questionnaire the scores ranged from 0 to 9, with a mean of 4.00 (SD = 2.30). We found a significant stimulus category effect, $F(2,46) = 32.74, \epsilon = .80, p < .001$. Bonferroni corrected comparisons showed that participants had less fear of birds than of either spiders or snakes (both p -values $< .001$). The difference between fear of spiders and fear of snakes was not significant ($p = .120$).

3.2. Valence and arousal ratings

The mean valence and arousal ratings for spider, snake, and small bird pictures are given in Table 1. There were significant effects for both valence, $F(2,46) = 71.86, \epsilon = .96, p < .001$, and arousal ratings, $F(2,46) = 30.36, \epsilon = .93, p < .001$. Bonferroni corrected comparisons revealed that both spider and snake pictures yielded significantly lower valence and higher arousal ratings when compared to bird pictures (all p values $\leq .001$). Spider pictures yielded significantly lower valence ($p = .022$) and higher arousal ratings than snake pictures ($p = .006$).

3.3. P1

For the P1 amplitude, the main effect of stimulus category was marginally significant, $F(2,46) = 3.15$, $\epsilon = .922$, $p = .057$. This main effect was qualified by a significant interaction of electrode and stimulus category, $F(8,184) = 5.26$, $\epsilon = .398$, $p = .002$. Subsequent single electrode analyses revealed that there was a significant stimulus category effect at Oz ($p < .001$) but not at the other electrodes (all p -values $> .21$). As can be seen in Fig. 2, the P1 amplitude at Oz was significantly smaller for snake pictures than for bird pictures ($p = .001$) and for snake pictures than for spider pictures ($p < .001$). The mean P1 amplitudes for spider versus bird pictures did not differ ($p = .813$).

For the P1 latency, there was a main effect of stimulus category, $F(2,46) = 6.76$, $\epsilon = .784$, $p = .006$, that was qualified by a significant interaction of electrode and stimulus category, $F(8,184) = 3.17$, $\epsilon = .457$, $p = .021$. Single electrode analyses revealed that the stimulus category effect was only found at O1, Oz and O2 (all p -values $\leq .001$). At PO3 and PO4 no stimulus category effect was found (both p -values $> .21$). At O1, Oz, and O2 the P1 latency in response to snake pictures was consistently shorter than in response to bird pictures (all post hoc p -values = $.001$). The P1 latency difference between snake and spider pictures was only significant at Oz ($p = .026$). At Oz the P1 latency was 121 ms for bird pictures, 115 ms for snake pictures and 118 ms for spider pictures.

Table 1. Participants' mean arousal and valence ratings (and standard deviations).

Condition	Valence (SD)	Arousal (SD)
Spider	2.85 (1.10)	3.98 (1.87)
Snake	4.00 (1.97)	2.92 (1.92)
Small bird	6.98 (1.27)	1.25 (0.46)

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

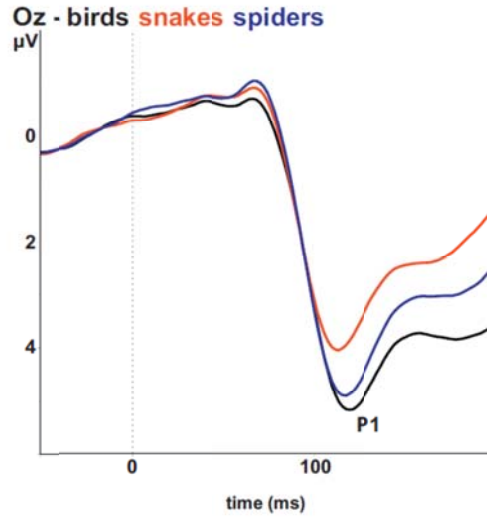


Fig. 2. The P1 peak at Oz for bird (black line), snake (red line), and spider (blue line) pictures. Negativity is up.

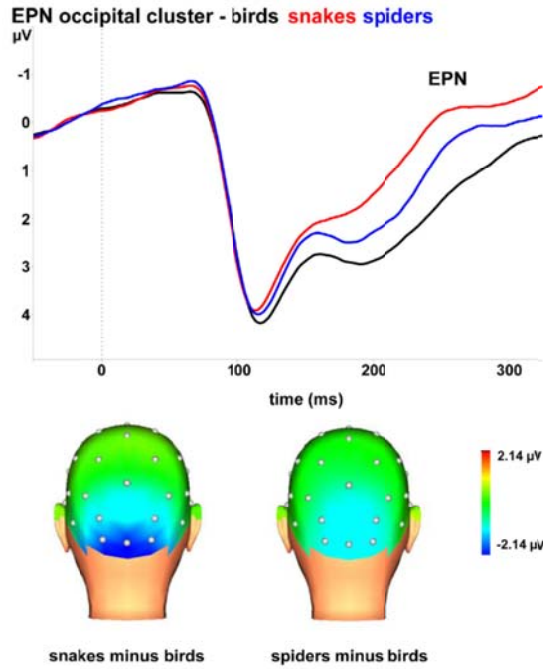


Fig. 3. Top: EPN (225–300 ms) potentials in response to snake (red lines), spider (blue lines), and bird pictures (black lines) at the occipital cluster (O1, O2, PO3, PO4). Negativity is up. Bottom: Topographic map of the difference between EPN amplitudes evoked by snakes vs. birds (left) and spiders vs. birds (right).

3.4. EPN

Because we found a significant stimulus category effect for the P1 amplitude at Oz, we only analyzed the EPN at lateral O1, O2, PO3, and PO4 electrodes (for which no significant P1 effects were found). For the 225–300-ms EPN amplitude measures we found a significant effect of stimulus category, $F(2,46) = 24.71$, $\epsilon = .960$, $p < .001$. As illustrated in Fig. 3, snake pictures elicited a larger EPN than spider pictures ($p = .011$) and bird pictures ($p < .001$), whereas spider pictures elicited a larger EPN than bird pictures ($p = .003$).¹ The ANOVA also revealed a significant electrode \times stimulus category interaction, $F(6,138) = 6.49$, $\epsilon = .591$, $p < .001$. As can be seen in Fig. 3, the effects of stimulus category are most pronounced at occipital electrodes (O1 and O2), while the effects are present to a lesser degree at occipito-parietal electrodes (PO3 and PO4).

3.5. LPP

For the 500–900-ms LPP amplitude measures we found a significant stimulus category effect, $F(2,46) = 8.06$, $\epsilon = .878$, $p = .002$. Fig. 4 shows that both snake ($p = .014$) and spider pictures ($p = .002$) elicited a larger LPP than bird pictures. The difference between spiders and snakes (collapsed across electrodes) was not significant ($p = .728$). In addition, there was a significant interaction of stimulus category and electrode, $F(8,184) = 3.26$, $\epsilon = .623$, $p = .009$. Subsequent single electrode analyses yielded significant stimulus category effects for all electrodes in the parietal cluster (all p -values $< .009$) except for P4 ($p = .082$). In case of significant stimulus category effects at single electrodes, both snake (all p -values $< .029$) and spider pictures (all p -values $< .009$) elicited a larger LPP than bird pictures. No significant LPP amplitude differences between snake and spider pictures were found at single electrodes.

¹ When we subtracted the P1 amplitudes from the EPN area measures to control for potential P1 effects, all pairwise comparisons for the stimulus category effect remained significant (all p -values $\leq .021$).

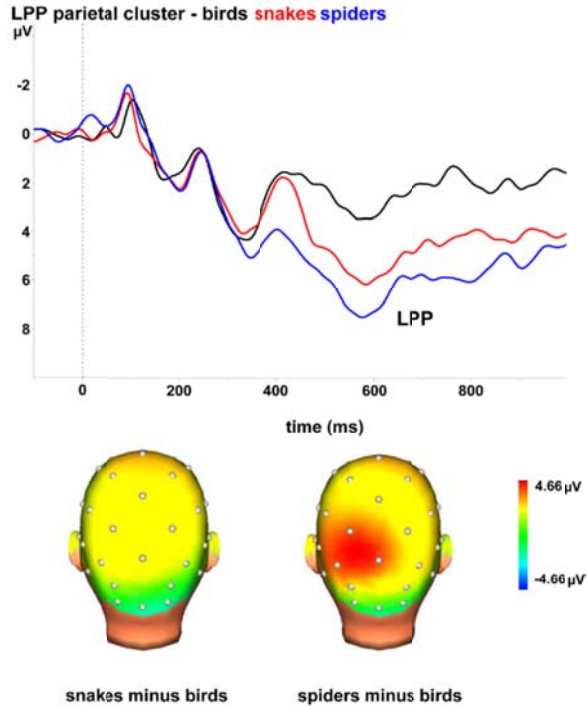


Fig. 4. Top: LPP potentials (500–900 ms) in response to snake (red lines), spider (blue lines), and bird pictures (black lines) at the occipital cluster. Negativity is up. Bottom: Topographic map of the difference between LPP amplitudes evoked by snakes vs. birds (left) and spiders vs. birds (right).

3.6. Correlational analysis

The correlations between the ERP cluster measures and the fear scores to the different stimulus categories are given in Table 2. There was a significant correlation ($r = -.61$) between the EPN cluster amplitude for spider pictures and the fear of spider score. Because the EPN is a negative deflection in the EEG signal, this indicates that participants who reported to have greater fear of spiders, had enhanced EPN activity, compared to participants with less self-reported fear of spiders. For snake and bird pictures, no significant correlations were found between fear scores and EPN amplitudes. For the LPP, no significant correlations were found. From Table 2, it can be seen that there was an insignificant but moderate correlation between fear of spiders and the LPP cluster amplitude ($r = .33$, $p = .121$).

Table 2. Pearson's correlations between fear scores on the spider, snake, and small bird questionnaires, and EPN amplitude (at the lateral occipital cluster) and LPP amplitude (at the parietal cluster) and each corresponding animal category ($n = 24$).

Component	Spider	Snake	Small bird
EPN	-.60*	.26	.18
LPP	.33	.02	.01

* $p = .002$

4. Discussion

In the present research we examined the hypothesis that in non-phobic individuals, more early attention is automatically allocated to snakes than to spiders by means of early (P1 and EPN) and late (LPP) attention-related brain potentials. As results of previous studies have been mixed, we had no specific hypothesis regarding the emotional modulation of the P1. Because snakes may phylogenetically be more fear-relevant than spiders, we expected larger EPN amplitudes in response to snake pictures than in response to spider pictures, and the smallest EPN amplitudes in response to small-bird pictures. We expected larger LPP amplitudes for snake and spider pictures compared bird pictures. Because the effects of attention may be comparable for snakes and spiders at later stages of processing, we expected no or only small differences between LPP amplitudes in response to snake and spider pictures.

At Oz, the P1 amplitudes were smaller but they peaked earlier in response to snake pictures when compared to bird and spider pictures. At lateral occipital electrodes, the P1 amplitude was not modulated by stimulus category. This latter outcome is consistent with previous RSVP studies that found no emotional modulation of the P1 (Junghöfer et al., 2001; Van Strien, Franken, & Huijding, 2009). We had no specific hypothesis regarding the P1, but the emotional modulation of the P1 amplitude at Oz is in line with a previous study, in which we found smaller P1 amplitudes at Oz to unpleasant emotional pictures from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005) than to pleasant ones (Van Strien, Langeslag, et al., 2009). P1 peak latencies at Oz were shortest for snake pictures, which

might support the snake detection hypothesis, as it suggests faster attentional capture of snake stimuli than of spider and bird stimuli. It should be noted however that the latency differences between the stimulus categories were very small. It is possible that the P1 peak amplitude in response to snake pictures was just reached in shorter time because the P1 peak was smaller in response to snake vs. spider pictures. The specificity of the P1 modulation at Oz needs further research.

At lateral occipital electrodes, we found significant differences between EPN amplitudes in response to spider, snake, and bird pictures. Snake and spider pictures elicited a larger EPN compared to bird pictures. This result suggests that humans share a tendency to preferentially direct attention toward potentially threatening animal stimuli, which may reflect natural selective attention that is associated with motivational systems of avoidance and approach (Schupp, Flaisch, et al., 2006). As expected, snake pictures elicited a more enhanced EPN compared to spider pictures, indicating that relatively more fast and automatic attention is directed toward snake pictures than toward spider pictures. This is in support of Isbell's (2006) theory, stating that snakes have had a crucial role in shaping the primate brain, and that, as a result, snakes still automatically draw attention in human beings.

Because in the present study spider pictures were rated as more negatively valenced and more arousing than snakes, the EPN results cannot be explained in terms of conscious valence and arousal ratings of the pictures. This is consistent with the view that this early component reflects unintentional and unconscious processing of emotional cues (Schupp, Flaisch, et al., 2006).

At parietal and centroparietal electrodes, both snake and spider pictures elicited larger LPP amplitudes compared to bird pictures. Although visual inspection of the grand averages (Fig. 4) suggests a larger LPP in response to snake compared to spider pictures, the difference between these two stimulus categories was not significant. The LPP results indicate that snake and spider pictures evoke a comparable level of sustained attention, which is higher for both fear evoking categories than for birds. As suggested by Michalowski et al. (2009) the enlarged LPP amplitudes to the fear-relevant stimuli may be related to the preparation of defensive

action. Snake and spider stimuli rather than small-bird stimuli may potentially evoke such preparation.

Concerning the association between the extent of conscious fear of snakes and spiders, and ERP amplitudes for pictures of these animals, we found that the EPN to spider pictures correlated significantly with the extent of self-reported fear of spiders. This is in accordance with a previous study investigating the emotional modulation of the EPN by spider pictures (Van Strien, Franken, & Huijding, 2009) and suggests that greater fear of spiders is accompanied by enhanced early attentional capture of visual spider stimuli. Spider fearful persons may therefore have attentional mechanisms that are automatically focusing more on phobia-relevant stimuli, which causes them to detect the presence of a spider faster and more habitually, compared to non-fearful persons.

Contrary to expectations, there was no significant correlation between self-reported fear of snakes and EPN amplitudes. Persons with high snake fear are faster to detect snake targets than non-fearful participants (Öhman et al., 2001). This larger early attentional capture should have been reflected in enhanced EPN amplitude for snake pictures. Remarkably, Lipp and Derakshan(2005) employing a dot-probe task, found a relation between self-reported spider fear and bias to spider pictures, but no relation between self-reported snake fear and bias to snake pictures. This failure to find a relationship could not be attributed to low or restricted snake fear scores in their sample. In the present sample, snake and spider fear scores also exhibited comparable means and ranges, so the lack of association between snake fear and EPN amplitude is not due to reduced or restricted fear scores. A possible explanation for the lack of association in the present research may be that snake fear is less reliably reported by our participants than spider fear. In Northwestern Europe, people will normally never be confronted with real-life snakes running wild, so their self-reported fear is probably based on an imaginary encounter with a snake. This explanation is not inconsistent with the notion of the innate and automatic nature of snake processing.

Also in contrast to expectations, fear scores were not associated with LPP amplitudes, although we found a moderate but nonsignificant correlation between fear of spiders and LPP amplitude in response to spider pictures. It may be that other factors such as disgust sensitivity

also influence the ERP amplitudes. The (non)association between self-reported animal fear and disgust on the one hand, and EPN and LPP components on the other hand, awaits further research.

We did not expect to find correlations between the bird questionnaire scores and ERP amplitudes, because non-emotional stimuli will hardly capture automatic attention. The absence of correlations between bird fear and EPN amplitudes most probably is a result of participants not having any fear of these birds.

In the present research, the EPN task always preceded the LPP task. We chose this fixed order because our key hypothesis concerned the EPN, and we wanted to submit our participants to the EPN task in an uncontaminated fashion. Theoretically, there may have been carry-over effects from the EPN task to the LPP task, but it is not likely that habituation effects have been the reason for the lack of significant LPP amplitude differences between snakes and spiders. Like the EPN, the LPP appears to be insensitive to habituation, as in the study of Codispotti, Ferrari, and Bradley (2006) the affective modulation of the LPP remained intact across many stimulus repetitions. It should also be noted that in the present LPP task the LPP amplitudes to both snake and spider pictures remained larger relative to bird pictures.

Other factors than predatory pressure, such as formal pictorial properties may have influenced the ERP results. Whereas task differences and differences in low-level visual features between stimuli may interact with the emotional modulation of the P1, the emotional modulation of the EPN appears to be more robust (Hajcak et al., 2012). Junghöfer et al. (2001) found that with an RSVP procedure the emotional modulation of the EPN was independent of spatial frequency and complexity. Employing a non-speeded presentation of IAPS pictures, Bradley and colleagues (Bradley, Hamby, Löw, & Lang, 2007) found that picture complexity (i.e., simple figure-ground compositions versus complex scenes) affected early posterior ERPs, with less occipital negativity in the 150–250 ms time window for complex scenes. Their data further suggested that the LPP reflects picture emotionality rather than complexity. In the present research, we used picture categories with comparable (low) complexity. The pictures in each category showed a single specimen in the foreground, which will give less variation in complexity than for instance IAPS pictures. In addition, the emotional modulation of the EPN

and LPP is larger for simple than for complex compositions (Nordström & Wiens, 2012). Given the relatively simple figure-ground compositions of the three stimulus categories, it seems unlikely that picture complexity has confounded the present ERP effects. However, other factors, such as familiarity with the species, may have influenced the (late) ERP results.

Compared to men, women generally report more fear of snakes and spiders and it is conceivable that women are more prone to phobias for these evolutionarily fear-relevant stimuli because of the potential survival cost to their child (Rakison, 2009). Given that the present sample contained only females, it remains to be investigated whether men will show the same EPN and LPP effects to snake and spider pictures.

The current study directly compared ERPs in response to snake and spider pictures in non-phobic women. The present findings show that more early visual attention is allocated to snakes and spiders than to birds and that this automatic allocation of early visual attention is stronger for snakes than for spiders. This outcome fits well with Isbell's (2006) theory, which states that the neural circuitry for defense behavior was initially designed to deal with snakes. The differential modulation of the EPN by snakes and spiders is also compatible with the proposal of Soares et al. (2009) that snake detection is more dependent on bottom-up processes whereas spider detection is more dependent on top-down processes. The LPP amplitudes indicate that sustained visual attention is larger for phylogenetic fear stimuli, such as snakes and spiders, than for neutral stimuli. While snakes draw more early attention than spiders, the sustained attention is similar for both categories. Interestingly, spider fear was associated with the EPN amplitudes for spider pictures, whereas snake fear was not associated with the EPN amplitudes for snake pictures. The results suggest that ancestral priorities modulate the early capture of visual attention and that early attention to snakes is more innate and independent of reported fear.

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