

Curvilinear shapes and the snake detection hypothesis: An ERP study

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Abstract

Consistent with the snake detection hypothesis, previous ERP studies have established a larger early posterior negativity (EPN) in response to pictures depicting snakes than to pictures depicting other creatures. Here, we examined to what extent the curvilinear shape of the snake's body drives the larger EPN. To this end, we employed pictures of threatening and nonthreatening species with or without typical curvature. Participants watched a random rapid serial visual presentation of snake, worm, spider, and beetle pictures. The EPN was scored as the mean activity (225–300 ms after picture onset) at occipital and parieto-occipital electrodes. Across electrodes, the EPN was significantly larger for snake pictures than for spider, worm, and beetle pictures, and for spider and worm pictures than for beetle pictures. The results suggest that curvilinear body shapes may partly drive the enhanced EPN. However, the unique cortical response to snakes is not fully explained by this mechanism, and is most probably also determined by other threat-relevant cues.

Descriptors: Early posterior negativity (EPN), Snake fear, Spider fear, Evolution, Snake detection hypothesis

Snakes appear to draw more automatic visual attention than any other living creature. According to the snake detection hypothesis (Isbell, 2006, 2009), snakes have a long evolutionary coexistence with primates and their predecessors and may have been their first predators. This predatory pressure on primate evolution caused evolutionary changes in the primate visual system allowing rapid visual detection of these well-camouflaged animals. There is ample evidence that in humans the visual detection of snakes is faster than of other, less life-threatening stimuli (Öhman, Flykt, & Esteves, 2001; Öhman & Mineka, 2001). From an evolutionary perspective, a fear module that is activated automatically by stimuli posing deadly threat and that is largely independent of conscious cognition would be highly adaptive. The amygdala may be the key structure that is dedicated to this fear module (Mineka & Öhman, 2002).

Recently, several studies have provided direct electrophysiological evidence for the snake-detection hypothesis in primates and humans (He, Kubo, & Kawai, 2014; Van Le et al., 2013; Van Strien, Eijlers, Franken, & Huijding, 2014; Van Strien, Franken, & Huijding, 2014). Van Le and colleagues (2013) measured neuronal responses in the medial and dorsolateral pulvinar of macaque monkeys that were kept in the laboratory and had no chance to encounter snakes before the experiment. Their study demonstrated the

existence of pulvinar neurons that responded selectively faster and stronger to snakes stimuli than to angry and neutral monkey faces, monkey hands, or geometric shapes. As the authors noted, the pulvinar is part of a fast visual information processing pathway from the retina and superior colliculus to the amygdala, allowing the rapid automatic visual detection of fear-related stimuli (Morris, Ohman, & Dolan, 1999; Tamietto & de Gelder, 2010).

In two previous studies, we examined the snake detection hypothesis in humans using ERPs. In the first study (Van Strien, Eijlers et al., 2014), participants watched the random rapid serial visual presentation (RSVP; see Junghöfer, Bradley, Elbert, & Lang, 2001) of 600 snake pictures, 600 spider pictures, and 600 bird pictures at a rate of three pictures per second. An ERP component peaking around 225–300 ms after stimulus onset, the so-called early posterior negativity (EPN), was measured at lateral occipital sites. The EPN amplitude was largest for snake pictures, intermediate for spider pictures, and smallest for bird pictures. The EPN reflects the early selective visual processing of emotionally significant information, a process that is not altered by habituation (Schupp, Flaisch, Stockburger, & Junghöfer, 2006). It is associated with the functioning of the basic motivational systems of approach and avoidance and is augmented particularly by stimuli of evolutionary significance (Schupp, Junghöfer, Weike, & Hamm, 2003).

In the second ERP study with the RSVP paradigm (Van Strien, Franken, & Huijding, 2014), we examined (a) whether the preferential activity in early visual processes is specific to snakes or is a categorical reptile effect, and (b) whether disgusting animals such as slugs enhance early visual processing as well. We found that the

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Figure 1. Illustrative examples of the snake, worm, spider, and beetle stimuli used in the present research. For copyright reasons, the depicted photographs are public domain (pixabay.com); they are similar to the actual stimuli, but were not used in the experiment.

EPN was significantly larger to snake pictures than to pictures of other reptiles and pictures of slugs. There was no association between EPN amplitudes and reported fear and disgust for the different species.

Furthermore, a RSVP study with a Japanese sample demonstrated larger EPN amplitudes to brightness-equated grayscale pictures of snakes compared to spiders (He et al., 2014). Taken together, the results of the above studies suggest that ancestral priorities modulate the early capture of visual attention, and that this attention appears to be innate for snake stimuli and independent of consciously reported fear.

Here, we address the question of the extent to which the typical curvilinear body shape of snake stimuli causes the enlarged EPN. This specific visual feature may have been absent in the other animal images that we have employed until now, and might drive the rapid detection of snakes in particular. LoBue (2014) examined whether such a simple low-level cue is sufficient in producing fast detection in the absence of threat. In a series of visual search tasks, LoBue demonstrated that simple curvilinear lines are detected more rapidly than rectilinear lines. According to LoBue, this low-level perceptual bias may have developed specifically for the detection of snakes and still draw attention to shapes that are snakelike. Although LoBue argues that curvilinear features are also relevant to spider detection because the spider's legs may be made up of curved configurations, the curvilinear shape of a snake's body is clearly different from the body shape of spiders. That is, spiders may show some curvature at a local feature level, but not at a global, whole body level. In the present study, we therefore employed pictures of spiders as fearful, but noncurvilinear stimuli. In addition, we employed pictures of worms as curvilinear, non-fearful stimuli and pictures of beetles as noncurvilinear, nonfearful

stimuli. To maintain ecological validity, we used photographs of real snakes, spiders, worms, and beetles (see Figure 1). Note that in this article we use the term curvilinear body shape to designate the elongated, limbless, and winding bodies of snakes and worms.

Noteworthy, LoBue (2014) found that the latencies to detect curvilinear targets dropped further when fear was experimentally induced in participants by a fearful video clip. This suggests that rapid threat detection is not only driven by low-level cues, but results from several interacting perceptual and emotional factors.

Given the fast attentional capture of snake pictures and the large EPN in response to snake pictures, it is interesting to learn to what extent the EPN in response to snake pictures is driven by the curvilinear body shape of snakes. To examine the influence of curvilinear animate body shapes on the EPN, we employed the RSVP of pictures of threatening and nonthreatening species with or without typical body curvature (i.e., snakes, worms, spiders, and beetles). In addition, participants filled out fear and disgust questionnaires for these species, and rated the valence and arousal of the individual pictures. Based on our earlier research, we expected the largest (most negative) EPN amplitudes in response to snake pictures, intermediate EPN amplitudes in response to spider pictures, and the smallest EPN amplitudes to beetles. If curvilinear body shapes enhance the EPN also in nonthreatening species, the EPN amplitudes in response to worms should be larger (more negative) than in response to beetles. If the larger EPN to snakes is only driven by curvilinear body shape, the EPN amplitude in response to worms should be comparable to the EPN amplitude in response to snakes. If other visual features or contextual factors also drive the larger EPN in response to snakes, the EPN amplitude will be smaller in response to worms than in response to snakes.

Method

Participants

Participants were 24 university students (11 men, 13 women) with normal or corrected-to-normal vision. One man and one woman were left-handed, the others were right-handed by self-report. Ages ranged from 18 to 29 years, with a mean age of 20.71 years. They participated for course credits. The study was approved by the departmental ethics committee. All participants provided informed consent.

Questionnaires and Task

Prior to the experimental run, participants rated their fear of snakes, worms, spiders, and beetles on a 15-item questionnaire for each category, with possible scores ranging from 0 (*no fear*) to 45 (*very high fear*). They also rated their disgust for each category on an eight-item questionnaire with possible scores ranging from 0 (*no disgust*) to 48 (*very high disgust*; for details, see Van Strien, Franken et al., 2014).

Participants were seated in a dimly lit room and were told to attentively watch the continuous RSVP of 450 snake pictures, 450 worm pictures, 450 spider pictures, and 450 beetle pictures. For each stimulus category, there were 10 different pictures that were shown 45 times. Pictures were obtained from various Internet sites. Each picture showed a complete specimen against a natural background (see Figure 1). The pictures were shown at a distance of 120 cm on a 20" PC monitor with a resolution of $1,024 \times 768$ pixels. Pictures had a size of 600×450 pixels, and were displayed against a medium gray background. The presentation rate was three pictures per second, with no blank between pictures. The pictures were presented randomly within each cycle of 40 unique pictures (45 cycles), hence transition probabilities among stimulus categories were comparable (see Flaisch, Junghöfer, Bradley, Schupp, & Lang, 2008) and repetitions of the same category were allowed. Identical to the paradigm employed in our previous studies, the 1,800 pictures were presented in a single block without rest.

Following the experimental run, participants completed a computerized Self-Assessment Manikin (SAM) questionnaire (Bradley & Lang, 1994) regarding valence and arousal ratings of all pictures on a 9-point scale.

EEG Recording and Data Analysis

EEG activity was recorded using a BioSemi Active-Two system from 32 pin-type active Ag/AgCl electrodes mounted in an elastic cap. Electrooculogram (EOG) activity was recorded from active electrodes placed above and beneath the left eye, and from electrodes at the outer canthus of each eye. An additional active electrode (common mode sense) and a passive electrode (driven right leg) were used to comprise a feedback loop for amplifier reference. The EEG and EOG signals were digitized with a 512-Hz sampling rate, a low-pass filter of 134 Hz, and 24-bit A/D conversion.

Offline, the EEG signals were referenced to an average reference and phase-shift-free filtered with a band-pass of 0.10–30 Hz (24 dB/oct). Correction for horizontal and vertical eye movements was done using the Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983). ERP epochs were extracted with a 380-ms duration and beginning 50 ms before stimulus onset. The ERP signals were defined relative to the mean of this 50-ms prestimulus baseline period. Average ERPs were computed for each participant and each condition (snake, worm, spider, beetle). Epochs with a

Table 1. Participants' Mean Fear, Disgust, Valence, and Arousal Ratings

Stimulus category	Fear (SD)	Disgust (SD)	Valence (SD)	Arousal (SD)
Snake	9.75 (7.20)	20.21 (9.94)	4.80 (2.09)	4.14 (1.91)
Worm	10.71 (5.25)	30.83 (8.33)	3.20 (1.73)	3.17 (1.62)
Spider	14.33 (12.23)	23.83 (10.61)	2.83 (1.64)	5.38 (2.23)
Beetle	8.79 (5.91)	23.13 (8.44)	3.75 (1.82)	3.40 (1.80)

Note. Fear scores can range from 0–45, and disgust scores from 0–48. Valence and arousal ratings are based on a rating scale from 1 to 9.

baseline-to-peak amplitude difference larger than 100 mV on any channel were omitted from averaging.

Statistical Analyses

For the fear, disgust, valence, and arousal ratings, repeated measures analyses of variance (ANOVAs) were employed with stimulus category (snake, worm, spider, beetle) as a factor. For the EPN component, a repeated measures ANOVA was conducted, with stimulus category (snake, worm, spider, beetle) and electrode (O1, Oz, O2, PO3, PO4) as factors. At the electrodes included in the analysis, the EPN is typically modulated by stimuli of evolutionary significance, with the effect being larger at occipital than at parieto-occipital sites (Van Strien, Franken, & Huijding, 2014). When appropriate, Greenhouse-Geisser correction was applied. To explore the relationship between reported fear and disgust on the one hand, and the EPN amplitude on the other, we calculated the correlations between questionnaire scores and EPN amplitudes for snakes, worms, spiders, beetles, respectively. To reduce the total number of correlations, we employed one occipital cluster (comprising O1, O2, Oz, PO3, and PO4) for the EPN amplitude measure.

Results

Ratings

The mean fear, disgust, valence, and arousal ratings for snake, worm, spider, and beetle pictures are given in Table 1. For the fear ratings, the stimulus category effect was significant, $F(3,69) = 3.92$, $\epsilon = .571$, $p = .034$. Bonferroni-corrected pairwise comparisons only yielded a borderline significant difference between spider and beetle scores ($p = .068$). For the disgust ratings, the stimulus category effect was also significant, $F(3,69) = 9.86$, $\epsilon = .902$, $p < .001$. Bonferroni-corrected comparisons showed that worms were rated as more disgusting than spiders, beetles, and snakes (all p values $\leq .018$). Further, the stimulus category effects were significant for both valence, $F(3,69) = 12.17$, $\epsilon = .777$, $p < .001$, and arousal, $F(3,69) = 14.60$, $\epsilon = .844$, $p < .001$. Bonferroni comparisons revealed that worm, spider, and beetle pictures were rated as more unpleasant than snake pictures (all p values $\leq .010$). Spider pictures were more arousing than snake, worm, and beetle pictures (all p values $< .023$).

EPN

Figure 2A shows the grand-averaged EPN potentials at the occipital cluster (O1, Oz, O2, PO3, PO4) for snake, worm, spider, and beetle pictures. Snake pictures yielded the most negative-going wave form, compared to the other picture categories. The ANOVA revealed a significant stimulus category effect, $F(3,69) = 70.62$,

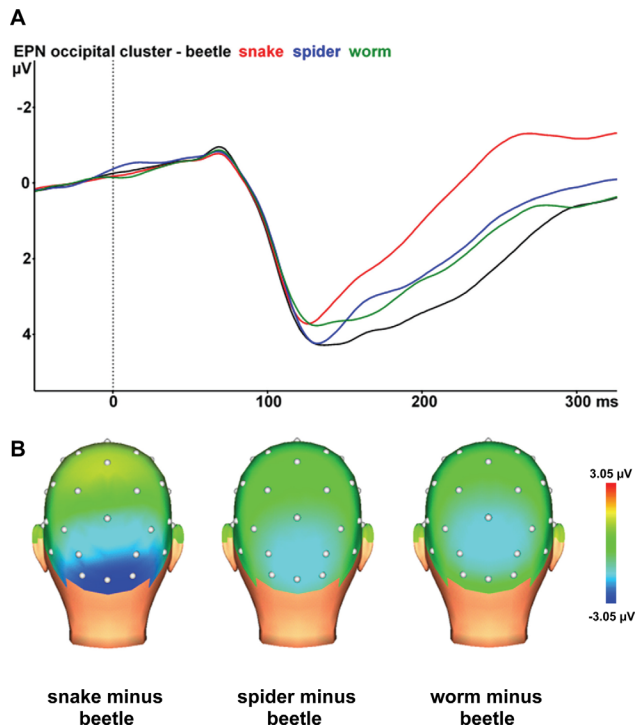


Figure 2. A: The early posterior negativity (EPN) in response to snake (red line), spider (blue line), worm (green line), and beetle pictures (black line) at the occipital cluster (O1/2, Oz, PO3/4). B: Topographic maps of the differences in EPN mean amplitudes (225–300 ms) between snake versus beetle pictures (left), spider versus beetle pictures (middle), and worm versus beetle pictures (right).

$\epsilon = .813$, $p < .001$. Bonferroni-corrected pairwise comparisons revealed that the EPN was significantly more negative for snake pictures than for the other categories (all p values $< .001$). Worm and spider pictures evoked a more negative EPN than beetle pictures (both p values $\leq .006$). For worm and spider pictures, no significant difference in EPN amplitude emerged ($p = .877$).

The interaction of stimulus category and electrode was also significant, $F(12,276) = 6.96$, $\epsilon = .389$, $p < .001$. As can be seen from Figure 2B, the stimulus category effects are most pronounced for the snake versus beetle contrast at the occipital electrodes (O1, Oz, and O2). Subsequent single-electrode analyses revealed significant stimulus category effects at all electrodes (all p values $< .001$). Bonferroni-corrected pairwise comparisons revealed that snake pictures elicited larger EPN amplitudes than worm, spider, and beetle pictures at all electrodes (all p values $\leq .020$). Spider pictures elicited larger EPN amplitudes than beetle pictures at all electrodes (all p values $\leq .003$) and worm pictures at Oz ($p = .030$). Worm pictures elicited larger EPN amplitudes than beetle pictures at PO3, PO4 (both p values $< .001$), and O1 ($p = .036$).

Correlation Analyses

There were no significant correlations between the EPN cluster amplitude measures and the fear and disgust ratings for snakes, worms, spiders, and beetles.

Discussion

In the present research, we examined the influence of curvilinear animal shapes on the EPN amplitude, as snakes typically elicit

larger, more negative amplitudes than other animate categories. We employed a RSVP of snake, worm, spider, and beetle pictures, and recorded the EPN in response to these four categories. These four categories represent phylogenetically threatening and non-threatening species with or without typical body curvature.

As expected, snake and spider pictures elicited enhanced EPN amplitudes compared to beetle pictures, and snake pictures elicited a larger EPN amplitude compared to spiders. This clearly replicates the results of our previous EPN research with snake and spider pictures (Van Strien, Eijlers et al., 2014; Van Strien, Franken, & Huijding, 2014). These differential EPN amplitudes at occipital and parieto-occipital sites suggest that human attention is preferentially directed toward phylogenetically threatening animate objects, with snakes capturing more automatic attention than spiders, and spiders capturing more automatic attention than beetles.

Across occipital and parieto-occipital electrodes, worm pictures elicited larger EPN pictures than beetle pictures but smaller EPN amplitudes than snake pictures. The curvy shape of worms may have driven the larger EPN amplitude for worms compared to the equally innocuous beetles. The midway EPN amplitude for worms between beetles and snakes suggests that superior threat detection of snake stimuli is not only driven by the curvature of snakes, but most probably also by other threat-relevant physical and contextual cues.

Body curvature appears to enhance the EPN in response to animate objects. Larger EPN amplitudes are thought to indicate increased source activity in the visual cortex (Schupp et al., 2003) as a result of activating projections from the amygdala to the visual areas (Dolan, 2002; Tamietto & de Gelder, 2010). Simple geometric forms such as a down-pointing V can indicate threat and activate the amygdala (e.g., Larson, Aronoff, Sarinopoulos, & Zhu, 2009). It is not clear to what extent simple curvilinear shapes yield amygdala activation. Curvature as such appears to be a basic feature of rapid visual detection (Wolfe, Yee, & Friedman-Hill, 1992), so the attentional capture may be not amygdala based but sheer object based (see Pourtois, Schettino, & Vuilleumier, 2013). Nevertheless, the visual advantage of curvilinear shapes may have had survival value in human evolution, especially for snake detection (Isbell, 2006). The amygdala-related fear module may interact with other attention networks to extract relevant fear (or other emotion) cues that activate the visual cortex by amygdalocortical projections. Such an amygdala-based gain control on visual processing could be reflected by the EPN in the 200–300 ms time window and might explain why the EPN is not only modulated by low level visual features such as curvature, but also by symbolic stimuli with acquired emotional significance such as emotional words (Kissler, Herbert, Peyk, & Junghofer, 2007) or gestures (Flaisch, Hacker, Renner, & Schupp, 2011).

It can be argued that generic physical characteristics other than the curvilinear body shape may have driven the larger EPN for snakes, in particular, factors such as animal size, within-species variation, and differences in background. Regarding size, snakes are larger than spiders, beetles, and worms. Therefore, the larger EPN for snakes could reflect a general fear of larger animals. In a previous study, however, we compared pictures of snakes to pictures of crocodiles and found a much larger EPN in response to snakes than in response to crocodiles (Van Strien, Franken, & Huijding, 2014). In view of this result, it is not very likely that the larger EPN for snakes simply reflects a fear of larger animals. Also, our snake stimuli may have been more varied than the stimuli in the other three categories, which may have been more similar within each category. The larger EPN for snakes could thus reflect a kind of novelty effect due to the larger variation in snake pictures

compared to the variation in, for instance, worm pictures. However, such a novelty account can be ruled out as we have found that snake pictures again elicited a much larger EPN when compared to pictures of small birds (Van Strien, Eijlers et al., 2014). These bird pictures did differ within their category at least as much as did snake pictures. Finally, the background for snake pictures may have been different from the backgrounds in the other picture categories. In the present research, the backgrounds in the snake, beetle, and worm pictures were more or less comparable and existed mainly of sand, rocks, leaves, or grass, as did the backgrounds of other reptiles in our previous research (Van Strien, Franken, & Huijding, 2014). The backgrounds of spiders were less sharp, as were the backgrounds of bird pictures in previous research. In the RSVP study of He et al. (2014), brightness-equated grayscale pictures were used, which must have reduced the possible influences of factors such as background and within-category variation (e.g., in color). Consistent with our research, these authors also obtained larger EPN amplitudes in response to snake pictures when compared to spider pictures. In summary, we have found definitely larger EPN amplitudes in response to snake pictures compared to pictures in a large range of other species. These categories did or did not differ in animal size, species variation, and backgrounds, leaving these factors as primary cause for the larger EPN in response to snake pictures implausible.

We measured the EPN at occipital (O1, Oz, O2) and parieto-occipital (PO3, PO4) electrodes and found a significant interaction of stimulus category and electrode. The pattern of larger EPN amplitudes for snake compared to spider and beetle pictures and larger EPN amplitudes for spider compared to beetle pictures was consistent across all electrodes. Larger EPN amplitudes for worm compared to beetle pictures were predominantly found at the parieto-occipital electrodes. This suggests that the supposed modulation of the EPN by curvilinear shapes involves a higher level of visual processing. As the largest EPN snake effects were found at occipital electrodes, another probably more basic low-level visual feature specific to snakes may also have influenced the EPN. Recently, it has been proposed that many poisonous animals possess a characteristic spectral composition, with more high-contrast energy at midrange spatial frequencies (Cole & Wilkins, 2013; Le, Cole, & Wilkins, 2015). It could be that snakes exhibit such a spectral composition. Preliminary results from our laboratory demonstrate that pictures of animals and objects with high-contrast energy at midrange spatial frequencies selectively elicit enhanced EPN amplitudes at occipital, but not at parieto-occipital sites (Van Strien & Van der Peijl, 2015).

Snakes were rated as less unpleasant than the other categories, and spiders were rated as more arousing than the other categories.

These valence and arousal ratings are comparable with the ratings in our previous studies. In our first study (Van Strien, Eijlers et al., 2014), we found the highest (most pleasant) valence scores for small birds, yet this category elicited the smallest EPN amplitudes. Therefore, in our series of experiments with animal stimuli, participants' conscious arousal and valence measures appear not to be related to the EPN.

Self-reported fear of spiders was somewhat higher than fear of the other categories, but this difference was not significant. In our previous studies, fear was also nonsignificantly higher for spiders compared to the other categories. Worms were rated as more disgusting than snakes, spiders, and beetles. In a previous study (Van Strien, Franken, & Huijding, 2014), slugs were also rated as more disgusting than snakes and spiders. In that study, the EPN was lowest for slugs. Thus, in the present study, it seems unlikely that the EPN amplitude that we found for worms was enhanced by disgust. In addition, the correlation analyses did not yield significant correlations between the fear and disgust ratings for the various species and the EPN cluster amplitude measures. This lack of a correlation is in accordance with previous research (Van Strien, Franken, & Huijding, 2014). Consciously reported fear, disgust, valence, and arousal ratings do not seem to be systematically associated with the EPN amplitude, which supports the view that the EPN reflects the automatic first-stage processing of emotional cues (e.g., Schupp et al., 2006).

In our research on the modulation of the EPN by evolutionarily-significant stimuli, we use realistic photographs of snakes, spiders, and other animals to maintain ecological validity. After all, the brain mechanisms for rapid threat detection evolved in a complex natural setting. An inherent limitation of the use of natural stimuli is that visual features are less well controlled. As discussed above, it is unlikely that in our series of experiments generic factors such as animal size, within-species variation, and background differences have driven the larger EPN in response to snake stimuli compared to other animal stimuli. Nevertheless, to find out very specific factors that drive the EPN in response to phylogenetic threat, it is worthwhile to also conduct experiments with more controlled stimuli, for instance, by means of grayscale pictures with blank backgrounds, or by means of very simple shapes such as employed by LoBue (2014).

To conclude, employing random RSVP of snake, spider, worm, and beetle pictures, we found the largest EPN in response to snake pictures. Worm pictures elicited larger EPN than beetle pictures, suggesting that curvilinear shapes may partly drive the enhanced EPN. The boosted EPN response to snake pictures, which fits in with Isbell's (2006, 2009) snake detection hypothesis, most probably is also determined by other threat-relevant cues than the snake's typical curvilinear body shape.

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