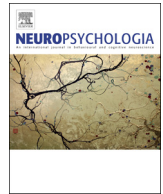




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Pattern matters: Snakes exhibiting triangular and diamond-shaped skin patterns modulate electrophysiological activity in human visual cortex



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ABSTRACT

The neural and perceptual mechanisms that support the efficient visual detection of snakes in humans are still not fully understood. According to the Snake Detection Theory, selection pressures posed by snakes on early primates have shaped the development of the visual system. Previous studies in humans have investigated early visual electrophysiological activity in response to snake images vs. various alternative dangerous or non-dangerous stimuli. These studies have shown that the Early Posterior Negativity (EPN) component is selectively elicited by snake or snake-like images. Recent findings yielded the complementary/alternative hypothesis that early humans (and possibly other primates) evolved an aversion especially for potentially harmful triangular shapes, such as teeth, claws or spikes. In the present study we investigated the effect of triangular and diamond-shaped patterns in snake skins on the ERP correlates of visual processing in humans. In the first experiment, we employed pictures of snakes displaying either triangular/diamond-shaped patterns or no particular pattern on their skins, and pictures of frogs as control. Participants observed a random visual presentation of these pictures. Consistent with previous studies, snakes elicited an enhanced negativity between 225 and 300 ms (EPN) compared to frogs. However, snakes featuring triangular/diamond-shaped patterns on their skin produced an enhanced EPN compared to the snakes that did not display such patterns. In a second experiment we used pictures displaying only skin patterns of snakes and frogs. Results from the second experiment confirmed the results of the first experiment, suggesting that triangular snake-skin patterns modulate the activity in human visual cortex. Taken together, our results constitute an important contribution to the snake detection theory.

1. Introduction

Fear and phobias related to snakes are very common in humans (Agras et al., 1969; Fredrikson et al., 1996; King, 1997; Öhman and Mineka, 2003; Sagan, 1977). Primates, including humans, have been shown to be able to rapidly detect snakes (Öhman et al., 2001; Shibasaki and Kawai, 2009) against a natural background. According to the “Snake Detection Theory” (Isbell, 2009; 2009), selection pressures posed by snakes on early primates are responsible for the modification and expansion of the visual system, where natural selection favored those individuals that were better able to detect and avoid snakes.

Some researchers have presented the idea that constrictor snakes have propagated the evolution of a visual Snake Detection Module (Isbell, 2009; 2009). The idea, however, is subject to debate as larger primates, such as early humans, were probably not the regular prey for

even the largest pythons, although constrictor snakes may have occasionally targeted human infants and small children as prey. A putative ancestral Snake Detection Module may have been lost (i.e. no longer useful) or may have been refined subsequently. In support for the latter idea, venomous snakes, such as vipers, were likely as abundant as today in Africa (Cadle, 1988) when hominids and other primates were in their early stages of evolution. Efficient detection and avoidance of these venomous snakes may be challenging, but may drastically enhance survival.

Ambush predators, such as vipers, blend within their environment, and have evolved cryptic and disruptive coloration to be invisible to their prey, for example, triangular-like patterns on their skins. It has also been suggested that those triangular patterns may be aposematic signs that protect the snakes, for example, from avian predators (Niskanen and Mappes, 2005; Valkonen et al., 2011a, 2011b).

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However, whether cryptic or aposematic, both prey and potential predators may have developed an attentional bias towards those characteristics that help to detect snakes more efficiently.

In today's Africa, approximately 60% of all snake bites are caused by members of the *Viperidae* family. In the drier regions of the African continent, the saw-scaled vipers (also known as *Echis* or carpet vipers) are responsible for up to 90% of all snake bites (Mackessy, 2010), while the puff adder (*Bitis arietans*) is responsible for most of the human deaths over the continent (Mallow et al., 2003). All these venomous snakes dangerous to humans show clear triangular or diamond-shaped patterns on their bodies, and therefore the snake's body pattern represents a rather reliable index of their hazard. From an evolutionary perspective, it is reasonable to assume that the ancestral relatives of these current species would have looked similar during primate (and human) evolution in Africa. Our primate ancestors would thus have benefited from recognizing and avoiding dangerous snakes based on their skin patterns, and this ability may have been passed on to future generations.

Animal studies have found many lines of evidence supporting the theory regarding a specific visual sensitivity to snakes. A study on macaques (*Macaca fuscata*) (Van Le et al., 2013a, 2013b) revealed a class of neurons (pulvinar neurons) that responded selectively faster and more strongly to pictures of snakes. Pulvinar neurons are part of a neural pathway that quickly processes visual information from the retina via the superior colliculus, allowing for rapid visual detection of fear-related stimuli (Morris et al., 1999; Tamietto and de Gelder, 2010).

Behavioral studies on the sensitivity of primate vision to snakes are consistent with the aforementioned studies. Captive rhesus macaques (*Macaca mulatta*) showed enhanced responses to snake stimuli even when the stimuli were only partially visible (Etting and Isbell, 2014). In natural settings, snakes are difficult to perceive as their skin patterns (either disruptive coloration, crypsis or a combination of both, see Cuthill et al., 2005) allow them to blend within the surrounding vegetation and other natural features (soil, rocks, etc.). Therefore, it is plausible that it would be advantageous for potential prey to be able to detect the presence of snakes by detecting a small visible section of their body only. Although snakes show characteristic and well-recognizable physical features, such as a long curvilinear body, the absence of legs, and slithering movements, these characteristics may not be a completely reliable visual cue, especially in the presence of disruptive coloration patterns (Cuthill et al., 2005). However, smaller but relevant threat cues, such as snake skin patterns (for example, scalation), may represent more reliable indicators of the presence of these potentially dangerous reptiles. In a recent study, wild vervet monkeys (*Chlorocebus pygerythrus*) were able to detect very small snake cues in a visual task (as small as 2.5 cm of snake skin; see Isbell and Etting, 2017). The experiment proved that snake scales alone (in absence of curvilinear shapes as well as other snake-like features) were sufficient for the detection of the threat. Snake skin features thus seem to have a role in snake perception. Further, another study found that white-faced capuchin monkeys (*Cebus capucinus*) were more efficient at detecting snake models presenting scales on their body than detecting the same models without scales (Meno et al., 2013).

It is also worth noting that some non-venomous snakes may have evolved physical coloration and characteristics comparable to venomous species, in order to be perceived as dangerous by possible predators, and therefore to be avoided as prey. This phenomenon is called Batesian mimicry (see e.g. Greene and McDiarmid, 1981; Owings et al., 2002; Aubret, F. & Mangin, 2014). In Batesian mimicry, venomous species with aposematic signals (e.g., triangular patterns, intense colors, sounds, etc.) are used as a model for imitation by many of non-dangerous animal species (such as insects, snakes, cephalopods, birds, etc.). Consequently, the color patterns of the scales may not be a completely reliable identification index of the venomousness of a snake.

Furthermore, some studies (Grassini et al., 2018; Van Strien, Christiaans, Franken and Huijding, 2016) have shown that curvilinear

shapes do in fact attract human attention. It is probably the case that multiple physical characteristics of snakes (including their curvilinear shape and their skin patterns) drive the enhanced detection for snake stimuli, rather than a single characteristic.

Recent EEG studies have tested the Snake Detection Theory in humans (He et al., 2014; Grassini et al., 2016; Grassini et al., 2018; Van Strien, Eijlersm, Franken and Huijding, 2014; Van Strien, Franken and Huijding, 2014; Van Strien, Christiaans, Franken and Huijding, 2016; Van Strien and Isbell, 2017; Langeslag and Van Strien, 2018). All these studies have found that snake images are selectively responsible for the modulation of an ERP component, the Early Posterior Negativity (EPN), peaking around 200 ms after stimulus onset.

The EPN is shown as a relative negativity detected from electroencephalography over the occipital scalp. The EPN is determined as the difference between the electrophysiological activity in response to experimental and control condition (Schupp et al., 2006). The EPN reflects visual processing of emotionally significant visual stimuli (Luck and Kappenman, 2011; Olofsson et al., 2008), and is not sensitive to habituation to the stimuli (Schupp et al., 2006). The EPN represents selection of visual stimuli for further processing and it is associated with the basic motivational systems of approach and avoidance (Schupp et al., 2004). Specifically, the EPN has been reported in studies investigating the electrophysiology of emotional stimuli with an evolutionary significance, such as erotic or violent pictures (Schupp et al., 2003).

An EPN has been observed for pictures of snakes vs. pictures of other animals such as birds, non-threatening reptiles such as turtles, other curvilinear animals such as worms, other disgust-eliciting animals such as slugs, other threatening reptiles such as crocodiles, and even with other fear-evoking animals such as spiders (Van Strien et al., 2014b, 2016; Van Strien et al., 2014a). An EPN has also been observed for faces with emotional vs. neutral expressions (e.g., Holmes et al., 2005; Holmes et al., 2008). The EPN is particularly pronounced for angry expressions, as an EPN has been observed for angry vs. neutral faces, angry vs. happy faces, and even angry faces vs. faces with other negative expressions such as sadness and fear (Calvo and Beltrán, 2013; Mühlberger et al., 2009; Rellecke et al., 2012; Schupp et al., 2004a). Langeslag (2018) found that EPN is also modulated by facial expression, and that faces showing open mouths elicited a greater EPN compared to faces with closed mouths. This effect may be related to the exhibition of teeth (triangular-like visual stimuli) in the open-mouth faces. Furthermore, mouth-open faces displaying anger produced the strongest EPN (unlike anger in mouth-closed faces), suggesting that the visibility of the teeth specifically contributed to the EPN.

A direct link between the EPN and the allocation of early automatic attention in response to threat has been provided by a study employing the face in the crowd task with angry and happy faces (Feldmann-Wüstefeld et al., 2011). These authors found an advantage for angry faces in their behavioral results together with an EPN for angry faces. The EPNs for snakes (vs. control stimuli) and angry (vs. control) faces suggest that snakes and angry faces capture early automatic attention, which enables fast mobilization of defense and is highly adaptive (Öhman, 2009). Grassini et al. (2019) found an enhancement of EPN in perception of Urban (vs. Natural) images, and interpreted this modulation to be associated with the higher level of stress that humans commonly reported in conjunction with urban environments compared to the relaxation usually reported in conjunction with natural settings, and related to evolutionary human adaptation to natural settings. Again, this interpretation argues for an evolutionarily hypothesis of EPN.

Previous studies have not found any correlation between the subjective levels of fear elicited by snakes and the amplitude of the EPN (e.g. Grassini et al., 2016; Grassini et al., 2018; Van Strien and Isbell, 2017). This supports the view that EPN reflects an automatic processing of visual stimuli, independent from subjective experience of fear.

Furthermore, even if most of the studies have not controlled for low-

level visual features in the images, He et al. (2014), and Grassini et al. (2016) showed that similar modulation of EPN by snake images is possible also using, respectively, gray-scaled pictures and color pictures controlled for luminance and contrast. The study of Grassini et al. (2018) showed that low-level visual features of the stimuli (e.g. spatial frequency) may play a role in the modulation of EPN, but they do not explain the whole effect exhibited in response to snake images. Taken together, the results of electrophysiological studies in humans suggest that snake stimuli selectively modulate early visual attentional processes.

Other early electrophysiological responses have been shown to be sensitive to emotional stimuli (see Olofsson et al., 2008), however, sometimes with inconsistent results. The N1 component (peaking around 100 ms from stimulus onset) has been investigated by previous research as an index modulated in response to snake stimuli (Grassini et al., 2018). This component was reported to be very sensitive to low-level visual features of the pictures, such as spatial frequency (e.g. Grassini et al., 2018; Groen et al., 2017), and many studies analyzing EPN in response to evolutionarily stimuli have decided to omit this component completely from the analysis (e.g. Van Strien, & Van der Peijl, 2018), or to integrate the later part of the N1 with EPN, considering the two components as related to the same neural activity (Langeslag and Van Strien, 2018).

Whether human brain activity is influenced by the triangular or diamond-shaped patterns often present in snake skins has never been studied specifically, and such a study could generate refinements to the Snake Detection Module hypothesis. The study of Souchet and Aubret (2016) supported this idea, as already school children perceived simple drawings of snakes with triangular patterns on their body as less pleasant compared to similar drawings without the pattern.

In the present study, our primary goal was to test whether human brain activity is influenced by the patterns of snake skins. We compared ERPs in response to photos of snakes featuring triangular patterns (commonly found in venomous vipers in Nordic countries) with ERPs to photos of snakes featuring no patterns but just scales of their bodies. These two conditions were also compared to a baseline stimulus (frog photos). If the human visual system is specialized to be sensitive to triangular shapes, we would expect a selective modulation of EPN for images of snakes featuring triangular patterns on their body compared to snakes without such patterns and control condition. In Experiment 1 we employed pictures of full animal bodies (photos of snakes and frogs including their surrounding environment). In Experiment 2 we used photos of skin patterns of the animals, similar to Van Strien and Isbell (2017).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Participants were 31 university students (24 women and 7 men) with normal or corrected-to-normal vision. All participants self-assessed to be right-handed. Participants' age ranged from 19 to 35 years (mean = 24.87; SD = 3.60). They received credits for an introductory psychology course or movie vouchers as compensation. The study was conducted with the understanding and written consent of each participant, in accordance with the Declaration of Helsinki.

2.1.2. Stimuli

The stimuli were presented with E-Prime software (Psychology Tools, Pittsburgh, PA) on a 19-in. LCD monitor with a resolution of 1024 × 768 pixels and 75-Hz screen refresh rate (1 refresh ≈ 13.3 ms). The stimuli were images of snake species with triangular/diamond-shaped patterns (hereinafter referred to as “snakes with patterns”) of the *Vipera aspis* (venomous with patterns) and *Natrix maura* (non-venomous with patterns), images of snakes without triangular/diamond-shaped



Fig. 1. From top-left to bottom-right, examples of: *Natrix maura* (non-venomous with patterns), *Vipera aspis* (venomous with patterns), *Pseudonaja textilis* (venomous without patterns), *Zamenis longissimus* (non-venomous without patterns), and two green frogs (*Lithobates clamitans*). The first two snake species show clear triangular patterns in their bodies. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

skin patterns (hereinafter referred to as “snakes without patterns”) of the species *Zamenis longissimus* (non-venomous without patterns) and *Pseudonaja textilis* (venomous without patterns). For each snake category (patterned vs non-patterned), one venomous species and one non-venomous species were selected. This was done to test, using subjective ratings, whether the subjects perceived the venomous snakes or the snakes with patterns as more threatening than non-venomous snakes or snakes without patterns.

Images of frogs of various species were used as control stimuli (examples in Fig. 1). The size of the images were 600 × 450 pixels, or 9.8 × 7.4 degrees of visual angle to the subject. The images were presented on a gray background. Altogether, 12 images per snake species were selected from photos taken by the authors of the article or their collaborators (thus, a total of 24 images for snakes presenting triangular patterns and 24 images for snakes that did not present triangular patterns), and 12 frog images were selected from free-to-use stock images on the internet. The number of individual images used were in line with previous similar studies (see Van Strien et al., 2014a,b; Grassini et al., 2016; Grassini et al., 2018). The number of individual images of frogs was 12, while for each category of snakes the number of individual images was 24 (12 per snake species). This is due to the fact that grouping the 4 snake species into 2 categories was decided post-hoc, as there were no behavioral nor electrophysiological differences within the two species of snakes with patterns and the two of snakes without patterns. This may, however, raise a concern about a potential repetition suppression effect such that responses to frog stimuli would be diminished relative to snake condition, or oppositely, a pop-out effect for frog images. However, EPN time-window was found resistant to habituation to the stimuli (Schupp et al., 2006). Furthermore, the comparison of snakes vs. frogs was not the primary aim of our study, as the differences between EPN for snakes and for non-dangerous animals

has been already widely studied in general (see e.g. Van Strien et al., 2014a,b; Grassini et al., 2016), and specifically also for snakes vs. frogs (see Grassini et al., 2018).

The luminance histogram of the images was equalized using Matlab (The MathWorks, Natick, MA) and the SHINE toolbox (Willenbockel et al., 2010). The luminance equalization was performed separately for each RGB layer, after which the layers were recombined to form a color image (in the same way than in Grassini et al., 2016 and Grassini et al., 2018). Examples of the stimuli are depicted in Fig. 1.

The stimuli of snakes with patterns and snakes without them, were analyzed and compared post-hoc, to identify low-level uncontrolled differences in the stimuli that may have driven the difference revealed by our presented electrophysiological results (colorfulness, RGB color components, and spatial frequencies).

2.1.3. Procedure

Participants were asked to attend a total 1040 trials, belonging into 3 stimuli categories (snakes with patterns, snakes without patterns, and frogs). Those trials were shown in two identical experimental blocks of 520 trials each. Each one of the images employed in the experiment was shown 8 times per block (total of 480 trials). Additionally, 40 trials were randomly selected from the 520 trials and were followed by a question asking the participant to rate the level of fear elicited by the last image.

Each individual picture was displayed in random order and remained on the screen for 800 ms (60 frames). Each stimulus was preceded by a fixation dot in the center of the screen of a random duration between 300 and 500 ms. The fixation dot was employed in the attempt to reduce eye movements of the subjects and therefore to improve the overall quality of the data. Furthermore, the introduction of the fixation dot had the purpose to avoid that brain activity related to different trials would overlap and therefore introduce noise in the data. A variable duration of the fixation dot was used to decrease brain activity due to participants' rhythmic readiness to the stimuli in the presentation. A question appeared on the screen at a random interval and requested the participant to rate the level of fear elicited by the animal on a scale from 0 to 9. The image preceding the question was selected randomly among all the image samples, balanced among the animal species (5), and in total the question appeared 40 times per block. Participants were instructed to answer the question using a standard computer keyboard. Trials preceding the questions were analyzed together with the others. In Fig. 2 an example of the procedure is shown. A stimulus duration of 800 ms exceeds the duration usually employed in previous studies on

this topic (in similar studies stimulus duration is around 300 ms, see Grassini et al., 2018). We decided to employ a longer stimulus duration to allow the participants to adequately perform the subjective rating task: too short a stimulus would not have allowed the subject to evaluate the elicited fear for the stimulus. The question about level of fear was introduced to measure whether the participants judged the venomous snakes or snakes exhibiting skin patterns as more fear-eliciting than the other snake species or frogs.

2.1.4. Data acquisition

The same equipment with the same settings was used for both experiments, and the data were preprocessed in identical fashion. EEG was recorded from 64 scalp sites, positioned according to the 10-10 electrode system, using a cap with sintered Ag/AgCl active electrodes (Easycap GmbH, Herrsching, Germany). NeurOne 1.3.1.26 software and Tesla #MRI 2013011 and #MRI 2013012 amplifiers (Mega Electronics Ltd, Kuopio, Finland) were used for data collection. Signal was referenced online to Cz and the ground electrode was placed on AFz. Eye movements were recorded with four additional bipolar electrodes. The recording sampling rate was 500 Hz.

2.1.5. EEG data pre-processing

EEG data was processed offline using MATLAB scripts (v. R2014b; The MathWorks, Inc., Natick, MA) and with the EEGLAB toolbox version 14.1.1 (Delorme and Makeig, 2004). Data edges were trimmed from 1000 ms before the first marker to 1000 ms after the last one (beginning and end of the experiment), to remove noisy and not relevant data sections.

Data was high-pass filtered at 0.1 Hz using a Hamming windowed-sinc FIR filter (EEGLAB function “pop_eegfiltnew.m”), and then down-sampled to 256 Hz. Line noise and its harmonics were attenuated using the CleanLine plugin for eeglab, as it has demonstrated to more preserve data integrity compared to a traditional notch filter (EEGLAB function “pop_cleanline”, see Mullen, 2012). Bad data sections in the continuous EEG recording, as well as bad electrodes were then automatically removed or attenuated using the Artifact Subspace Reconstruction method from the Clean Rawdata EEGLAB plug-in (EEGLAB function “clean_rawdata”, Kothe, 2013; Piazza et al., 2016). Data were then re-referenced to average of all the electrodes, and epoched (−300 to 800 ms from stimulus onset), then baseline correction was applied from −300 to 0 ms before the onset of the stimulus. Segments containing artifacts were then rejected using kurtosis of activity (i.e. to detect peaky distribution of activity), parameters chosen were 5 SD

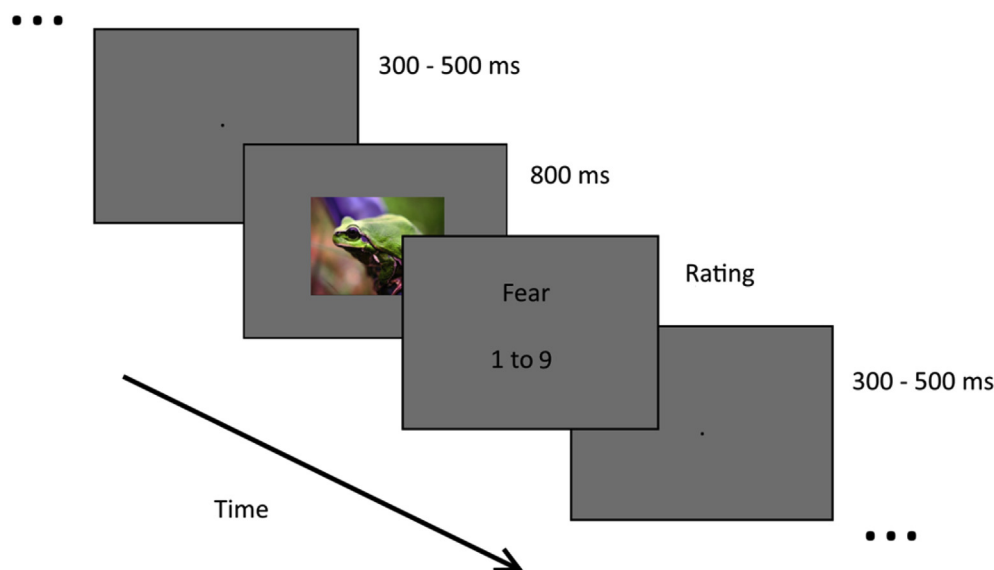


Fig. 2. Example of experimental procedure. First, a fixation dot appeared for a variable duration (from 300 to 500 ms), then the stimulus was shown for 800 ms. At random intervals, a question was presented, asking the participant to rate the level of fear elicited by the last stimulus. The following trial started after rating was made.

from the mean for both single and all-channel limits (for more info please see EEGLAB function `pop_rejkurt.m`). The remaining data were submitted to extended Infomax independent component analysis (ICA, EEGLAB function “`pop_runica.m`”) to identify and subsequently remove Independent components representing eye-blink, eye-movement, heart-beat artifacts and other non-neural activity in the data. ADJUST 1.1.1 (EEGLAB function “`ADJUST.m`”, Mognon et al., 2011; Pontifex et al., 2017) was used to automatically identify and eliminate artefactual ICs. Finally, the previously removed bad electrodes were interpolated using spherical interpolation (EEGLAB function `pop_interpolate.m`).

Data pre-processing and artifact removal pipeline was developed in line with the recommendation of Swartz Center for Computational Neuroscience (EEGLAB developed) fellow Makoto Miyakoshi (see https://scn.ucsd.edu/wiki/Makoto's_preprocessing_pipeline, version retrieved on 20.06.2018).

2.1.6. Data analysis and statistics

IBM SPSS 21 (IBM Corp., New York, NY) was used for statistical analysis.

Fear ratings were compared between stimulus categories with one-way repeated measures ANOVA using stimulus category as a factor (5 levels: four snake species and frogs), to test whether the participants rated venomous or patterned snakes as more fear-eliciting than non-venomous or non-patterned snakes. The fear scores given to the images during the presentation were first averaged per snake species (4), and frogs, the scores ranged from a minimum of 1 to a maximum of 9.

For the electrophysiological signal, we focused on the differences over the posterior brain regions (scalp area where EPN typically peaks, see Luck and Kappenman, 2011). EEG epochs corresponding to different stimulus categories (snakes with patterns, snakes without patterns, and frogs) were compared for the average amplitude in EPN time-window. The EPN and the N1 time-windows were identified upon visual inspection of the ERPs. Brainwaves were analyzed using a traditional calculation of the mean amplitude (uV) for the time windows of interest EPN (250–350 ms). Waves representing the average of the occipital electrode cluster were then computed to help visualize the activity differences (pooled across PO7, PO3, POz, PO4, PO8, O1, Oz, and O2 electrodes). The selected time window was similar to the one used in previous studies in the same field (see e.g. Grassini et al., 2018; Olofsson et al., 2008; Van Strien, Eijlers, et al., 2014; Van Strien, Franken, et al., 2014). The N1 was statistically analyzed, using the same analysis method as for EPN. Visual inspection of the scalp topographies of the brain activity differences in EPN, especially for the snakes with patterns vs. snakes without patterns, revealed the effect to be stronger in centro-occipital electrodes than in centro-lateral electrodes. To test this difference statistically, we computed two occipital clusters for the analysis of the EPN, a centro-occipital cluster (POz and Oz), and a centro-lateral cluster (PO7, PO3, PO4, PO8, O1, and O2). After artifact rejection, 88% of the ERP trials were considered valid and were analyzed.

For EPN and N1 amplitudes, 3×2 repeated measures ANOVAs were conducted with the stimulus category (3 levels: snakes with patterns, snakes without patterns, frogs) and cluster (2: centro-occipital, latero-occipital) as factors. In all the ANOVAs, when the sphericity assumption was violated, Greenhouse-Geisser correction was applied. When Greenhouse-Geisser was applied, we report in the article corrected p values and uncorrected dfs.

Post-hoc additional analyses were performed for colorfulness of images (Hasler and Suesstrunk, 2003), RGB color layers (Matlab function `imread()`, please consult the Matlab manual for image processing for more info), and spatial frequency band powers (Delplanque et al., 2007). For the latter analysis, the images were first decomposed into red, green and blue layers, and then the estimated power of these color layers was averaged to get the mean index of energy for each image category and frequency band. The power scores were then normalized (z-scores) among frequency bands to allow comparisons between

frequency bands and experiments 1 and 2. The wavelet decomposition works by dividing the picture in two (first level), then again in two (second level), and so on. To find the size of pixel of the smallest cycle (i.e. highest frequency), we divided the number of pixels of the smallest dimension (450 pixels) by two, for eight times (highest spatial frequency 2 px/c). The results are presented in the analysis section and in Fig. 6A and B (supplementary figures). The p-values for post-hoc comparison repeated measure t-tests presented throughout the article are corrected using the Bonferroni method.

2.2. Experiment 1 - results

2.2.1. Fear ratings

The average scores were: 4.64 (SD = 2.08) for *Natrix maura*, 4.56 (SD = 2.12) for *Vipera aspis*, 4.53 (SD = 2.11) for *Pseudonaja textilis*, and 4.50 (SD = 2.16) for *Zamenis longissimus*, and 2.43 (SD = 1.60) for frogs.

ANOVA revealed a statistically significant difference between categories, $F(4,120) = 87.19$, $p < 0.001$, $\eta_p^2 = 59$. Fear scores for the snake species did not differ from each other ($ps = 1$), but they all differed from frogs ($ps < 0.001$).

These results suggest that the participants did not consciously experience more fear toward snakes with triangular patterns compared to snakes without patterns, and that they did not experience more fear toward venomous snakes compared to non-venomous snakes.

2.2.2. ERPs

ERPs of the brain activity in centro-occipital and latero-occipital clusters are shown in Fig. 3 A. Fig. 3B shows the topographic maps of the brain activity differences between the experimental conditions.

For EPN, the interaction for stimulus category X electrode cluster was statistically significant, $F(2,60) = 12.92$; $p < 0.001$, $\eta_p^2 = 30$.

Paired-sample t-tests were performed to identify the stimulus categories in which the difference in activity topography occurred. We computed the ERPs differences for each stimuli combination (snakes with patterns vs. snakes without pattern; snakes with patterns vs. frogs; snakes without patterns vs. frogs), and compared the difference between the two electrode clusters. The tests revealed that the difference for snakes with patterns vs. snakes without patterns was larger in centro-occipital than in latero-occipital electrode clusters, $t(30) = -4.61$, $p < 0.001$, contrarily, the difference in latero-occipital electrode cluster was larger than in centro-occipital electrode cluster for snakes without patterns vs. frogs, $t(30) = 4.99$, $p < 0.001$. The difference for snakes with patterns vs. frogs was not observed between the two electrode clusters ($p = 0.46$).

Successively, difference between stimulus categories in the two electrode clusters were analyzed separately. In the centro-occipital electrode cluster, the main effect for stimulus category was statistically significant, $F(2, 60) = 68.34$; $p < 0.001$, $\eta_p^2 = 70$. Post-hoc repeated measures t-tests revealed that all the stimulus categories differed from each other ($ps < 0.001$), with the snakes with patterns eliciting the most prominent EPN negativity, followed by the snakes without patterns, and frogs.

In the latero-occipital electrodes, the main effect for stimulus category was also statistically significant, $F(2, 60) = 99.67$; $p < 0.001$, $\eta_p^2 = 77$. Results from post-hoc t-test mimicked closely the ones reported for the centro-occipital cluster, with all the stimulus categories differing from each other ($ps < 0.001$), with the snakes with patterns eliciting the most prominent EPN negativity, followed by the snakes without patterns, and frogs.

For the N1 component, the main effect for stimulus category was statistically significant $F(2,58) = 82.48$; $p < 0.001$, $\eta_p^2 = 74$. Post-hoc comparisons showed that all the three categories differed from each other statistically significantly ($ps < 0.001$), with the snakes without patterns producing the most prominent negativity in N1, followed by the snakes with patterns, and frogs.

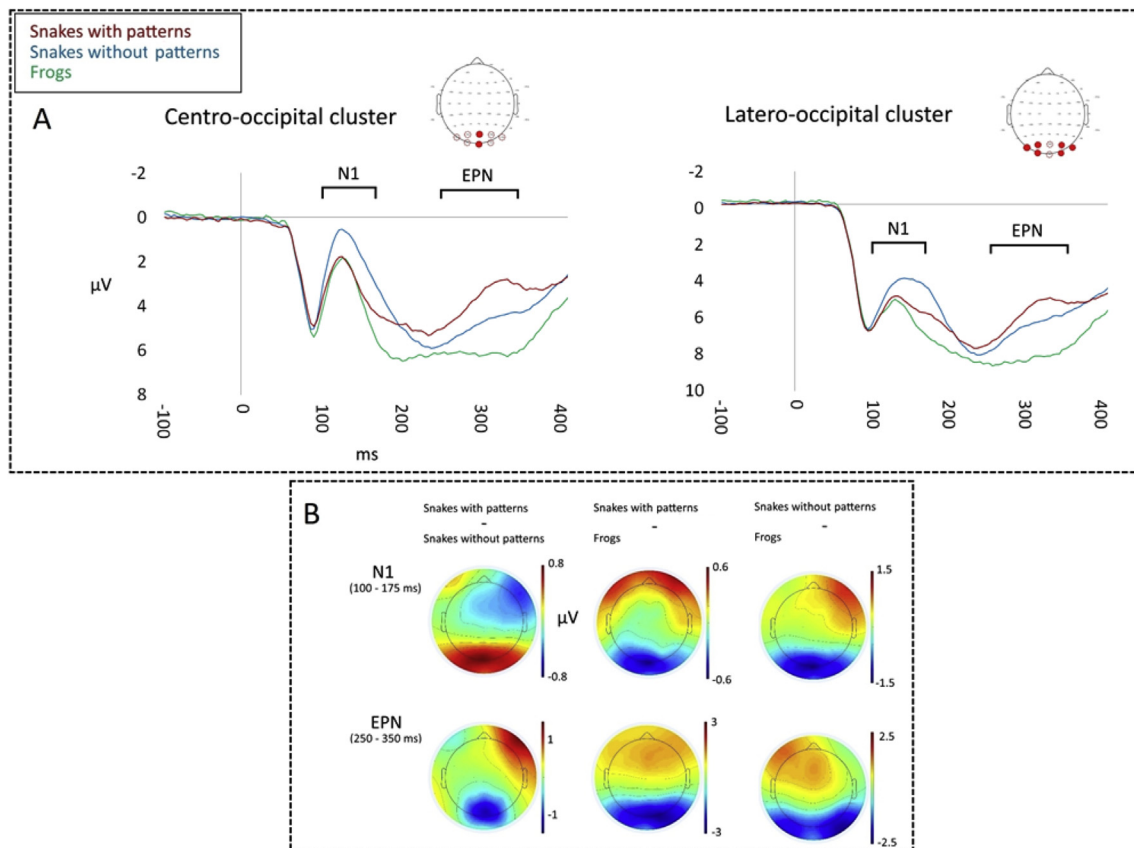


Fig. 3. Panel A shows ERPs obtained averaging the brain activity over two electrode clusters (left: centro-occipital, right: latero-occipital) for snakes with patterns (red line), snakes without patterns (blue line), and frogs (green line; control condition). The electrodes considered for the computation of the three presented electrode clusters are illustrated on the EEG maps presented on the top-right corner of Panel A. Panel B shows the differences in scalp distribution of brain activity between stimulus categories in N1 (100–175 ms) and EPN (250–350 ms), based on subtractions of the average amplitudes in response to each stimulus category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2.3. Post-hoc snake stimuli analysis

Colorfulness did not differ between the snake categories ($p = 0.845$). The stimuli did not differ in magnitude in any of the RGB layers (Red, $p = 0.221$, Green, $p = 0.704$, Blue, $P = 0.497$). The spatial frequency analysis did not show any statistical differences in any of the frequency power analyses ($p_s > 0.096$), the latter analysis is presented in the [Supplementary Figure 6A](#).

2.3. Experiment 1 discussion

The results of Experiment 1 show an increase in EPN amplitude which was specific not only for snake stimuli, but also sensitive for triangular snake skin features. Furthermore, differences between the stimulus categories depended on the scalp topography examined, as revealed from the interaction effect between stimulus category and electrode cluster. Snakes without patterns elicited more prominent negativity in latero-occipital cluster compared to the centro-occipital cluster. However, the results of the first experiment may have been influenced by systematic biases in the images (e.g., different body shapes or postures, or difference in the background environment between the snake species). Therefore, we designed a second experiment where we presented only sections of the bodies of the animals depicted in the photos of Experiment 1 (similarly than in [Van Strien & Isbell, 2017](#)). The aim of the second experiment was to be a conceptual replication of the first experiment, and at the same time an attempt to exclude the possibility that some systematic bias may have influenced our results in the first experiment.

3. Experiment 2

3.1. Methods

3.1.1. Participants

Participants were 29 university students (19 women and 10 men) with normal or corrected-to-normal vision. All participants self-assessed to be right-handed. Participants' age ranged from 19 to 36 years (mean = 24.79; SD = 5.06). Compensation and ethical procedure were identical to Experiment 1.

3.1.2. Stimuli

The stimuli were presented using the same equipment described in Experiment 1 and in an identical experimental setting. The stimuli used were images of snake skins with triangular patterns (*Natrix maura* and *Vipera aspis*; snakes with patterns), snake skins without triangular patterns (*Pseudonaja textilis* and *Zamenis longissimus*; snakes without patterns) and frog skins (see examples in [Fig. 4](#)). Other aspects of the experimental presentation and image pre-processing were kept identical to those described in Experiment 1 (see [Fig. 2](#)).

3.1.3. Procedure

The procedure was identical to that in Experiment 1. (see [Fig. 2](#)), but the images revealed only skin patterns of the animals (see [Fig. 4](#)). The participants were asked to rate their fear level towards the animal they thought the skins belonged to.

3.1.4. Data analysis and statistics

Data analysis and statistical analyses were carried on in a similar



Fig. 4. From top-left to bottom-right, examples of skin patterns for *Natrix maura*, *Vipera aspis*, *Pseudonaja textilis*, *Zamenis longissimus* and two species of frogs. It is possible to identify the characteristic patterns in the first two snake skins.

fashion as in Experiment 1. After artifact rejection, 92% of the ERP trials were considered valid and then analyzed.

Visual inspection of the brainwaves (see Fig. 5) suggested to select slightly different time-windows for analyses compared to the time-windows analyzed in Experiment 1. For this experimental setup, EPN was analyzed in the classical EPN time-window as reported by several previous studies (225–300 ms; see e.g. Van Strien et al., 2014), while N1 was analyzed from 150 to 225 ms from the stimulus onset.

3.2. Experiment 2 - results

3.2.1. Fear ratings

Average reported fear scores were 4.38 for *Natrix maura* (non-venomous, with patterns), 4.36 (SD = 2.30) for *Vipera aspis* (venomous, with patterns), 4.23 (SD = 2.17) for *Pseudonaja textilis* (venomous, without patterns), 4.27 (SD = 2.27) for *Zamenis longissimus* (non-venomous, without patterns), and 3.92 (SD = 1.75) for frogs.

Repeated measures ANOVA revealed no statistical differences between the stimulus categories, $F(4,120) = 2.08$, $p = 0.157$.

The results suggest that the participants did not consciously feel more fear toward skins of venomous snakes compared to skins of non-venomous snakes, or toward snake skins with patterns compared to snake skins without patterns.

3.2.2. ERPs

For EPN, the interaction for stimulus category X electrode cluster was statistically significant, $F(2,56) = 16.10$; $p < 0.001$, $\eta_p^2 = 37$. Paired-sample t-tests were performed to identify the stimulus categories in which the difference in activity topography occurred. We computed the ERPs differences for each stimuli combination (snakes with patterns vs. snakes without pattern; snakes with patterns vs. frogs; snakes without patterns vs. frogs), and compared the difference between the two electrode clusters. The tests revealed that the difference for snake skins with patterns vs. frogs was larger for latero-occipital than in

centro-occipital electrode clusters, $t(28) = 3.26$, $p = 0.003$, and for snake skins without patterns vs. frogs, $t(28) = 3.26$, $p < 0.001$, but not for snake skins with patterns vs. snake skins without patterns, ($p = 0.08$).

Successively, differences between stimulus categories in the two electrode clusters were analyzed separately. In the centro-occipital electrodes, the main effect for stimulus category was statistically significant, $F(2, 56) = 9.35$; $p < 0.001$, $\eta_p^2 = 25$. Post-hoc t-test revealed that the snake skins with patterns statistically significantly differed both from the snake skins without patterns ($p < 0.001$), and from frog stimuli ($p = 0.028$). Snake skins without patterns did not differ from frogs ($p = 0.790$).

Over the latero-occipital cortex, the main effect for stimulus category was also statistically significant, $F(2, 56) = 13.68$; $p < 0.001$, $\eta_p^2 = 33$. The results from post-hoc t-tests were similar to the results for centro-occipital cluster in Experiment 1: all the stimulus categories differed from each other, with the snake skins with patterns eliciting the most prominent EPN compared to snake skins without patterns ($p = 0.003$) and frogs ($p = 0.001$), and snake skins without patterns and frogs not differing in the EPN amplitude ($p = 0.482$).

For the N1 component, the main effect for stimulus category was statistically significant $F(2,56) = 48.35$; $p < 0.001$, $\eta_p^2 = 68$. Post-hoc comparisons revealed that all the three categories statistically significantly differed from each other ($ps < 0.002$), with the snake skins without patterns producing the most prominent N1, followed by the snake skins with patterns, and frogs.

3.2.3. Post-hoc snake stimuli analysis

Colorfulness did not differ between snake skins with patterns and snake skins without patterns ($p = 0.196$). The stimuli did not differ in the red color layer ($p = 0.43$). However, the snake skins with patterns showed a stronger green, $t(34) = 2.35$, $p = 0.025$, CI 0.002 0.024), and blue, $t(34) = 4.81$, $p < 0.001$, CI 0.06 1.491) color intensity. The spatial frequency analysis did not reveal statistical differences in any of the frequency power analyses ($ps < 0.096$), the latter analysis is presented in Supplementary Figure 6B.

4. Discussion

To investigate the effects of different snake patterns on the human early attentional processes we used Early Posterior Negativity (EPN) over the occipital lobe as an index of the underlying brain activity. EPN reflects visual processing of emotionally significant visual stimuli (Luck and Kappenman, 2011; Olofsson et al., 2008), and previous studies have found that this component is specifically modulated by evolutionarily relevant stimuli (Schupp et al., 2003). We also analyzed differences in the earlier N1 component.

In Experiment 1, we presented pictures displaying full-body photos of snakes showing triangular/diamond-shaped skin patterns, snakes without triangular patterns, and frogs. In Experiment 2 we employed close-up pictures of snake skins with and without triangular patterns, and frog skins.

In the first experiment, pictures of full bodies of snakes with triangular patterns elicited the largest EPN while pictures of full bodies of snakes without these patterns elicited intermediate EPN, and full bodies of frogs the smallest EPN. These results demonstrate an increase in EPN amplitude specific not only for snake stimuli, but also sensitive for triangular/diamond-shaped snake skin features. Behavioral data showed that the observers did not rate the venomous snakes as more fear-eliciting compared to non-venomous snakes, or snakes presenting triangular patterns on their body as more fear-eliciting compared to those without patterns.

In the second experiment, instead of using pictures of the whole animals, we used close-up images of the same snake species that were used in the first experiment. Images of snake skins with patterns showed a difference in EPN both when compared to images of snake

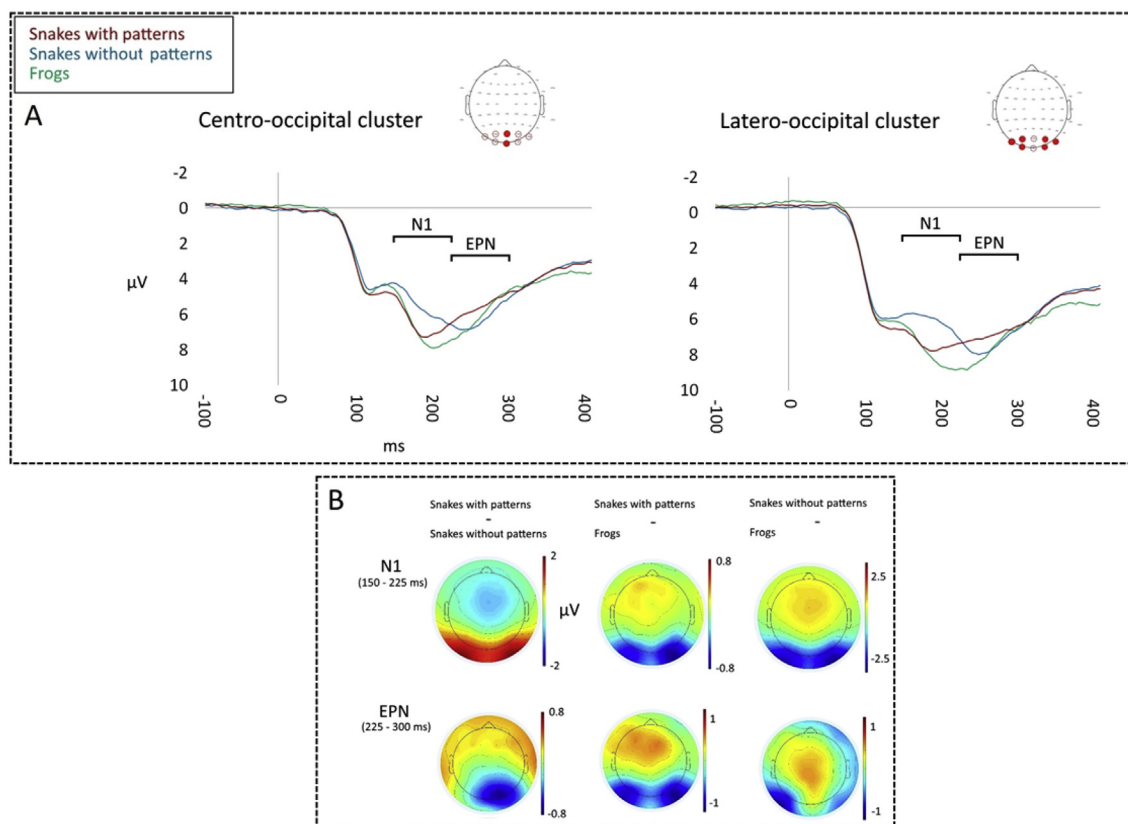


Fig. 5. Panel A shows ERPs obtained averaging the brain activity over two electrode clusters (left: centro-occipital, right: latero-occipital) for snake skins with patterns (red line), snake skins without patterns (blue line), and frogs (green line; control condition). The electrodes considered for the computation of the three presented electrode clusters are illustrated on the EEG maps presented on the top-right corner of Panel A. Panel B shows the differences in scalp distribution of brain activity between stimulus categories in N1 (150–225 ms) and EPN (225–300 ms), based on subtractions of the average amplitudes in response to each stimulus category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

skins without patterns and frog skin images. However, images of snake skins without patterns did not differ from frogs, unlike in experiment 1. This difference may be due to the fact that the human visual system had less information available in Experiment 2 to detect a potentially dangerous snake body from a non-dangerous frog stimulus. While in Experiment 1 the visual system had the possibility to recognize and categorize the animals as they were represented in full body, in Experiment 2 this was impossible, as the animals were not easy to recognize from close-ups of their skins. However, the images of snake skins with patterns still had a visible and recognizable signature, and the visual system could still have used this low-level image characteristic to identify potential danger (even though this may have happened on unconscious level as there were no differences in fear ratings in the behavioral results).

The results of our two experiments replicate previous EPN findings which were obtained by employing pictures of fully visible animals (e.g. Van Strien et al., 2014a,b). Further, our results extend the previous findings and indicate that human attention is preferentially directed towards snakes featuring triangular skin patterns compared to snakes without these patterns, or frogs. Specifically, our second experiment is in agreement with behavioral animal studies (Etting and Isbell, 2014; Isbell and Etting, 2017) which have shown that non-human primates react to partially exposed snake models. In real world, snakes are often hidden in the vegetation, and the ability to detect partially visible snakes is highly relevant to survival.

Studies of non-human primates (Van Le et al., 2013; Van Le et al., 2016) have proposed that some subcortical neurons may be specialized for detecting snakes, and therefore modulate early processing of visual stimuli (Morris et al., 1999; Shibasaki and Kawai, 2009). Alternatively or additionally to this theory, as proposed already by Van Strien and

Isbell (2017), particular patterns of snake skins may be able to trigger specific neural networks in the visual cortex that are particularly sensitive to specific line orientation or to diamond-shaped patterns (Shibasaki and Kawai, 2009; Tamietto and de Gelder, 2010). Our study suggests that these neural mechanisms are particularly sensitive to the diamond-shaped or triangular patterns which are commonly found in venomous snakes around the world, although also in non-venomous snakes which may mimic the patterns of more dangerous species.

From visual inspection of the obtained brain waveform, we found a difference in brain activity between the stimulus categories around 150 ms from the stimulus onset (roughly visual N1 time-window), and therefore we conducted data analyses also for the N1 component. These analyses suggested stronger attentional capture for snakes without patterns, compared to snakes with patterns and frogs. However, previous studies (see He et al., 2014; Grassini et al., 2016; Grassini et al., 2018; but also Olofsson et al., 2008 for a review) have shown that brain activity before 200 ms from the stimulus onset may not be directly related to attentional priorities driven evolutionarily by snakes. Evolutionarily non-threatening stimuli (e.g. butterflies, see Grassini et al., 2016) were also shown to modulate the N1 time-window in a similar manner than snake stimuli, and the N1 time-window was shown to be very sensitive to spatial frequency power difference between visual stimuli (see Grassini et al., 2018). Furthermore, the difference in the N1 modulation may be due to a systematic bias in some low-level visual features of the images we employed. However, post-hoc analyses aimed to assess whether there was any systematic low-level bias between images of the snakes without patterns and the snakes with patterns. Analyses of colorfulness (Hasler and Suesstrunk, 2003), RGB color layers, and mean power in spatial-frequency bands of the images (Delplanque et al., 2007) failed to find clear biases in low-level

characteristics, with the exception of differences for the blue and green color layers in Experiment 2. Images of snake skins without patterns showed higher power in the higher spatial frequencies. While this difference failed to reach statistical significance, it may still have had some influence on the electrophysiological activity, as shown by a wide body of literature investigating the relationship between visual ERPs and the spatial frequency power of the stimuli (see De Cesarei, Mastria and Codispoti, 2013; Holmes et al., 2005; Yang and Chan, 2015). Specifically, difference in the high spectrum of the spatial frequency has been shown to particularly affect early ERP components, such as N1 (as suggested by Grassini et al., 2018). However, as we did not have an a-priori hypothesis for the N1 modulation, any attempt of interpretation is only speculative.

In experiment 1, the analysis for centro-occipital and latero-occipital electrode clusters in the EPN component showed different scalp topography for the reported differences between stimulus categories. Snakes with patterns showed a more central EPN activity compared to snakes without patterns, while the difference between snakes without patterns and frogs was more pronounced in the latero-occipital electrode cluster. To explain this phenomenon, we suggest that the processing of the triangular shapes may be associated with stronger recurrent activation of early visual areas (involving V1), or with attentional amplification of visual processes in early visual areas related to processing the visual details (angular shapes in this case). A stronger activity in lateral areas (as showed in Experiment 1 by snakes without patterns vs. frogs) may be related to higher-level cognitive processes, such as stimulus categorization, and therefore more related to the semantic discrimination of the snake images from the frog images. The statistical analysis of ERPs showed that differences in signal lateralization were not present in Experiment 2 for snakes with patterns vs. snakes without patterns - however, the scalp maps show again rather clearly the more centralized activity for snakes with patterns. In Experiment 2, snakes without patterns showed a more prominent lateral activity vs. frogs, similarly than in Experiment 1, supporting the idea that occipito-lateral areas may be involved in the processing of snakes without patterns vs. frogs. In Experiment 2, a more lateralized activity was also individuated for the comparison of snakes with patterns vs. frogs. We interpreted this result in line with the understandings above: as well as snake skins, frog skins also contain patterns and colors that may resemble those of dangerous animals, and to distinguish dangerous from non-dangerous stimuli the brain has to employ higher level cognitive processes.

The present study was aimed to investigate early, evolutionarily-driven brain dynamics provoked by evolutionarily relevant animal stimuli (snakes). Therefore, analysis of later ERP components (e.g. P3, and LPP) did not fit within the scope of the present study. These later components are related to higher-level and slower cognitive functions, such as sustained attention (Luck & Kappenman, 2012).

In both experiments, fear scores were low also towards snakes (average below 5 on a scale from 1 to 9), suggesting that the majority of the participants did not particularly feel fear towards these animals. In Experiment 1, self-reported fear for the two categories of snakes was higher than fear level reported for frogs, and there was no difference between the fear scores in the two snake categories. Behavioral data from Experiment 2 suggested also that participants did not rate differently the fear level for the animals from which the skin patterns were extracted, even though dangerous (snakes) and non-dangerous (frogs) animals were rated. These results are reasonable, as the skin patterns of frogs that we employed may sometimes resemble those of dangerous animals (see Fig. 4). However, in both experiments, differences in EPN were found between all the three stimulus categories, and what is of particular importance, between snakes with patterns vs. snakes without patterns. These results, together with those of previous studies that found a lack of association between snake fear and EPN amplitudes (Van Strien et al., 2014a,b, 2016; Van Strien, Franken and Huijding, 2014; Grassini et al., 2016, 2018) suggest that the attentional bias

towards evolutionary threatening stimuli (indexed by EPN) is activated independently from conscious fear perception and may indicate the innate nature of early attentional capture by snakes.

The experiment 2 was developed as a conceptual replication of the first experiment. However, the design of the second experiment, due to its nature, had some limitations (e.g. photo magnification ratio, and extraction of the animal in the figure from its ecologically valid environment). Furthermore, as we used the pictures utilized in experiment 1 to produce the close-up pictures employed in experiment 2, it is possible that low-level uncontrolled variables (e.g. a systematic bias in lighting, or image colors) may have, to some extent, affected the results of our second experiment.

In the present study we used naturalistic stimuli (i.e., realistic pictures), equalized only for luminance and contrast level. It could be argued that other low-level visual features, such as color and spatial frequency, might be crucial for the modulation of EPN and should be controlled for. We decided to equalize the stimuli only for luminance (similarly as in our previous study, see Grassini et al., 2016), trying to keep an equilibrium between ecological validity and experimental control. Similar previous studies (e.g. Van Strien and Isbell, 2017) used more natural stimuli, privileging ecological validity over control, while others (e.g. He et al., 2014; Grassini et al., 2018) used black and white pictures trying to control for the image colors, or used stimuli equalized for spatial frequency power. In spite of the different uncontrolled variables, all these studies provided convergent evidence and showed a distinct EPN effect for snakes.

The study has the limitation of not dealing with snakes that present different skin markings (or patterns) than triangular or diamond-shapes. Other types of patterns may be responsible for similar attentional capture than the one reported in the present study for the snakes with triangular or diamond-shapes. This deserves future investigation. A further limitation is that the present study did not employ a traditional Rapid Serial Visual Presentation (RSVP) paradigm, employed by previous studies on electrophysiology of snake perception (e.g. Van Strien et al., 2014a,b; Grassini et al., 2016). The different experimental paradigm employed may have shifted the onset of the studied ERP components, and made our results more difficult to interpret within the framework of previous investigations. However, the present design allowed the participants to better give subjective ratings for the presented pictures and to have a more relaxed experimental session (longer stimuli duration compared to the RSVP, and less ocular fatigue), and the introduction of a fixation point (usually not employed in a classical RSVP paradigm) should have reduced the eye-movement related artifacts. Furthermore, if the EPN is a robust phenomenon, it should be elicited in any theoretically relevant experimental condition, and its existence should not be dependent on any a single stimulation paradigm, such as RSVP.

From an evolutionary perspective, the ability to rapidly recognize dangerous stimuli (e.g., venomous snakes hiding in the grass vs. other kind of reptiles) on the basis of their skin patterns might have been an evolutionary advantage, and therefore may have shaped human early visual processes. Yet, there are other scenarios we cannot exclude. Other factors than skin patterns may have influenced the human attentional preference toward triangular-like patterns. Triangular patterns are often present in other threatening stimuli that may have had evolutionary importance (e.g. sharp tooth profile, claws, daggers, sharp stones, etc.). In this view, humans may have benefited from a multi-purpose attentional bias toward triangular shapes, and this bias may also have served in detecting dangerous venomous snakes.

In conclusion, using visual presentation of either full pictures of snakes exhibiting triangular-like patterns, snakes without these patterns and frogs, or partly exposed bodies with identifiable skin patterns from these three categories of animals, we found that images showing the triangular patterns elicited an enhanced EPN compared to pictures of non-patterned snakes and pictures of frogs. Our findings are consistent with and constitute an important addition to the Snake Detection

Hypothesis.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2019.05.024>.

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