



Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli



Simone Grassini ^{a,b,*}, Suvi K. Holm ^a, Henry Railo ^{a,b}, Mika Koivisto ^{a,b}

^a Department of Psychology, University of Turku, Finland

^b Centre for Cognitive Neuroscience, University of Turku, Finland

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ABSTRACT

Snakes were probably one of the earliest predators of primates, and snake images produce specific behavioral and electrophysiological reactions in humans. Pictures of snakes evoke enhanced activity over the occipital cortex, indexed by the “early posterior negativity” (EPN), as compared with pictures of other dangerous or non-dangerous animals. The present study investigated the possibility that the response to snake images is independent from visual awareness. The observers watched images of threatening and non-threatening animals presented in random order during rapid serial visual presentation. Four different masking conditions were used to manipulate awareness of the images. Electrophysiological results showed that the EPN was larger for snake images than for the other images employed in the unmasked condition. However, the difference disappeared when awareness of the stimuli decreased. Behavioral results on the effects of awareness did not show any advantage for snake images.

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1. Introduction

Snakes were one of the earliest predators of primates, and snake images appear to automatically draw more visual attention than other dangerous animals. Snakes have been living together with primates and their ancestors since prehistoric eras. According to the snake detection hypothesis (Isbell, 2006, 2009), the predatory pressure of these reptiles on primates may have caused evolutionarily driven changes in the primate visual system, which allows quick detection of these predators, thus increasing the chances of survival. The literature on the topic confirms that humans detect snake images faster than other animal stimuli (see Öhman, Flykt, & Esteves, 2001; Öhman & Mineka, 2001). From an evolutionary perspective, a fear module specifically activated by stimuli of a crucial importance for survival would be highly adaptive.

The amygdala may be the key structure dedicated to processing threatening stimuli (Mineka & Öhman, 2002). In macaques, pulvinar neurons respond faster and stronger to snake stimuli compared

to other threatening or neutral images (Van Le et al., 2013). Pulvinar neurons may be part of a fast visual pathway that connects the retina and the superior colliculus to the amygdala. This pathway may enable rapid automatic visual detection of fear-related stimuli (Morris, Öhman, & Dolan, 1999; Tamietto & de Gelder, 2010).

Recently, several studies have provided electrophysiological support for the snake detection hypothesis in humans (He, Kubo, & Kawai, 2014; Van Le et al., 2013; Van Strien, Eijlers, Franken, & Huijding, 2014; Van Strien, Franken, & Huijding, 2014; Van Strien, Christiaans, Franken & Huijding, 2016). In four studies, Van Strien and colleagues examined the snake detection hypothesis in humans using event-related potentials (ERPs). The first study (Van Strien, Franken, & Huijding, 2014) showed an ERP component peaking at 225–300 ms after stimulus onset over the occipital scalp area (Early Posterior Negativity, EPN). The EPN amplitude was larger for snake pictures, intermediate for spider pictures and significantly lower for bird pictures. In a second study, Van Strien, Eijlers et al. (2014) and Van Strien, Franken et al. (2014) demonstrated that the EPN effect is not evoked by reptiles in general and that it is not directly related to the feeling of disgust or fear. Pictures of snakes elicited larger EPN compared to pictures of slugs and other dangerous and non-dangerous reptiles. The third study compared the ERPs produced by snake pictures with those produced by worm

* Corresponding author at: Department of Psychology, University of Turku, Assistentinkatu 7, 20014 Turku, Finland.

E-mail address: simone.grassini@utu.fi (S. Grassini).

pictures and demonstrated that the curvilinear shape of the snakes is not directly responsible for the enhanced EPN (Van Strien et al., 2016). Finally, a study using gray-scaled images showed no difference between spiders and other animal stimuli except snakes (He et al., 2014), contradicting previous findings (Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014). Furthermore, the results of He et al. (2014) showed a smaller snake advantage, as compared with the other studies.

Altogether, the results suggest that ancestral priorities may modulate early capture of visual attention. EPN has been suggested to reflect the early selective visual processing of emotional information that is not altered by habituation to the stimuli (Schupp, Flaisch, Stockburger, & Junghofer, 2006). Furthermore, EPN is modulated by motivational systems of approach and avoidance and it is sensitive to evolutionarily crucial stimuli (Schupp, Junghofer, Weike, & Hamm, 2003). A difference in the modulation of the EPN by snakes and spiders (He et al., 2014; Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014) is in line with the idea that snake detection is to a large degree driven by bottom-up flow of information, while the detection of other dangerous stimuli (e.g. spiders) depends on top-down processes (Soares et al., 2014; Kawai & Koda, 2016).

Van Strien et al. (e.g. Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014) reported that the EPN effect is modulated by ancestral priorities rather than consciously reported fear or arousal. However, these studies refer to consciousness as emotional awareness (conscious feelings) or conscious top-down processing (cognitive control) and not to subjective visual perception. On the basis of the argument that the snake detection advantage is automatic, evolutionary in origin and based on ancestral priorities, we found it reasonable to test whether or not this effect could be produced by unconscious visual processing.

There are currently no published studies that have investigated whether or not unaware images (e.g. of snakes) can produce the enhanced EPN deflection. However, previous studies have shown that masked snake images produce physiological effects (electrodermal responses) in phobic participants even under backward masking conditions that make the stimuli less visible (Öhman & Soares, 1993, 1994). Snake images seem to be more likely to be detected compared to other animals in challenging attentional conditions (Soares, Lindström, Esteves & Öhman, 2014). Furthermore, LoBue (2014) found an attentional bias toward dangerous stimuli due to perceptual, cognitive and emotional effects. Especially related to the detection of snakes, curvilinear shapes were easier to recognize compared to straight lines. Threatening words such as “snake” also produced faster responses when compared to non-threatening words.

On the other hand, even if the EPN represents an evolutionarily-driven electrophysiological reaction, the EPN itself might not be independent from subjective visual perception of the stimuli. For example, the EPN (225–300 ms) is a mid-latency evoked potential (Foxe & Simpson, 2002) and unconscious processing of emotional stimuli has been indexed in earlier components than EPN, over occipito-temporal areas (see e.g. Pegna, Landis, & Khateb, 2008; Smith, 2012). However, the debate about the possibility of unconscious processing of emotional images is still ongoing (see the recent meta-analysis by Hedger, Gray, Garner, & Adams, 2016).

Furthermore, the EPN temporally and spatially overlaps with a well-known electrophysiological marker of subjective visual awareness called the Visual Awareness Negativity (VAN) (see Koivisto & Revonsuo, 2010; Koivisto et al., 2008; Railo, Koivisto & Revonsuo, 2011; Koivisto & Grassini, 2016; Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo, 2016), which suggests that the EPN might reflect aware perception.

Finally, there are some methodological problems with the studies done so far. The previous EPN studies, with the exception of the

study of He et al. (2014), face the limitation that the images were not equalized for contrast and luminance, making it possible that low level visual features associated with snake images may explain the effects. However, He et al. (2014) used gray scaled images, while colors might be important for the detection of threatening stimuli.

In the present study we strove to improve the current knowledge on the topic by studying (1) whether or not previous ERP results can be replicated using colored images, equalized for contrast level and luminance, and (2) whether or not conscious perception of the stimuli is crucial for the snake images to evoke the EPN effect. Previous studies describe the EPN effect of snake images as evolutionarily driven and “automatic” (see Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014), implicitly suggesting that such an effect might not require subjective visual awareness of the stimulus. The present research attempts to address this problem in a comprehensive way.

2. Methods

2.1. Participants

Participants were 27 university students (4 men, 23 women) with normal or corrected-to-normal vision. All participants were right-handed (Oldfield, 1971). Their age ranged from 19 to 29 years, with a mean age of 23.41 years (SD = 2.49). They participated in order to obtain course credits in introductory psychology at the University of Turku. The study was conducted with the understanding and written consent of each participant, in accordance with the Declaration of Helsinki, and was accepted by the Ethics Committee of The Hospital District of Southwest Finland.

2.2. Questionnaires

Before the experimental session, the participants were asked to rate their fear of snakes, spiders, birds and butterflies on questionnaires that were adaptations of the Spider Phobia Questionnaire (SPQ; Klorman, Weerts, Hastings, Melamed, & Lang, 1974; Muris & Merckelbach, 1996; Muris, Merckelbach, Ollendick, King, & Bogie, 2002), translated in Finnish. Each questionnaire contained 15 statements regarding fear of the animals displayed in the images that were employed in the study. For every statement, the participant had to rate ‘yes’ or ‘no’, and the score on each animal questionnaire could range from 0 (no fear) to 15 (very high fear). Furthermore, for every animal category, the participants were asked to indicate their familiarity with the animal by asking them how often they had seen the animal. This was done in order to examine possible effects of habituation. The score ranged from 0 (very rarely) to 10 (very often).

Finally, after the experiment, the participants were asked to rate from 0 to 10 the arousal provoked by every image presented during the experimental session.

2.3. Stimuli

Stimuli were presented using E-prime 2.0 software on a 19-in. CRT monitor with 1024 × 768 pixel resolution and 85 Hz screen refresh rate (1 refresh ≈ 12 ms). The stimuli were snake, spider, bird or butterfly images of the size of 600 × 450 pixels (Fig. 1), 9.8 × 7.4 cm from 1.5 m. 30 images per animal type were selected from free-to-use stock images on the internet. Snake, spider and bird images were employed in previous studies (see e.g. Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014), and were included in the present study to facilitate comparison with earlier studies. Butterfly images were included as non-threatening stimuli that feature colorful patterns that may resemble those of snakes. Using butterfly images we controlled for the possibility that

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