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Revisiting “The Malicious Serpent”: Phylogenetically Threatening Stimulus Marked in the Human Brain

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Abstract

Twenty years ago, Öhman and Mineka’s publication “The Malicious Serpent” emphasized the selective pressure ancestral reptiles would have on early mammals’ visual system, specifically the development of a set of subcortical structures that would provide snake-like images privileged access to the amygdala. This process would occur automatically and allows for quick defensive reactions. Based on criticisms directed to the snake detection research, we created five questions that guided the discussion in this review. Evidence suggests the existence of a set of subcortical structures that promote prompt detection of snakes and sustained attention, but difficulties arise due to the complex interconnectivity of cortical and subcortical structures and multiple threat responses. Gaps in the research are identified as potential for future investigation.

Keywords
fear module, Snake Detection Theory, visual system, primate evolution

Introduction

In 2003, Öhman and Mineka published “*The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear,*” an article suggesting that ancestral reptiles played an important role in the evolution of the mammalian class, acting as source of selective pressure. This pressure would have been particularly important for the order primates (including humans), especially when the evolution and adaptation of their visual systems related to coping with threat-related stimuli are considered (Isbell, 2009; Öhman & Mineka, 2003). One of the results of this selection and adaptation process would be the specialization of the basic mammalian fear module (FM), a “*behavioral, mental and neural system that has evolved to assist mammals in defending against threats such as snakes*” (Öhman & Mineka, 2003, p. 7). These would include a set of subcortical structures involved in visual detection which would facilitate and sustain the defensive responses.

Despite their seminal work and proposals, Öhman and Mineka (2003) left many open questions, speculative arguments, and hypotheses that were only addressed in the

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subsequent years by other authors, using research and technology that were not previously fully available at the time. Not surprisingly, recent research has also brought forth direct criticisms of snake detection studies in primates. The main aim of the present review is to compile the state-of-the-art advancements and critiques on this issue since the original publication of their paper.

Key Arguments

According to Öhman (2000, 2005), fear is an emotional state that motivates individuals to deal with threatening events. It involves attentional, perceptual, and physiological changes, supposedly at the function of increasing the chances of an organism successfully coping with danger (Öhman, 2005). Although the flexibility of the definition of the word fear can cause misinterpretation (Adolphs et al., 2019), as we will see later in the next sections, it is reasonable to think that fear, in many of its definitions, has been shaped under selective pressures and natural selection (e.g., Bolles, 1970; Seligman, 1970, 1971). Consequently, the descendants of the ancestors who underwent this selection would be better prepared to optimize their survival and reproduction because of these fear-related mechanisms.

The Preparedness Theory (Seligman, 1970) suggests that such mechanisms would be enhanced to respond to certain types of stimuli that would be associated with ancestral threats. This idea came from the observation that certain phobias are easily acquired after one or a few aversive exposures to the feared object, persisting even after the information that the situation is harmless. Hence, it is argued that, in the face of evolutionary pressures, neural mechanisms that would predispose the acquisition of fear and resistance to its extinction in the face of certain stimuli would have been naturally selected, and then inherited by us precisely because they helped ensure the survival of our ancestors (Mineka & Öhman, 2002; Seligman, 1970). This is taken as an explanation of why phobias to certain animals (e.g., spiders and snakes) and social phobias are very common, while phobias to stimuli apparently with no evolutionary relevance have lower incidence (Mineka & Öhman, 2002). However, some studies have argued that the preparedness effect is not robust, although it is usually concluded that there is evidence for selective processing of fear-relevant stimuli (e.g., Åhs et al., 2018).

Öhman and Mineka (2001, 2003) focused their investigation on the human fast visual attention to snakes and on the neural pathway responsible for such behavior. It is known that the neurons that depart from the retina project into two major structures in the brain, the lateral geniculate nucleus and the superior colliculus. From the lateral genicutate nucleus signals are routed to the primary visual cortex and then to other visual areas in the brain (Kaas & Huerta, 1989; Soares, Kessel et al., 2017). The superior colliculus would forward the signals to the pulvinar and then the pulvinar would transfer the signal to the amygdala, without involvement of the cortex (Elorette et al., 2018; Kragel et al., 2021; Rafal et al., 2015; Soares, Kessel et al., 2017). Regarding this latter pathway, Ledoux (1996) proposed that the superior colliculus-pulvinar pathway (which he called the "low road" of affective stimuli) would transmit threatening signals to the amygdala, implying faster autonomic and behavioral responses.

Furthermore, the visual input that reaches the superior colliculus comes mostly through magnocellular and koniocellular channels, which produce signals of low spatial frequency. Thus, the information necessary for the efficient activation of this pathway would have a low level of visual detail. Although the evidentiary basis for the neural characteristics of the FM was not yet complete (indeed, still debatable to this day), the authors speculated that it would help mammals to detect and react threatening stimuli. Furthermore, the FM would become specialized depending on the ecological niche of different species and could respond more intensely to different threatening images.

In the case of primates, behavioral findings pointed to snakes as a special threatening stimulus, capable of elicit or condition fear responses vicariously or even when not consciously perceived (Cook & Mineka, 1990; Öhman & Soares, 1998). Therefore, Öhman and Mineka (2003) argued that snakes would constitute an "archetypal stimulus" that could preferentially trigger the FM to elicit defensive responses. Mineka and Öhman (2002) believed that FM specialized neuronal circuitry would (1) rely on limbic structures, (2) be amygdala-centered, and (3) have the constituents of the low road as neuronal support. Based on later studies, currently the FM would include the superior colliculus and pulvinar nucleus (together dubbed the "low road"), the amygdala, locus coeruleus, substantia nigra, the periaqueductal grey matter, and the nucleus cuneiform.

The Snake Detection Theory (Isbell, 2006, 2009) came to further suggest that the visual specialization in the early primates arose in response to selective pressure exerted initially by predatory constricting snakes. Later, the brains of anthropoid primates took a particular evolutionary course due to venomous snakes such as the ones from the *Viperidae* and *Elapidae* taxa. Some primate taxa would have developed a greater visual sensitivity to cues related to these reptiles and the capacity to adopt faster appropriate behaviors as part of the snake avoidance strategy (Isbell, 2006, 2009). Consequently, some individuals would survive longer and deal better with the environment and will be more likely to pass on their genes to the next generations. The descendants of these individuals would inherit the genetic information partially responsible for the characteristics that minimized the deleterious action of the threat agent, even if some of the threats are no longer selective pressures with any, or the same, impact as before.

Although all these arguments are widely used as references for many studies, there were several issues that warranted further investigation. Upon preliminary analysis of the advancements and common critiques of the aforementioned issues in the literature, we have formulated five guiding questions with the aim of summarizing the current state-of-the-art in this research field and inspiring future studies. Our first question delves into the evidence of a specialized neural circuitry for the visual detection of snakes. Then, we examine the behavioral evidence for distinct responses elicited by snakes in primates and their innate origins. Next, we explore the specific snake characteristics that contribute to faster visual detection and reaction times, as well as the presence of a larger early posterior negativity (EPN). Lastly, we investigate how the context and the definition of key concepts may potentially impact data interpretation.

Is There Evidence of a Specialized Neural Circuitry for the Visual Detection of Snakes?

Neurophysiological arguments indeed suggest that some salient visual information associated with snakes would be brought from the retina to the amygdala, through the low road (i.e., the colliculo-pulvinar pathway), bypassing the visual cortex in primates (Elorette et al., 2018; Kragel et al., 2021; Rafal et al., 2015; Soares, Maior et al., 2017). Consequently, the activation of the low road/FM would mediate faster initial attention allocation, visual detection, and first behavioral and physiological responses to the stimuli that acted as a selective pressure. Despite all this, increasing evidence indicates the relevance of multiple waves and pathways across the cortical and subcortical areas for fear processing (involving threat evaluation, detection, identification, and defensive responses) (Li & Keil, 2023; Pessoa & Adolphs, 2010). In any case, due to the extensive connections between subcortical and cortical regions, the visual information would be coordinated and amplified (Pessoa & Adolphs, 2010; Shipp, 2003) and would contribute to visual attention (Saalmann & Kastner, 2009; Serences & Yantis, 2006).

In fact, studies using EEG showed larger EPN amplitudes for snake images when compared with images of crocodiles, turtles, spiders, and slugs (He et al., 2014; Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014). These results were interpreted by the authors as reflecting larger early automatic attention capture. However, as the stimuli tested in these EEG studies were task-relevant, they did not necessarily reflect exogenous (automatic) attention capture. With this in mind, Soares, Maior et al. (2017) recorded EEG data during a letter discrimination task while non-task relevant snake (threatening), spider (threatening, subjectively evaluated as more arousing and unpleasant than snakes), and bird (non-threatening) images were presented. The authors found that snake images elicited larger early (P1) exogenous attention-related brain potential amplitudes in comparison to birds, and no differences in P1 amplitudes were found between spiders and birds. Interestingly, the authors also reported that spiders gained the same relevance as snakes as the focus of attention in late attention-related potential when stimuli were presented for 180 ms, and elicited greater amplitudes in late-related potential when stimuli were presented for 360 ms.

These studies seemed to be aligned with the findings of Le et al. (2013), which demonstrated that medial and dorsolateral pulvinar neurons of lab-reared Japanese monkeys (*Macaca fuscata*) responded more quickly and strongly to images of snakes than responded to the presentation of other, neutral or threatening, visual stimuli. Later, Le et al. (2016) found a significant increase in the strength of gamma oscillations in the pulvinar neuronal activity of Japanese monkeys in the early phase when images of snakes were presented. On the other hand, an increase in the strength of gamma oscillations in the pulvinar happened in the late phase when the stimuli were images of monkey faces. Recently, Dinh et al. (2022) recorded Japanese monkeys' amygdalar neurons activity and found that they responded faster and stronger to snake images than to other predators' images as well.

Thus, many studies seemed to indicate that subcortical structures have decisive roles in response to some kinds of fear-relevant visual stimuli (e.g., Le et al., 2013; Maior et al., 2011). However, there are different hypotheses related to threat and fear processing. Li and Keil (2023), for example, suggested that the extant literature about threat processing is incompatible with the privileged threat processing in the amygdala and with the amygdala providing instructions in threat processing to the sensory cortex. Instead, the authors find it more likely that a quick threat processing would initially involve a threat evaluation in the sensory cortex, then a threat processing in the threat network, and, finally, an advanced threat processing in a multiple large-scale brain network.

It is possible that the same subcortical structures allegedly related to the early visual detection of snakes play different roles in different phases of perception. Almeida et al. (2015), for example, while investigating the roles of spatial demands (central vs. peripheral vision) during fMRI tasks, suggested that the superior colliculus, pulvinar and amygdala, subcortical structures that have foveal representation, play different roles in snakes' bodies visual processing. The authors found increased amygdala responses to images of snakes' bodies presented in the center or in the periphery of the left hemifield. The superior colliculus and pulvinar presented a similar pattern. Thus, Almeida et al. (2015) argued that mechanisms of central and peripheral vision share the same structures in routing implicit or explicit relevant threatening information and claim that their "*findings suggest multiple phylogenetic fingerprints in the responses of subcortical structures to fear-relevant stimuli*" (Almeida et al., 2015, p. 2). Roles played by the superior colliculus, pulvinar, and amygdala could facilitate the detection of snakes in the periphery of the visual field (capture of exogenous attention) and, once the image was brought to the foveal visual field (central), the same structures would play other roles in the exchange of information with cortical areas, in the maintenance of endogenous (explicit) attention and in identification. In a way, the data and discussion proposed by Almeida et al. (2015) draw the focus from the idea that the superior colliculus, pulvinar, and amygdala are structures primarily related to implicit and emotional processing and create a bridge to ideas that propose both preattentive and conscious roles of these same structures, through a rich network of connections between cortical and subcortical areas (Pessoa & Adolphs, 2010).

Despite the discussion about the brain mechanisms behind this, there is indeed evidence of differentiated neuronal processing for snakes. However, there is still doubt about how the functioning of these mechanisms would be translated into behavior. This idea is dealt with in the next question.

Do Snakes Really Generate Differentiated Behavioral Responses in Primates?

As the FM would be particularly sensitive to snake features, as suggested in studies described in our previous question, it would be important to investigate the behavioral output of these mechanisms today. Öhman and Mineka (2003) argued that the primate observer would notice and react faster towards snakes. Moreover, this visual detection and reaction would happen independent of cognitive control. For example, Öhman et al. (2001) found that participants responded faster to a picture of a snake or a spider (threatening stimuli) among matrices of four or eight flowers or mushrooms (non-threatening stimuli) than to pictures of a flower or a mushroom among serpents or spiders. Further, the participants were equally fast responding to the threatening stimuli among eight or three distractors, which was not true for the detection of the non-threatening stimuli, as these elicited significantly faster responses among three threatening distractors. These reports fit the propositions expressed in the FM/ Snake Detection Theory (Isbell, 2006, 2009; Öhman & Mineka, 2003). However, results from other studies offered different explanations, as discussed below.

Brosch and Sharma (2005) and Blanchette (2006), for example, compared phylogenetic (that may have caused anatomical/physiological/behavioral impact as a result of a long ecological/evolutionary relationship throughout several generations) and ontogenetic (that may have caused impact because of development and experience of one individual, throughout its life span) fear-relevant (something that may cause fear) and fear-irrelevant stimuli in visual search tasks and found no evidence that the phylogenetic visual stimuli have an advantage in detection. These results seemed to suggest that the threat component was causing the faster responses. However, Blanchette (2006) also argued that "*it is possible that the detection of recent threats is based on mechanisms that are different and that have evolved more recently, while the detection of ancient threats is based on another set of mechanisms, using subcortical pathways"* (p. 1500). The authors concluded that, with their data set, it was impossible to state whether there were different processes for different types of stimuli. Brosch and Sharma (2005) discuss something similar and argue that the effects caused by an ontogenetic threat could make the effect caused by a phylogenetic threat become less evident or disappear due to different processes. Besides that, Lipp et al. (2004) questioned the suitability of visual search tasks to investigate attentional capture by fear-relevant stimuli, as we will see in the next couple of paragraphs.

It is known that while an individual is aware of a threat, levels of arousal and valence can affect cognitive performance (Reul & de Kloet, 1985), especially when a participant is actively looking for, and responding to, a particular stimulus, as in a visual search task. On the other hand, the responses due to arousal and valence would not exclude the effect of a FM shaped by evolution, although they may obscure the differences between the behavioral effects caused by both.

For example, humans reacted to images of snakes in striking postures faster than to images of snakes in resting postures (Masataka et al., 2010). In the same vein, macaques (*Macaca mulatta*) reacted more strongly to snake models in striking postures than to non-striking postures (Etting & Isbell, 2014). In keeping with these results, Le et al. (2014) showed that pulvinar neurons fired more strongly to snakes in striking postures, compared to non-striking ones. Although EEG studies could not find correlations between fear, arousal, and event-related potentials in response to snakes (Grassini et al., 2016; Van Strien, Eijlers et al., 2014; Van Strien, Franken et al., 2014), it seemed that human and non-human primates somehow could match their responses to the threat level. It is not yet clear which characteristics are responsible for the efficiency in the visual detection of snakes in different configurations.

Thus, it is possible that different methodologies might be measuring different processes (e.g., visual detection, subjective fear, conscious perception of threat, conscious motor responses) or an outcome of all of them. There is a considerable amount of cross-talk between cortical and subcortical systems, with possible interactions between cognitive, affective, and motor responses to different signals (Pessoa et al., 2021) and separating different components of fear responses is not a simple task.

To minimize the effect that experience with a threatening stimulus could cause, studies that measured reactions before visual awareness were developed. Snakes have been shown to elicit distinctively faster reactions when presented outside of visual awareness for a few moments through the continuous flash suppression (CFS) technique (Tsuchiya & Koch, 2005). Gomes et al. (2016) showed that the image of snakes and spiders are consciously perceived faster than those of birds (breaking-CFS; Jiang et al., 2007), but when the task is performed with the participant's non-dominant eye (arguably a stronger suppression condition), only snakes had an advantage over birds. Indeed, spiders were more negatively rated in valence and arousal than snakes and low-level features (luminance and spatial frequency) were controlled, therefore it was unlikely that the differences in arousal, valence, luminance, or spatial frequency were responsible for these results. In another experiment, using the random image structure evolution (RISE; Sadr & Sinha, 2004) technique, Kawai and He (2016) found results pointing in the same direction as humans discerned degraded images of snakes more accurately than the images of other animals (birds, cats, and fishes) under the same conditions. These results indicate that the advantage in the response to snakes compared to the reaction to other stimuli, including other animals, was significant, especially when the stimuli were presented in degraded perceptual conditions since these studies simulated camouflaged snakes. Gomes et al. (2018) when presenting images of snakes and birds with manipulated spatial frequency, obtained results that indicated that the conscious perception of snake images occurred faster when these images were presented in low spatial frequency (global shape, no details, blurred image), but not in high spatial frequency (detailed contours). The difference between the detection of snakes and other stimuli would be more pronounced in more challenging visibility conditions, as Soares et al. (2014) had already suggested when performing a series of tasks that hindered the visual detection of spiders (another common object of phobias and rated negatively by the general population) and snakes.

In summary, our second question led us to the work of Öhman et al. (2001), to some methodological considerations that arose from there (e.g., Blanchette, 2006; Brosch & Sharma, 2005; Lipp et al., 2004), and to the data obtained after methodological adaptations. The suitability of visual search tasks, the existence of mechanisms (other than FM) possibly responsible for the responses found by Öhman et al. (2001), the nature of stimuli used in comparison with snake images, the lack of weighting on arousal and valence, the conscious (and possibly influenced by subjectivity) way of giving the answers to the tasks, and the lack of control of the low-level features of the stimulus guided the creation of new methodologies. These new methodologies have apparently filtered and eliminated some of the variables that could be influencing the results and many studies continue to show a bias for faster and more efficient detection of snake images compared to other visual stimuli (e.g., Gomes et al., 2016, 2018; Kawai & He, 2016).

Another important issue to be investigated is that behavioral/physiological responses to different stimuli may vary, depending on the intricate and inseparable interaction between ontogeny and the heritability of genetic information that may increase the chance of a particular outcome happening. Some researchers approached the issue and tried to unravel it, as described in the next section.

If Differences Exist, Are They Acquired Throughout Life, or Are They Genetically Inherited?

As suggested by Öhman and Mineka (2003), the FM relies on a specialized neural circuitry shaped by evolution, that would be automatically activated, among other, by snake features, independent of cognitive control. If the advantage in detecting/reacting to snakes was inherited evolutionarily, children with little or no experience with snakes would be expected to manifest the same or a similar pattern. However, most of the studies were usually done with adult human participants, who were supposed to have direct or indirect experiences with snakes and other threatening stimuli. Thus, one of the ways to begin to separate the attentional priority potentially generated by ontogeny from the attention produced by a supposed FM inherited and selective for certain evolutionary relevant stimuli would be to test naïve individuals to those stimuli.

Then, LoBue and Deloache (2008) tested children between 3 and 5 years of age and adults in visual search tasks and obtained results consistent with those found by Öhman et al. (2001) for all ages. Another study found that infants under one year old oriented their attention to snakes faster than to flowers (Bertels et al., 2018). In the same vein, LoBue et al. (2017) found that infants (4–24 months) fixed their gaze more quickly on snakes and probes that appeared in the position of snakes than on frogs and probes that appeared in their place. LoBue et al. (2017) also found that the same infants visually fixated on probes faster after viewing trials that contained an angry face compared to trials that contained a happy face. There was no difference in results between different ages in the experiment involving snakes (vs. frogs), but there were differences between different ages in the experiment employing facial expressions. According to the authors, this would suggest an inborn predisposition to detect and/or react to snakes while the processing of faces would depend more on age and development. Later, neural responses to snake images were found to be more widespread and higher in amplitude when compared to neural responses obtained from the presentation of frogs and caterpillars' images to 7–10-month-old human infants, suggesting, once again, an inborn predisposition to rapidly detect snakes (Bertels et al., 2020, 2023). However, according to Bertels et al. (2023), although there seems to be an innate device that provides the detection of snakes already by infants less than one year of age, as there is maturation of the visual system, neural responses are more intense.

Similarly, if snakes really acted as an evolutionary pressure that shaped the primate visual system before the emergence of the human species, it would be expected that other primates from the same evolutionary branch would also respond quickly to snakes. Thus, by using lab-reared Japanese monkeys as subjects, Shibasaki and Kawai (2009) showed that snakes among flowers were detected faster than the reverse. Kawai and Koda (2016) showed that snake-naïve lab-reared Japanese monkeys reacted to a single snake picture among eight animal pictures (koalas) more quickly than a koala among snakes. However, when snakes' images were replaced by spiders, no such difference in the reaction was observed.

These results seem to indicate that the images of snakes provoke similar reactions in individuals of different primate species and different ages, which does not seem to be the case when other visual stimuli are tested. It is true that few primate species were tested so far, and that studies with infants demand adaptations, making the comparisons between studies somewhat limited. In addition, many of these studies have the same limitations that are the major sources of criticism directed to visual search tasks to investigate an inherited predisposition to visually detect a stimulus.

It is also worth noting that Öhman and Mineka (2003) did not state that the FM would necessarily generate fear of snakes and the visual cues that provide fast visual detection of snake images might not be associated with arousal or subjective fear. Therefore, at least when it comes to early and automatic visual detection *per se*, we are not necessarily discussing threat/fear processing.

What Characteristics Are There in Snakes to Elicit Privileged Neural Processing and Fast Behavioral Responses?

Some of the main questions raised by Öhman and Mineka (2003) in "*The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear*" orbit around the relationships between the sensory mechanisms of visual detection and the characteristics of snakes that would activate these mechanisms. The authors speculated that since the processing of visual information by the pathways preceding the cerebral cortex is coarse, the visual characteristics of snakes that would facilitate their detection and response should be basic and simple. That is, the complex configuration of the various characteristics responsible for what is meant visually by a snake would require more complex cortical processing, while the rapid and initial reaction, responsible by visual detection, would be based on simple characteristics, like the elongated and curvilineal shape.

In fact, images of objects and animals that have curvilinear shapes (e.g., snakes and coiled wires) cause a faster behavioral response than other visual stimuli (LoBue, 2014; LoBue & DeLoache, 2011). Van Strien et al. (2016), for example, found that a larger EPN on occipital and parieto-occipital electrodes was caused by images of snakes (longer and more curvilinear) than by spiders and worms images (with not so long and curved limbs and body axis, respectively), and spider and worms elicited larger EPN than beetles.

Curiously, Gayet et al. (2019) compared the detection efficiency to bicycle and to car images (as bicycles and cars have a similar perimeter/surface ratio of snakes and non-elongated animals, as birds, respectively) using the breaking-CFS (Jiang et al., 2007) and found a significant advantage to the detection of bicycles when the images were low-pass filtered or unfiltered (images with low spatial frequency components). These results are very similar to what Gomes et al. (2018) found when using the same methodology while investigating snake image detection compared to bird image detection. Gayet et al. (2019), in a criticism of Gomes et al. (2018), concluded that if there is a specialized subcortical pathway that favors the detection of snakes, and consequently also favors the detection of bicycles, "*this pathway capitalizes on shape detection rather than fear detection*" (Gayet et al., 2019, p. 930). If true, this statement would exclude the need for subjective experience and arousal for the initial higher efficiency in the primate visual detection of higher perimeter-to-surface ratio stimuli. In a reply to Gayet et al. (2019), Gomes et al. (2019, p. 936) argued *that "stimuli shape is one prime feature for this fast-initial processing, relevant for grabbing early visual attention."*

Although the shape of snakes seems to be paramount for early visual detection, Van Strien et al. (2016) stated that other threat-relevant cues should be involved in the strong cortical response. Van Strien and Van der Peijl (2018) suggested that the high-contrast energy at midrange spatial frequencies, typical of some poisonous animals (Cole & Wilkins, 2013), seems to enhance the EPN at the occipital electrodes. Grassini et al. (2019) also argue something beyond the snake's shape that could be relevant to the primate's responses to snake images. The authors found that images of snakes with a diamond shape scales pattern on their skins elicited a higher EPN than a snake with no such pattern. Furthermore, when using only images of the diamond shape scales' skin pattern (and no other snake features), compared to images with no such pattern, the EPN was larger as well.

Interestingly, Beligiannis and Van Strien (2019) found that blurred and non-blurred snake pictures elicited, respectively, higher EPN than blurred and non-blurred spider and bird images, and that non-blurred images of snakes elicited much higher EPN than blurred images of snakes, suggesting that EPN in response to snake images is larger when local characteristics (e.g., scales) are clearly visible. These findings add valuable information to the Snake Detection Theory investigation, once the elongated/curvilinear global shape of snakes represents a low spatial frequency attribute, and the snake scales pattern represents a high spatial frequency attribute. In a way, these data seem to corroborate with Pessoa and Adolphs (2010), when they take into account that there may be several cortical and subcortical pathways for emotional processing.

In addition, snakes may be found in different configurations, that is, coiled, stretched, wrapped around trunks or branches, or in striking position. As noted above, some studies have shown differential responses to some configurations (Etting & Isbell, 2014; Le et al., 2014), which indicate that curvilinear shapes may not be the sole driving visual input. Few studies, nonetheless, have evaluated the impact of scale and color patterns in fast visual detection. For instance, Wombolt and Caine (2016) showed a moderate effect of scaled patterns in eliciting visual assessment in marmosets. Using EEG data, Bertels et al. (2023) showed that color information is not required for rapid visual detection of snakes by 6–11-month-old humans. Given that some of these features may be less conspicuous in low-spatial resolution, especially in low-luminance contexts, it is likely that their impact is not critical for early detection, although some impact seems to exist at some point (e.g., Grassini et al., 2019). Maybe a temporal comparison of neural responses to elongated shapes and scale patterns could bring valuable clues about different reactions to different snake features and about the importance of each feature to different phases of perception and reaction.

How Can the Context and the Definition of Key Concepts Interfere With the Data Interpretation?

It is important to strictly define the concepts of what is being investigated since fear and detection seem to be words that may have very flexible interpretations. For example, Öhman and Mineka (2003) suggested that the FM would involve subcortical structures. This suggestion holds a conceptual problem regarding the flexibility of the definition of fear. Fear, while subjective experience, would be a product of cortical cognitive circuits, and some authors, to avoid misinterpretation, rather use the term "defensive survival circuit" instead of "FM," to name this set of subcortical structures (Ledoux, 2014, 2021). That is, the activation of the defensive survival circuit/FM would help to modulate conscious feelings, like fear, but these feelings would depend on cortical processing. The integration of these subcortical structures with cortical regions would later give rise to complex behaviors based on emotions and subjective experiences to better cope with the surroundings and increase survival chances (Ledoux, 2014, 2021; Pessoa et al., 2021). Anyway, the misuse and poor definition and contextualization of the word fear to indicate automatic, exogenous, implicit attention-grabbing can create noise in the discussion. There is an ample and heated discussion about the definition of emotions, especially about the lack of clarity in what people (including scientists) mean by emotions (Adolphs et al., 2019).

On the other hand, it is curious that when authors make it clear that they are dealing with subjective fear that flourishes after the stimulus becomes evident, snakes of the Viperidae taxon, one of the taxa Isbell cited as possible selective pressure when she developed the Snake Detection Theory (Isbell, 2006), and one of the most poisonous groups of snakes, were identified as the snakes that elicit the most subjective fear in humans (Radlová et al., 2019). Curiously, these animals possess some very distinguishable characteristics, such as salient raised scales, while the fossorial serpents that elicited less subjective fear does not present this feature in a such salient and distinguishable way (Radlová et al., 2019). Later, a study using the same groups of snakes as visual stimuli, found that viperid snakes (subjectively evaluated as more frightening), when compared to fossorial non-venomous snakes (subjectively evaluated as less frightening), triggered higher skin resistance amplitude in human participants (Landová et al., 2020). These data seem to indicate that serpents could belong to distinct clusters of stimuli, and humans react differently to them, at least after the stimulus become overt. Furthermore, different snake features could affect different perceptual processes (elongated/curvilinear shape for early attention-grabbing and raised scales patterns to skin resistance/subjective fear). In this sense, snakes could be interpreted as a set of visual stimuli instead of only one stimulus depending on the objective of the study.

Ecological context and evolutionary history may create confounds as well. For example, many serpent species are ambush/seat-and-wait predators and remain cryptic in the environment (e.g., amid leaf litter) until they strike their preys, in a way that the visual sensitivity to snakes' overall shape could act as an evolutionary pressure on the snake's cryptic strategy. Thus, the more sensitive the prey is to the presence of a dangerous snake, the greater its chances of escaping, and the more cryptic is the snake, the greater the chances of the snake feeding or defending itself.

However, certain species of serpents are also primates' preys (e.g., Falótico et al., 2018). Moreover, natural selection on venomous snakes supposedly would have also favored the presence of cues throughout evolutionary history to keep predators away once the snake is detected (Ruxton et al., 2004). Thus, a complex arms race involving crypticity, visual sensitivity, and signaling has likely been going on for millions of years and different snake species could be easily or hardly detected depending on the ecological and evolutionary context (e.g., substrate, prey/predator sensory system). If the proposed methodology of a study does not observe this matter from ecological and evolutionary angles, it is possible that confounding variables could interfere with the results and their interpretation. For instance, although some primate species show obvious behavioral responses to partially exposed snakes (Etting & Isbell, 2014) and even to only 2.7 cm snakeskin (Isbell & Etting, 2017), there is an ample variety in behavioral responses to snakes, and some of these responses could be very subtle. Bearded capuchin monkeys (*Sapajus libidinosus*), for example, often perform mobbing behaviors, alarm calls, and particular facial expressions in encounters with snakes of potentially dangerous species (or mimics of dangerous species), while none of these behaviors were observed while the monkeys predate non-venomous snakes (Falótico et al., 2018). White-faced capuchin monkeys (*Cebus capucinus*) as young as 4 months old and older were less likely to respond to a white/no-scale patterned snake-like model than to dangerous snake species models (Meno et al., 2013a, 2013b).

Coelho et al. (2019) make very interesting points about modular theories and the mismatch between laboratory and ecological evidence. However, we emphasize that visual attention and detection are hard variables to measure, and specific details of visual detection are only possible to be investigated in very controlled environments, in a way that a trade-off between accuracy and ecological validity, unfortunately, has to be done when designing the experiments. The lack of vocalizations and obvious body movements does not mean necessarily that there is no visual detection or identification.

Zeller et al. (2022) also bring relevant criticisms toward the Snake Detection Theory literature and argued that laboratory research has biased the analysis towards snake stimuli and a limited number of primate and snake species. Indeed, as we have voiced elsewhere (Soares, Kessel et al., 2017), it is true that most neuroscientific studies, unfortunately, rely on very few experimental species for different reasons, and this is likely to be a limiting factor for the foreseeable future. However, there is little reason to suppose that the minor visual differences across snake species would critically modulate the saliency over the general visual features of venomous snakes, particularly in early detection. Furthermore, while many lab studies bias their comparisons by focusing on snakes and few, if any, other evolutionary-relevant stimuli, there are efforts to broaden the scope of comparison with conspecifics, raptors, and carnivores (e.g., Dinh et al., 2018; Le et al., 2013, 2016).

Conclusion

This article aimed to take the ideas expressed in the seminal publication of Öhman and Mineka (2003), as well as in the results of some previous publications that paved the way for that article (e.g., Mineka & Öhman, 2002; Öhman et al., 2001). It also aimed at examining the state-of-the-art on the matter, since the ideas suggested in the early 2000s still needed to go through tests, new methodologies, and questions which arose over time. After 20 years of research since the publication of "The malicious snake: Snakes as a prototypical stimulus for an evolved module of fear," new technologies and study designs have enabled the accumulation of information relevant to this debate.

Although, in an ecological sense, there is no reason to call a living being that is inserted in food webs "malicious," in a cultural sense it is totally understandable that a predator may be interpreted as evil and malicious by the descendants of its potential preys. So far, we have reasons to believe that this long-term ecological relationship has left genetic heritage in modern humans and non-human primates. Based on the state-of-the-art so far, Landová et al. (2020) suggested that future studies could create artificial stimuli to separate the influence that snakes' visual characteristics, cause on the attention and emotion of primate preys and predators. Öhman and Mineka (2003) had already suggested that delineating the characteristics responsible for the *fear* generated by images of snakes would enable the creation of a "*super fear stimulus*" that would depict an "*archetypal evil*" (Öhman & Mineka, 2003) as represented in the human brain.

Several studies suggest that the superior colliculus, pulvinar and amygdala, and, consequently, areas of the visual cortex, respond more intensely and more quickly to images of snakes (compared to other visual stimuli). These results are compatible with the idea that the presence of snakes, as selective pressure, produced changes in the visual system of modern primates (Isbell, 2006, 2009). This heritage, according to the suggestion of Öhman and Mineka (2001, 2003) would be a specialized primate FM, a set of subcortical structures that would help anthropoid primates to react quickly enough to increase the chances of survival in the face of significant predators to primate evolution. Concurrently, there does not seem to be much doubt that the extensive connections between cortical and subcortical structures are extremely relevant to the overall outcomes.

As for the behavioral manifestation that was due to the suggested neural mechanisms, a number of studies have recorded preferential/faster motor reaction to snakes. In view of the criticism directed to the methodology initially used to measure the outcomes of a possible functioning of the FM, and to the alternative explanations to the FM for a more efficient processing, different methodologies emerged. Breaking-CFS (Jiang et al., 2007) and RISE (Sadr & Sinha, 2004) methodologies, for example, were used to investigate the efficiency in the access of images to awareness. Different studies have also behaviorally investigated the spatial frequencies that could be efficiently transmitted by the low road and the FM (e.g., Gomes et al., 2018). The results usually point to a compatibility to the ideas expressed by the Snake Detection Theory and FM theoretical framework.

Regarding the contention between innate versus acquired on this topic, the reviewed literature suggests an important distinction. Although the number of studies is limited, very young human participants or lab-reared non-human primate subjects have shown faster responses to snakes, as discussed in our third question. Nevertheless, studies failed to show physiological manifestations of fear during the presentation of snakes to young children, suggesting then that the early attention-capture induced by snakes is not necessarily associated with fear. These results support the proposition that fast or preferential visual detection/reaction of snakes has been "hard-wired" in the phylogenetic history of anthropoid primates, regardless of emotion responses.

There is also evidence that the body shape of snakes is essential for the initial capture of attention. Different studies reveal that elongated/curvilineal images, with low area/border ratio would grab visual attention more efficiently. Subsequently, other visual characteristics, such as the arrangement and shape of scales, and the intense exchange of information between subcortical and cortical structures, would help maintain and amplify certain responses.

These outcomes would possibly be affected by the environmental context and idiosyncrasies, which would interfere with the perception of the stimulus and the manifestation of behavioral responses. These phases of perception, from detection to identification and reaction, the physiological and behavioral responses that characterize them, and the technical limitations to investigate them, should be contemplated in the design of the studies and in the interpretation of the results thereof.

In short, several studies conclude that the anthropoid primates tested react faster to images of snakes than to other stimuli. Future studies should separate the causes of this privileged reaction by filtering the variables that may be causing this effect: comparisons between capturing visual attention and manual motor activity, for example. Also, there is evidence that these reactions occur mostly due to a bottom-up process. Top-down participation however cannot be ruled out, although the extent this influence is yet to be determined. Further investigations on temporal patterns of activity in different brain structures during the presentation of threatening stimuli are also warranted. Finally, research on the area should incorporate a broader comparative approach, including diverse primate species and, perhaps more critically, other phylogenetically relevant threatening stimuli (e.g., carnivores, raptors). These would provide much needed data to shed light on the historical interactions between such species and how they may have contributed to the evolution of primate nervous system.

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References

Adolphs, R., Mlodinow, L., & Barrett, L. F. (2019). What is an emotion? *Current Biology*, *29*(20), R1060–R1064. https://doi.org/10.1016/j.cub.2019.09.008

Åhs, F., Rosén, J., Kastrati, G., Fredrikson, M., Agren, T., & Lundström, J. N. (2018). Biological preparedness and resistance to extinction of skin conductance responses conditioned to fear relevant animal pictures: A systematic review. *Neuroscience & Biobehavioral Reviews*, *95*, 430–437. https://doi.org/10.1016/j.neubiorev.2018.10.017

Almeida, I., Soares, S. C., & Castelo-Branco, M. (2015). The distinct role of the amygdala, superior colliculus and pulvinar in processing of central and peripheral snakes. *PLoS One*, *10*(6), e0129949. https://doi.org/10.1371/journal.pone.0129949

Beligiannis, N., & Van Strien, J. W. (2019). Blurring attenuates the early posterior negativity in response to snake stimuli. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, *146*, 201–207. https://doi.org/10.1016/j.ijpsycho.2019.09.002

Bertels, J., Bayard, C., Floccia, C., & Destrebecqz, A. (2018). Rapid detection of snakes modulates spatial orienting in infancy. *International Journal of Behavioral Development*, *42*(4), 381–387. https://doi.org/10.1177/0165025417693955

Bertels, J., Bourguignon, M., de Heering, A., Chetail, F., De Tiège, X., Cleeremans, A., & Destrebecqz, A. (2020). Snakes elicit specific neural responses in the human infant brain. *Scientific Reports*, *10*(1), 7443. https://doi.org/10.1038/s41598-020-63619-y

Bertels, J., de Heering, A., Bourguignon, M., Cleeremans, A., & Destrebecqz, A. (2023). What determines the neural response to snakes in the infant brain? A systematic comparison of color and grayscale stimuli. *Frontiers in Psychology*, *14*, 1027872. https://doi.org/10.3389/fpsyg.2023.1027872

Blanchette, I. (2006). Snakes, spiders, guns, and syringes: How specific are evolutionary constraints on the detection of threatening stimuli? *Quarterly Journal of Experimental Psychology*, *59*(8), 1484–1504. https://doi.org/10.1080/02724980543000204

Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, *77*(1), 32–48. https://doi.org/10.1037/h0028589

Brosch, T., & Sharma, D. (2005). The role of fear-relevant stimuli in visual search: A comparison of phylogenetic and ontogenetic stimuli. *Emotion (Washington, D.C.)*, *5*(3), 360–364. https://doi.org/10.1037/1528-3542.5.3.360

Coelho, C. M., Suttiwan, P., Faiz, A. M., Ferreira-Santos, F., & Zsido, A. N. (2019). Are humans prepared to detect fear and avoid snakes? The mismatch between laboratory and ecological evidence. *Frontiers in Psychology*, *10*, 2094. https://doi.org/10.3389/fpsyg.2019.02094

Cole, G. G., & Wilkins, A. J. (2013). Fear of holes. *Psychological Science*, *24*(10), 1980–1985. https://doi.org/10.1177/0956797613484937

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes*, *16*(4), 372–389. http://dx.doi.org/10.1037/0097-7403.16.4.372

Dinh, H. T., Meng, Y., Matsumoto, J., Setogawa, T., Nishimaru, H., & Nishijo, H. (2022). Fast detection of snakes and emotional faces in the macaque amygdala. *Frontiers in Behavioral Neuroscience*, *16*, 839123. https://doi.org/10.3389/fnbeh.2022.839123

Dinh, H. T., Nishimaru, H., Matsumoto, J., Takamura, Y., Le, Q. V., Hori, E., Maior, R. S., Tomaz, C., Tran, A. H., Ono, T., & Nishijo, H. (2018). Superior neuronal detection of snakes and conspecific faces in the macaque medial prefrontal cortex. *Cerebral Cortex (New York, N.Y.: 1991)*, *28*(6), 2131–2145. https://doi.org/10.1093/cercor/bhx118

Elorette, C., Forcelli, P. A., Saunders, R. C., & Malkova, L. (2018). Colocalization of tectal inputs with amygdala-projecting neurons in the macaque pulvinar. *Frontiers in Neural Circuits*, *12*, 91. https://doi.org/10.3389/fncir.2018.00091

Etting, S. F., & Isbell, L. A. (2014). Rhesus macaques (*Macaca mulatta*) use posture to assess level of threat from snakes. *Ethology*, *120*, 1177–1184. https://doi.org/10.1111/eth.12293

Falótico, T., Verderane, M. P., Mendonça-Furtado, O., Spagnoletti, N., Ottoni, E. B., Visalberghi, E., & Izar, P. (2018). Food or threat? Wild capuchin monkeys (*Sapajus libidinosus*) as both predators and prey of snakes. *Primates: Journal of Primatology*, *59*(1), 99–106. https://doi.org/10.1007/s10329-017-0631-x

Gayet, S., Stein, T., & Peelen, M. V. (2019). The danger of interpreting detection differences between image categories: A brief comment on "mind the snake: Fear detection relies on low spatial frequencies" (Gomes, Soares, Silva, & Silva, 2018). *Emotion (Washington, D.C.)*, *19*(5), 928–932. https://doi.org/10.1037/emo0000550

Gomes, N., Silva, S., Silva, C. F., & Soares, S. C. (2016). Beware the serpent: The advantage of ecologically-relevant stimuli in accessing visual awareness. *Evolution and Human Behavior*, *38*(2), 227–234. https://doi.org/10.1016/j.evolhumbehav.2016.10.004

Gomes, N., Silva, S., & Soares, S. C. (2019). "Threat-unrelated" properties: An ill-defined concept. A reply to "the danger of interpreting detection differences between image categories" (Gayet, Stein, & Peelen, 2019). *Emotion (Washington, D.C.)*, *19*(5), 933–937. https://doi.org/10.1037/emo0000632

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

Grassini, S., Holm, S. K., Railo, H., & Koivisto, M. (2016). Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. *Biological Psychology*, *121*(Pt A), 53–61. https://doi.org/10.1016/j.biopsycho.2016.10.007

Grassini, S., Valli, K., Souchet, J., Aubret, F., Segurini, G. V., Revonsuo, A., & Koivisto, M. (2019). Pattern matters: Snakes exhibiting triangular and diamond-shaped skin patterns modulate electrophysiological activity in human visual cortex. *Neuropsychologia*, *131*, 62–72. https://doi.org/10.1016/j.neuropsychologia.2019.05.024

He, H., Kubo, K., & Kawai, N. (2014). Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. *Neuroreport*, *25*(13), 1049–1053. https://doi.org/10.1097/WNR.0000000000000227

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/10.1016/j.jhevol.2005.12.012

Isbell, L. A. (2009). *The fruit, the tree, and the serpent*. Harvard University Press.

Isbell, L. A., & Etting, S. F. (2017). Scales drive detection, attention, and memory of snakes in wild vervet monkeys (*Chlorocebus pygerythrus*). *Primates*, *58*, 121–129. https://doi.org/10.1007/s10329-016-0562-y

Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science*, *18*(4), 349–355. https://doi.org/10.1111/j.1467-9280.2007.01902.x

Kaas, J.H., & Huerta, M.F. (1989). The subcortical visual system of primates. In H. D. Steklis, & & J. Erwin (Eds.), *Comparative Primate Biology Vol. 4*. New York, NY: Alan R. Liss.

Kawai, N., & He, H. (2016). Breaking snake camouflage: Humans detect snakes more accurately than other animals under less discernible visual conditions. *PLoS One*, *11*(10), e0164342. https://doi.org/10.1371/journal.pone.0164342

Kawai, N., & Koda, H. (2016). Japanese Monkeys (*Macaca fuscata*) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. *Journal of Comparative Psychology (Washington, D.C.: 1983)*, *130*(3), 299–303. https://doi.org/10.1037/com0000032

Kragel, P. A., Čeko, M., Theriault, J., Chen, D., Satpute, A. B., Wald, L. W., Lindquist, M. A., Feldman Barrett, L., & Wager, T. D. (2021). A human colliculus-pulvinar-amygdala pathway encodes negative emotion. *Neuron*, *109*(15), 2404–2412.e5. https://doi.org/10.1016/j.neuron.2021.06.001

Landová, E., Peléšková, Š, Sedláčková, K., Janovcová, M., Polák, J., Rádlová, S., Vobrubová, B., & Frynta, D. (2020). Venomous snakes elicit stronger fear than nonvenomous ones: Psychophysiological response to snake images. *PLoS One*, *15*(8), e0236999. https://doi.org/10.1371/journal.pone.0236999

Le, Q. V., Isbell, L. A., Matsumoto, J., Le, V. Q., Hori, E., Tran, A. H., Maior, R. S., Tomaz, C., Ono, T., & Nishijo, H. (2014). Monkey pulvinar neurons fire differentially to snake postures. *PLoS One*, *9*(12), e114258. https://doi.org/10.1371/journal.pone.0114258

Le, Q. V., Isbell, L. A., Matsumoto, J., Le, V. Q., Nishimaru, H., Hori, E., Maior, R. S., Tomaz, C., Ono, T., & Nishijo, H. (2016). Snakes elicit earlier, and monkey faces, later, gamma oscillations in macaque pulvinar neurons. *Scientific Reports*, *6*, 20595. https://doi.org/10.1038/srep20595

Le, Q. V., Isbell, L. A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R. S., Tomaz, C., Tran, A. H., Ono, T., & Nishijo, H. (2013). Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(47), 19000–19005. https://doi.org/10.1073/pnas.1312648110

Ledoux, J. E. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. Simon & Shuster.

LeDoux, J. E. (2014). Coming to terms with fear. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(8), 2871–2878. https://doi.org/10.1073/pnas.1400335111

LeDoux, J. E. (2021). As soon as there was life, there was danger: The deep history of survival behaviours and the shallower history of consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*, 20210292. https://doi.org/10.1098/rstb.2021.0292

Li, W., & Keil, A. (2023). Sensing fear: Fast and precise threat evaluation in human sensory cortex. *Trends in Cognitive Sciences*, S1364-6613(23) 00001-3. Advance online publication. https://doi.org/10.1016/j.tics.2023.01.001

Lipp, O. V., Derakshan, N., Waters, A. M., & Logies, S. (2004). Snakes and cats in the flower bed: Fast detection is not specific to pictures of fear-relevant animals. *Emotion (Washington, D.C.)*, *4*(3), 233–250. https://doi.org/10.1037/1528-3542.4.3.233

LoBue, V. (2014). Deconstructing the snake: The relative roles of perception, cognition, and emotion on threat detection. *Emotion (Washington, D.C.)*, *14*(4), 701–711. https://doi.org/10.1037/a0035898

LoBue, V., Buss, K. A., Taber-Thomas, B. C., & Pérez-Edgar, K. (2017). Developmental differences in infants' attention to social and nonsocial threats. *Infancy: The Official Journal of the International Society on Infant Studies*, *22*(3), 403–415. https://doi.org/10.1111/infa.12167

Lobue, V., & DeLoache, J. S. (2008). Detecting the snake in the grass: Attention to fear-relevant stimuli by adults and young children. *Psychological Science*, *19*(3), 284–289. https://doi.org/10.1111/j.1467-9280.2008.02081.x

LoBue, V., & DeLoache, J. S. (2011). What's so special about slithering serpents? Children and adults rapidly detect snakes based on their simple features. *Visual Cognition*, *19*(1), 129–143. https://doi.org/10.1080/13506285.2010.522216

Maior, R. S., Hori, E., Barros, M., Teixeira, D. S., Tavares, M. C., Ono, T., Nishijo, H., & Tomaz, C. (2011). Superior colliculus lesions impair threat responsiveness in infant capuchin monkeys. *Neuroscience Letters*, *504*(3), 257–260. https://doi.org/10.1016/j.neulet.2011.09.042

Masataka, N., Hayakawa, S., & Kawai, N. (2010). Human young children as well as adults demonstrate 'superior' rapid snake detection when typical striking posture is displayed by the snake. *PLoS One*, *5*(11), e15122. https://doi.org/10.1371/journal.pone.0015122

Meno, W., Coss, R. G., & Perry, S. (2013a). Development of snake-directed antipredator behavior by wild white-faced capuchin monkeys: I. Snake-species discrimination. *American Journal of Primatology*, *75*(3), 281–291. https://doi.org/10.1002/ajp.22106

Meno, W., Coss, R. G., & Perry, S. (2013b). Development of snake-directed antipredator behavior by wild white-faced capuchin monkeys: II. Influence of the social environment. *American Journal of Primatology*, *75*(3), 292–300. https://doi.org/10.1002/ajp.22109

Mineka, S., & Ohman, A. (2002). Phobias and preparedness: The selective, automatic, and encapsulated nature of fear. *Biological Psychiatry*, *52*(10), 927–937. https://doi.org/10.1016/s0006-3223(02)01669-4

Öhman, A. (2000). Fear. In G. Fink (Ed.), *Encyclopedia of stress* (2nd ed., pp. 15–19). Academic Press.

Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*(10), 953–958. https://doi.org/10.1016/j.psyneuen.2005.03.019

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, *130*(3), 466–478. https://doi.org/10.1037//0096-3445.130.3.466

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522. https://doi.org/10.1037/0033-295x.108.3.483

Öhman, A., & Mineka, S. (2003). The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. *Current Directions in Psychological Science*, *12*(1), 5–9. https://doi.org/10.1111/1467-8721.01211

Öhman, A., & Soares, J. F (1998). Emotional conditioning to masked stimuli: Expectancies for aversive outcomes following nonrecognized fear-relevant stimuli. *Journal of Experimental Psychology: General*, *127*(1), 69–82. http://dx.doi.org/10.1037/0096-3445.127.1.69

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11), 773–782. https://doi.org/10.1038/nrn2920

Pessoa, L., Medina, L., & Desfilis, E. (2021). Refocusing neuroscience: Moving away from mental categories and towards complex behaviours. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*, 20200534. https://doi.org/10.1098/rstb.2020.0534

Rádlová, S., Janovcová, M., Sedláčková, K., Polák, J., Nácar, D., Peléšková, Š, Frynta, D., & Landová, E. (2019). Snakes represent emotionally salient stimuli that may evoke both fear and disgust. *Frontiers in Psychology*, *10*, https://doi.org/10.3389/fpsyg.2019.01085

Rafal, R. D., Koller, K., Bultitude, J. H., Mullins, P., Ward, R., Mitchell, A. S., & Bell, A. H. (2015). Connectivity between the superior colliculus and the amygdala in humans and macaque monkeys: Virtual dissection with probabilistic DTI tractography. *Journal of Neurophysiology*, *114*, 1947–1962. https://doi.org/10.1152/jn.01016.2014

Reul, J. M., & de Kloet, E. R. (1985). Two receptor systems for corticosterone in rat brain: Microdistribution and differential occupation. *Endocrinology*, *117*(6), 2505–2511. https://doi.org/10.1210/endo-117-6-2505

Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding attack*. Oxford University Press.

Saalmann, Y. B., & Kastner, S. (2009). Gain control in the visual thalamus during perception and cognition. *Current Opinion in Neurobiology*, *19*(4), 408–414. https://doi.org/10.1016/j.conb.2009.05.007

Sadr, J., & Sinha, P. (2004). Object recognition and random image structure evolution. *Cognitive Science*, *28*(2), 259–287. https://doi.org/10.1016/j.cogsci.2003.09.003

Seligman, M. E. (1970). On the generality of the laws of learning. *Psychological Review*, *77*(5), 406–418. https://doi.org/10.1037/h0029790

Seligman, M. (1971). Phobias and preparedness. *Behavior Therapy*, *2*, 307–320. https://doi.org/10.1016/S0005-7894(71)80064-3

Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Sciences*, *10*(1), 38–45. https://doi.org/10.1016/j.tics.2005.11.008

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (*Macaca fuscata*): An evolutionarily predisposed visual system. *Journal of Comparative Psychology (Washington, D.C.: 1983)*, *123*(2), 131–135. https://doi.org/10.1037/a0015095

Shipp, S. (2003). The functional logic of cortico-pulvinar connections. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *358*, 1605–1624. https://doi.org/10.1098/rstb.2002.1213

Soares, S. C., Kessel, D., Hernández-Lorca, M., García-Rubio, M. J., Rodrigues, P., Gomes, N., & Carretié, L. (2017). Exogenous attention to fear: Differential behavioral and neural responses to snakes and spiders. *Neuropsychologia*, *99*, 139–147. https://doi.org/10.1016/j.neuropsychologia.2017.03.007

Soares, S. C., Lindström, B., Esteves, F., & Öhman, A. (2014). The hidden snake in the grass: Superior detection of snakes in challenging attentional conditions. *PLoS One*, *9*(12), e114724. https://doi.org/10.1371/journal.pone.0114724

Soares, S. C., Maior, R. S., Isbell, L. A., Tomaz, C., & Nishijo, H. (2017). Fast detector/first responder: Interactions between the superior colliculus-pulvinar pathway and stimuli relevant to primates. *Frontiers in Neuroscience*, *11*, 67. https://doi.org/10.3389/fnins.2017.00067

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101. https://doi.org/10.1038/nn1500

Van Strien, J. W., Christiaans, G., Franken, I. H., & Huijding, J. (2016). Curvilinear shapes and the snake detection hypothesis: An ERP study. *Psychophysiology*, *53*(2), 252–257. https://doi.org/10.1111/psyp.12564

Van Strien, J. W., Eijlers, R., Franken, I. H. A., & Huijding, J. (2014). Snake pictures draw more early attention than spider pictures in non-phobic women: Evidence from event-related brain potentials. *Biological Psychology*, *96*, 150–157. https://doi.org/10.1016/j.biopsycho.2013.12.014

Van Strien, J. W., Franken, I. H., & Huijding, J. (2014). Testing the snake-detection hypothesis: Larger early posterior negativity in humans to pictures of snakes than to pictures of other reptiles, spiders and slugs. *Frontiers in Human Neuroscience*, *8*, 691. https://doi.org/10.3389/fnhum.2014.00691

Van Strien, J. W., & Van der Peijl, M. K. (2018). Enhanced early visual processing in response to snake and trypophobic stimuli. *BMC Psychology*, *6*(1), 21. https://doi.org/10.1186/s40359-018-0235-2

Wombolt, J. R., & Caine, N. G. (2016). Patterns on serpentine shapes elicit visual attention in marmosets (*Callithrix jacchus*). *American Journal of Primatology*, *78*(9), 928–936. https://doi.org/10.1002/ajp.22563

Zeller, K., Garcia, C., Maille, A., Duboscq, J., Morino, L., Dezecache, G., & Bonnet, X. (2022). Primate–predator interactions: Is there a mismatch between laboratory and ecological evidence? *International Journal of Primatology*. https://doi.org/10.1007/s10764-022-00331-w