

To Fear or Not to Fear? – The Effect of Early Posterior Negativity on Reaction Times in Response to Threatening Animal Stimuli

Master's Degree Programme in Human Neuroscience Master's thesis Faculty of Medicine

> Author: Nelli Kraufvelin

> > 31.10.2023 Turku

The originality of this thesis has been checked in accordance with the University of Turku quality assurance system using the Turnitin Originality Check service.

Master's thesis

Subject: Master's Degree Programme in Human Neuroscience
Author: Nelli Kraufvelin
Title: To Fear or Not to Fear? – The Effect of Early Posterior Negativity on Reaction Times in Response to Threatening Animal Stimuli
Supervisor(s): Assistant Professor Henry Railo
Number of pages: 33 pages
Date: 31.10.2023

The snake detection theory (SDT) proposes snakes to have been the most important factor driving the evolution of the visually specialized, expanded brains of primates. Evidence from many studies has supported this idea, as it has been found that people are faster at detecting snakes among innocuous stimuli than they are at detecting innocuous stimuli in matrices of snakes or other threatening stimuli. In addition, electroencephalography (EEG) studies measuring electric potentials of the brain have found differential processing of snake pictures compared to other (innocuous and non-innocuous) animal stimuli, as they elicit particularly strong negative-going activity in the posterior channels at around 200-300ms after stimulus onset. This component called early posterior negativity (EPN) is known to be especially modulated by emotionally arousing stimuli. Faster reaction times to snakes as well as the EPN snake effect have been interpreted as evidence for the snake detection theory, yet no studies to date seem to have examined the possible correlation between the two. This study was conducted to investigate the matter. To increase the ecological validity to the results, a naturalistic paradigm was used. In this paradigm, participants reacted to snakes by standing in front of a large touch screen monitor, placing their finger on the screen before each trial. If an experimental stimulus was shown, the participants had to withdraw their arm away from the screen as fast as they could. Reaction times were measured both by simple reaction times measured from the moment that the participant's finger was removed from the screen, as well as acceleration, which was measured with an accelerometer that was attached to the participant's wrist. For the analyses, peak acceleration, which was calculated from the accelerometer data, was used. EEG was recorded throughout the experiment. As expected, snakes were found to elicit stronger EPN amplitudes compared to other animal stimuli. Moreover, a negative correlation between mean EEG amplitude at 200-300ms after stimulus onset, and reaction times, was found, meaning that stronger EPN was correlated with slower reaction times. This was opposite to what was expected, as faster reaction times as well as larger EPNs have both previously been associated with snakes. These surprising results suggest that the relationship between the EPN and reaction times is not as simple as assumed. It seems that the EPN is caused and modulated by a more complicated cognitive process than previously thought. The results from this study provide interesting and new insights into the EPN and its role in snake detection and otherwise. More research is needed to further these insights and provide even better understanding of this eventrelated component.

Key words: early posterior negativity, snake detection theory, mammalian fear module, EEG, ERP.

Table of contents

1	Introduction					
2	Bac	kground	6			
2	2.1	Theoretical Framework	6			
	2.1.1	The Mammalian Fear Module	6			
	2.1.2	Snake Detection Theory	6			
2	2.2	Electrophysiological Background	8			
	2.2.1	Electroencephalography	8			
	2.2.2	Event-related Potentials	9			
	2.2.3	Early Posterior Negativity	10			
3	Aim	S	12			
4	Met	hods and Materials	13			
4	l.1	Participants	13			
4	.2	Stimuli and Procedure	13			
4	.3	Instruments	14			
4	.4	Preprocessing	14			
4	.5	Data Analysis	15			
5	Res	ults	17			
5	5.1	Behavioral Results	17			
	5.1.1	Correlation Between RTs and Peak Acceleration	17			
	5.1.2	Reaction Times	17			
	5.1.3	Peak Acceleration	17			
5	5.2	Electrophysiological results	19			
	5.2.1	Visual Inspection	19			
	5.2.2	LME Analysis of the Electrophysiological Results	20			
6	Dis	cussion	22			
6	6.1	Behavioral Measures	22			
	6.1.1	Reaction Times	22			
	6.1.2	Peak Acceleration	23			
6	5.2	Early Posterior Negativity	23			
6	5.3	Future Work and Limitations	26			
7	Cor	clusions	27			
References						

1 Introduction

Humans and snakes have shared a particular relationship since the beginning of humankind (Isbell, 2009; Isbell, 2006). Being one of the most prominent predators of early primates, snakes exerted great pressure on the evolution of primate brains. According to the snake detection theory, this pressure was so immense that it became the reason for the evolution of the visually specialized, expanded brains seen in extant primates today (Isbell, 2009). Many studies have supported this theory, as both behavioral as well as cognitive neuroscience studies have found differential responses to snakes compared to other stimuli.

Many behavioral studies have shown that people detect snakes faster in matrices of innocuous stimuli than they detect innocuous stimuli in matrices of snakes or other threatening stimuli (DeLoache & LoBue, 2009; LoBue & DeLoache, 2008, 2010a; Lobue & Deloache, 2011). Moreover, similar responses have been observed already in younger than school-aged children, including 8- to 14-month-old infants, regardless of their prior exposure to snakes (LoBue & DeLoache, 2010b; Penkunas & Coss, 2013). These findings suggest an evolutionarily hard-wired mechanism for detecting snakes. Snakes are also one of the most common object of phobias (Blanchette, 2006; King, 2013), suggesting a universal tendency for snake fear.

Cognitive neuroscientific studies have also looked at brain responses to snakes. Many studies have found that snakes elicit strong electrophysiological responses compared to other animal stimuli (Beligiannis & Van Strien, 2019, 2020; He et al., 2014; Van Strien et al., 2016; Van Strien & Van der Peijl, 2018). This difference is seen regardless of the type of the compared animal stimuli; it is observed relative to more neutral animal stimuli, such as birds and butterflies, as well as disgusting stimuli such as slugs, and also compared to other threatening stimuli such as spiders (Van Strien, Franken, et al., 2014).

Though many studies have seen faster responses to snakes than to other stimuli, and others have found strong electrophysiological responses, no studies to date appear to have examined the possible correlation between the two. If found, this would be quite an important finding, as understanding the correlation between electrophysiological responses and the reaction times would provide a better understanding of the cognitive processes involved in the response.

Many previous experiments have used button-press tasks to report detection of stimuli. To increase the ecological validity of this experiment, a naturalistic paradigm was used. This experimental design involved a touch screen monitor, on which participants were asked to hold their finger until they saw an experimental stimulus and were instructed to withdraw their finger as soon as they saw the stimulus. To further increase the accuracy of the results, an accelerometer was used in addition to simple reaction times to measure peak accuracy of the withdrawal from the stimuli.

The next section will cover the background for the study. The first chapter will go over the behavioral and theoretical foundation by introducing the mammalian fear module and snake detection theory, and the second chapter will go over the electrophysiological background, where electroencephalography, event-related potentials, and early posterior negativity will be discussed.

2 Background

2.1 Theoretical Framework

2.1.1 The Mammalian Fear Module

Fear is a fundamental mammalian emotion, allowing to avoid and escape threats. These threats can be environmental, such as those caused by the elements, or brought on by other individuals, such as predators as well as aggressive conspecifics. Öhman and Mineka (2001) proposed a potential functional framework for the mammalian fear module, an evolved brain mechanism specialized for detecting and avoiding threats.

The mammalian fear module is described as a neural-behavioral module that is sensitive to evolutionarily important threatening stimuli. It is said to have four key characteristics: it is selective about the input it receives, automatic in its response, relatively impenetrable by other processes (encapsulation), and has a specialized neural circuitry. The fear responses generated by the mammalian fear module manifest and can be measured in three different dimensions: physiological, behavioral, and verbal-cognitive.

A key brain region suggested to be central to the mammalian fear module is the amygdala. The amygdala is a sub-cortical structure known to be involved in emotional responses, especially those involving fear (Calder et al., 2001). Its subcortical location suggests that the amygdala was in use by the mammalian ancestors long before the evolution of developed cortexes. Moreover, some studies have found amygdaloid neurons responding to very specific stimuli, for example, populations of cells in the primate amygdala have been found to be selectively responsive to faces (Desimone, 1991; Rolls, 1992).

Human infants have also been found to be especially attentive to threatening stimuli such as snakes, spiders, and angry faces (DeLoache & LoBue, 2009; LoBue, 2010a; LoBue & DeLoache, 2008, 2010, 2011; LoBue & Larson, 2010), suggesting that there are neural structures in place already in infancy that are selective to evolutionarily important threatening stimuli. However, other studies have not found the same effect of faster detection of threatening stimuli compared to those that are non-threatening (Demchenko et al., 2020; Tipples et al., 2002), making this claim somewhat uncertain.

2.1.2 Snake Detection Theory

Being one of the earliest predators of primates, snakes exerted great pressure on the evolution of their brains (Isbell, 2006). The snake detection theory suggests that this pressure was so

immense that it became the prime driving force for the evolution of the primate visual system. Primates differ from other mammals by being highly visually specialized, having expanded brains and greater orbital convergence. Isbell suggests that these features have evolved in response to having snakes as predators. Earlier theories suggested that these changes were due to the reaching and grasping behavior of primates (Napier and Walker, 1967; Cartmill, 1974; Bloch and Boyer, 2002; Kirk et al., 2003). However, according to the snake detection theory, detecting and avoiding snakes became so important for the early primates that it resulted in the evolution of such elaborate visual systems (Isbell, 2006).

Evidence from several studies seems to support the snake detection theory. For example, humans respond faster to snakes than to other fear-irrelevant simuli (Öhman et al, 2001; Penkunas and Coss, 2013). In the experiments by Öhman (2001), participants viewed image matrices and had to respond to incongruent stimuli. While these experiments did find that participants were able to detect fear-relevant stimuli faster than fear-irrelevant stimuli, the reaction times were slow (approximately 800-970 ms on average). The same methodology was used by Penkunas and Coss (2013), where children ages 3-8 detected images of snakes in matrices of lizards faster than they detected lizards in matrices of snakes. This effect was the same for children born in urban settings who did not have previous exposure to snakes, and children in rural settings who did have previous snake exposure. This suggests that earlier snake exposure is not necessary for young children to detect snakes faster than they can other non-threatening stimuli. Similarly, LoBue and DeLoache (2010) showed that even 8- to 14-month-old infants respond to snakes more rapidly than to images of flowers. Compared to images of frogs, the snake bias was not statistically significant, though a trend towards faster detection of snakes was found even then.

Primates also have been shown to react faster to snakes than to other stimuli (Kawai and Koda, 2016; Shibasaki and Kawai, 2009). Additionally, studies have shown that laboratory-reared monkeys learn to fear toy snakes through observing the fearful response of other monkeys but not fear-irrelevant stimuli such as toy flowers (Cook and Mineka, 1989; 1990). Laboratory-reared monkeys also spend more time looking at snake pictures compared to other stimuli (Bo et al., 2020). Öhman and Mineka (2003) also suggest snakes to be a stimulus that the fear module is especially sensitive to. However, they suggest that this is because of the lizard ancestors of snakes that were threats to the prehistoric mammals.

Some studies have compared people's reactions to snakes to other fear-relevant, but not evolutionarily primed stimuli. Fox, Griggs & Mouchlianitis (2007) showed that the visual attention of adults is captured by guns to the same extent as it is by snakes. However, a study by LoBue (2010) found that only dangerous objects that children had had experience with (such as medical syringes) captured their attention. This suggests that while snakes are a stimulus that people appear to have an inherent sensitivity to, the fear for other non-evolutionarily important threatening stimuli is learned and strengthened over time.

Though previous studies have been able to demonstrate that people react faster to snakes than many other stimuli, these studies have not used experimental paradigms that provide much ecological validity, as they do not very convincingly replicate natural behaviours such as escaping from threats. When encountering a threat in the wild, fast, automatic responses would be needed to avoid the potential threat. Thus, visual-search paradigms might not be the best tool to investigate natural responses to threatening stimuli such as snakes.

The snake detection theory and subsequent studies have established that humans and primates tend to respond to snakes faster than they do to other stimuli. Furthermore, this effect seems to take place even in younger children, including those that have not been exposed to snakes. This suggests an evolutionarily primed neural sensitivity to snakes.

2.2 Electrophysiological Background

2.2.1 Electroencephalography

Electroencephalography (EEG) is a neuroimaging method first developed in 1924 (Nunez & Srinivasan, 2006). Despite being a relatively old method, EEG is still useful today as it has many strengths and features that newer methods have not been able to replace.

EEG has many benefits including low cost, portability, and excellent temporal resolution. EEG's temporal resolution is in milliseconds (Luck, 2005), whereas functional magnetic resonance imaging (fMRI), for example, has a temporal resolution in the range of seconds. On the other hand, EEG has poor spatial resolution, and accurate source localization of the EEG signal is practically impossible, as each signal has an infinite number of possible origins (Nunez & Srinivasan, 2006).

EEG's excellent temporal resolution renders it useful for cognitive neuroscientific research, as the brain responses can be accurately timed with stimulus onset. This allows for insight into understanding the cognitive responses to a stimulus. Though the accurate location of the signal might not be possible to deduce, EEG experiments can still give us valuable information about the brain's functioning. Moreover, better source localization can be obtained by combining EEG with other modalities such as fMRI or MEG, which offer better spatial resolution.

The electric potentials recorded at the scalp in an EEG recording originate from electrical dipoles in the brain. These are formed by the pair of a negative electrical charge at the apical dendrites and a positive charge at the cell body (Luck, 2005). The charges generated at the dipole travel through the brain and skull all the way to the scalp, but they are dispersed laterally as they do so, causing blurring of the signal and making it harder to estimate the origin.

The electric potentials originate from postsynaptic potentials. For the signals to travel all the way from the brain to the scalp, there must be simultaneous activation of postsynaptic potentials across thousands or even millions of neurons, so that the signals summate and are not cancelled by each other. These neurons must also be spatially aligned and receive the same kind of input (excitatory or inhibitory) to allow for the summation of the signals. Most of the EEG signals arise from cortical pyramidal cells, as they are aligned perpendicular to the surface of the cortex. One factor that can prevent the travelling of the potentials to the scalp is the folding of the brain, which makes it difficult for the signals to summate.

2.2.2 Event-related Potentials

Event-related potentials (ERPs) are small changes in the EEG signal that happen in response to a stimulus (Blackwood & Muir, 1990). Many cognitive neuroscientific studies using EEG are ERP studies, as ERPs can provide valuable understanding of the cognitive processes happening in response to a stimulus.

Different components in the ERP waveform can be associated with specific responses to a stimulus, with earlier onset components often reflecting more automatic, "unconscious" responses, whereas later onset components are caused by more conscious, cognitive activity. Sometimes the ERP components are divided into "exogenous" and "endogenous" components depending on the latency (Luck, 2005), referring to the stimulus being either automatic in nature, solely depending on external factors, thus "exogenous", or depending on the internal response of the individual, hence "endogenous". This divide however is not very clear or

accurate, as it is difficult to determine a point after which a component becomes "conscious", or what even constitutes are conscious.

2.2.3 Early Posterior Negativity

Early posterior negativity (EPN) is an ERP component elicited in response to emotionally arousing stimuli (Schupp et al., 2003), thought to reflect early attentional capture. It takes place in the posterior electrodes at around 225-300ms after stimulus onset (Schupp et al., 2006), and is thought to be especially sensitive to evolutionarily important stimuli (Schupp et al., 2003). It, however, has not been found to be sensitive to valence; it is evoked by both pleasant and unpleasant stimuli. The EPN is also not subject to habituation, as it is not weakened through repetition.

The EPN has been found to be particularly strong to snakes, as snakes have been shown to elicit larger EPNs compared to other animal stimuli, including slugs, spiders, butterflies, other reptiles, and birds and butterflies (He et al., 2014; Van Strien, Franken, et al., 2014; Van Strien & Isbell, 2017; Van Strien & Van der Peijl, 2018). These findings suggest that snake pictures draw more early attention than other animals, including those that are also threatening.

The EPN snake effect has also been observed even when only parts of the snake are visible, such as the general shape of the snake (Beligiannis & Van Strien, 2019) or only the local features, such as snake skin patterns (Van Strien & Isbell, 2017). The effect is also seen in response to close-up shots showing only the snake's head (Beligiannis & Van Strien, 2020), which elicit higher EPNs than close-ups of other stimuli such as spiders. These findings suggests that it is not only the global features, such as the curvilinear shape, that modulate the EPN in response to snakes, but that local features, such as the snake skin patterns, also play a role.

The current idea is that the EPN reflects an automatic, unconscious reaction to emotionally salient stimuli, making it an exogenous ERP in the sense that it is not under voluntary control, even though it is a middle-latency potential. This can seem logical as the EPN does not habituate easily. However, unconscious processing is already known to occur over the occipito-temporal areas in earlier components than the EPN (Pegna, Landis, & Khateb, 2008; Smith, 2012). There is also a well-known ERP component called Visual Awareness Negativity (VAN) (Koivisto et al., 2016, 2016, 2016; Koivisto & Grassini, 2016; Railo et al.,

2011) that the EPN overlaps with. As the VAN indexes awareness of stimuli, it would be hard to say that the EPN would then reflect completely unaware stimuli. It could be thought that the EPN reflects unconscious processing of this emotional stimuli, yet there does not seem to be substantial evidence for it (Hedger et al., 2016).

3 Aims

The aim of the study was to see whether there is a correlation between reaction times and the EPN amplitude. To test this hypothesis, a naturalistic experimental design was used. In the experiment, the participants responded to experimental images by interacting with stimuli presented on a touch screen. To mimic a realistic encounter with a snake (or other animal), participants were instructed to withdraw their finger from the screen as fast as possible each time a target stimulus (any animal picture) was displayed. This procedure was thought to be better than a simple button press, as this would better mimic an encounter with a snake or other animal in the wild. Moreover, this touchscreen-based design allowed the participants to interact with the experimental stimuli more directly and faster than in a visual search task that has been used in many of the previous studies comparing people's reactions to snakes to non-threatening stimuli.

In addition to simple reaction times, an accelerometer was used to measure acceleration. Acceleration has not been measured in previous literature regarding the EPN snake effect, but it was added as it is possible that the fear module would affect both the reaction times as well as acceleration speed, as it helps to avoid the threat faster.

Thus, the hypotheses of the study were 1. That the reaction times as well as acceleration speed would be faster to snakes than to other stimuli, 2. That snakes would elicit the highest EPN amplitudes, and 3. That the EPN would positively correlate with both the peak acceleration as well as reaction times. These hypotheses were tested in the naturalistic paradigm chosen for the study.

4 Methods and Materials

4.1 Participants

30 participants were recruited for the study (5 male, 25 female). Three participants were removed during pre-processing due to missing or outlier data, with a total of 27 participants being included in the final analysis. Participants were all students at the University of Turku, and majority participated in exchange for course credits. All participants were right-handed and did not have a history of neurological disease. The participants were of ages between 18-40, with the mean age being 23.9. The participants gave informed consent before participation in the study. The study was conducted according to the principles of the Declaration of Helsinki and was approved by the Ethics Committee for Human Sciences at the University of Turku.

4.2 Stimuli and Procedure

The experiment had two types of stimuli: target stimuli included snake and spider images, while non-target stimuli included images of birds and butterflies. In addition, pictures without animals were used as control. These pictures were of mushrooms, pinecones, leaves, and flowers. Each category consisted of 28 images. The luminance histograms of all stimuli (each RGB layer) were matched with the SHINE toolbox (Willenbockel et al., 2010). The size of the pictures was 37,5 cm x 28 cm (resolution 600 x 450 pixels).

The participants were asked to sit in front of a 55" Phillips Signage Solutions Multi-Touch Full HD (55BDL4051T) touch screen monitor (resolution 1920 x 1080 and refresh rate). The experimental task was a go/no-go task, where participants had to react to all experimental stimuli (snakes, spiders, birds, butterflies). They were asked to put their finger on the screen start a trial, and to withdraw their finger from the screen by moving their whole arm back from the screen as fast as possible as soon as they saw an experimental (animal) stimulus. A blank screen with the word "start" appeared before each trial, with the trial being initiated as soon as the participant touched the screen. In case of a trial consisting of a control stimulus, the participant had to keep their finger on the screen until the next start screen appeared. Each trial consisted of one picture. Participants performed a short practice round before the actual experiment.

The stimuli were presented using Presentation software (v.22.0/05.10.20). The experiment was carried out in block design, with each block consisting of 112 trials (14 of each category),

and the stimuli being chosen randomly before each trial. The number of blocks slighty varied from participant to participant, as participants were instructed to complete as many blocks as they were able to complete within an hour. The arm movement involved made the experiment quite physically exhausting, causing some variation between participants. The number of blocks performed varied from 14 to 17, with the mode being 14.

4.3 Instruments

Arm movements were recorded with an MPU 6050 accelerometer that was attached on the participant's wrist. The sampling frequency of the accelerometer was 100Hz, and acceleration speed was measured in three dimensions. Before the experiment, the accelerometer was calibrated to be 0 m/s² when the participant was not moving their arm. The accelerometer was calibrated so that Earth's gravitational pull 9.1 m/s² did not show up in the measurements, which made the data easier to interpret. The accelerometer was controlled by two Arduino Uno (ATmega328P Arduino Uno R3 AVR® ATmega AVR MCU) units. One of the units was connected to a Dell Latidute E5540 laptop, on which Presentation was run, and the other one was connected to a laptop running a Cool Term win software, that was used to convert the accelerometer data into a text file. The units were also connected to each other to correctly save and synchronize the stimuli with the rest of the data.

EEG was recorded with 32 passive electrodes placed according to the 10-10 electrode system (EasyCap GmbH, Herrsching, Germany). Surface electromyograms (EMGs) were measured with two electrodes placed below and next to the left eye. The reference electrode was placed on the nose, and ground electrode on the forehead. EEG was recorded with a NeurOne Tesla amplifier using 1.4.1.64 software (Mega Electronics Ltd., Kuopio, Finland). Sampling rate was 500 Hz.

4.4 Preprocessing

All data was processed using MATLAB R2020b. First, the accelerometer data was read and segmented into trials and baseline corrected. Though the accelerometer measures acceleration in three dimensions, only one dimension (backward and forward) was included in the analysis. Peak acceleration was added to the EEG data as a marker. This data was then preprocessed with EEGLAB v2021.1 (Delorme and Makeig, 2004). First, a high pass filter with a cut-off frequency of 1 Hz was used, after which the data was run through a low pass filter with a cut-off frequency at 40 Hz. The EEG reference was changed to average reference, the data was epoched, and independent component analysis was run. IC label was used to

keep independent components that had at least 70% probability to originate from the brain. Outlier trials were rejected using joint probability with the criteria of three standard deviations. Finally, missing channels were interpolated.

After individual data was pre-processed, all data was compiled and grand averaged. First, condition, peak acceleration and reaction times were extracted from each individual trial. Then, each participant's data was added into a matrix. At this point, one participant with outlier ERPs was excluded from the analysis. A difference wave between the threatening (spiders, snakes) and non-threatening (birds, butterflies) animals was calculated to see whether there was an EPN. A butterfly plot was also used to visually inspect the data and to see whether there was EPN activation at the posterior electrodes around the 200-300 ms time window. After inspecting the data, posterior electrodes O1, O2 and Iz where EPN was most clearly visible were chosen to be included in the statistical analysis.

4.5 Data Analysis

Linear Mixed Effects (LME) analysis was used for both behavioral and electrophysiological data. LME was chosen for this study because it allows a look at the EPN's correlation with reaction times and peak acceleration on a trial-wise basis, instead of a between-conditions analysis that is usually used when calculating EPNs. The LME analysis also offers flexibility as both random as well as fixed effects can be entered in the same analysis.

For the behavioral data, LME analyses were done to see whether there were differences in the reaction times as well as acceleration between the different animal categories. First, an LME model looking at the reaction times was employed. Two models were tested for the analysis. The first model aimed to explain variation in reaction times by having the condition (animal) as main effect and individual variations within each condition was entered as a random effect (RT ~ animal + (1+animal|ID)) of RT ~ animal + (1+animal|ID). The second model was the same as the first except it also had variations between individual stimuli as random effects (RT ~ animal + (1+animal|ID) + (1|stimulus)). The more complicated model was deemed to explain the variation within reaction times better based on the Akaike information criterion (AIC), which was 97509 for the more complex model and 97731 for the simpler one.

The same approach was used for peak acceleration, but this time the simpler model (peak acceleration \sim animal + (1+animal|ID)) with only individual variation between categories as random effect was a slightly better fit (AIC 38255 versus AIC 38257). To see whether there

was a correlation between reaction times and acceleration speed, an LME analysis explaining reaction times with peak acceleration was used. For this analysis, the more complex model (touch RT ~ peak acceleration + (1+animal|ID) + (1|stimulus)) with both individual variations within each category as well as variations between individual stimuli was a better fit (AIC 89540 vs 89738).

For electrophysiological data, an LME analysis looking at the activity of the posterior O1, O2 and Iz electrodes was used to analyse the EPN activity. The activity of these electrodes within the 200-300 ms time window was used. A few models explaining activity in these posterior electrodes within the chosen time window were tested. First, the model EPN ~ RT*peak acceleration*condition + (1|ID) using EPN as intercept and interaction effects between the reaction times, peak acceleration and condition as fixed effects, and individual variation as a random effect was tested (AIC 41168). As there were no three-way interaction effects observed, two other models with simpler interactions were tested (EPN ~ 1 + RT*peak acceleration + RT*condition + peak acceleration*condition + (1|ID) with AIC of 41170 and EPN ~ 1 + condition + RT*peak acceleration + (1|ID) with AIC of 41164). As none of these models had significant interaction effects, a simpler model (EPN ~ 1 + RT + peak acceleration + condition + (1|ID) that explained EPN with only the individual fixed effects was used. This was also the best fit with AIC of 41162. Before performing the LME analyses, outliers for reaction times with the criteria of less than 250 ms and over 800 ms, and peak acceleration with the criteria of less than 1 m/s² and more than 25 m/s², were removed.

5 Results

5.1 Behavioral Results

5.1.1 Correlation Between RTs and Peak Acceleration

The linear mixed effects model explaining reaction times with peak acceleration showed no effect of peak acceleration on reaction times (t(7943) = -0.81, p = 0.42), meaning that there was no correlation between the two.

5.1.2 Reaction Times

According to the hypothesis, faster reaction times and a higher peak acceleration were expected in response to threatening stimuli. Results for the LME analysis examining the effect of condition on reaction times are shown in Table 1. No statistically significant differences were found between the categories, though the results were near-significant for snakes (t(8654) = -1.87, p = 0.06), which elicited the fastest reaction times. The butterfly condition was used as intercept, to which other categories were compared.

Table 1.

Linear mixed effects analysis for the effect of condition on reaction times. Butterfly condition used as intercept.

Name	Estimate	t	p	Lower 95% CI	Upper 95% CI
Butterfly	459.49	50.84	<.001	441.77	477.21
Snake	-11.98	-1.87	.06	-24.55	0.59
Spider	-3.00	-0.62	.53	-12.48	6.48
Bird	-2.45	-0.51	.61	-11.89	6.98

5.1.3 Peak Acceleration

Linear mixed effects analysis looking at the differences in peak acceleration between conditions are shown in Table 2. The differences in peak acceleration were significant for all categories, with snakes eliciting the highest peak acceleration, followed by spiders, butterflies, and birds, respectively. Butterfly condition was again used as intercept. Table 2.

Name	Estimate	t	р	Lower 95% CI	Upper 95% CI
Butterfly	10.38	15.73	<.001	9.09	11.68
Snake	0.70	2.34	.02	0.11	1.28
Spider	0.48	2.85	.004	0.15	0.81
Bird	-0.20	-2.14	.03	-0.39	-0.02

Linear mixed effects analysis for the effect of condition on peak acceleration. Butterfly condition used as intercept.

The behavioral results are visualized in Figure 1. There are visible differences in the peak acceleration between threatening and non-threatening conditions. Also, slightly faster reaction times can be seen for snakes, though as stated before, this difference was not quite statistically significant. The graph showing correlation between reaction times and peak acceleration shows no visible correlation, as was also found in the LME analysis looking at the correlation between the two.



Figure 1. Left is a scatter plot showing the relationship between reaction times (y-axis) and peak acceleration (x-axis). The middle and right graphs show the distribution and means for reaction times (middle) as well as peak acceleration (right) for each condition.

5.2 Electrophysiological results

5.2.1 Visual Inspection



Figure 2. Butterfly plot showing the difference waves between the threat (snake, spider) vs no-threat (bird, butterfly) conditions. Each line represents a different electrode.

Visual inspection of the butterfly plot (Figure 2) revealed clear negative polarization at the posterior channels in the 200-300 ms range, reflecting EPN activity. In addition, ERP waves calculated for each condition (Figure 3) showed a clear difference between the different categories, with birds eliciting clearly most positive amplitudes (least EPN). These results were seen as sufficient evidence for EPN. As already mentioned, electrodes O1, O2 and Iz were chosen for the EPN analysis, as these showed the clearest EPN.



Figure 3. Averaged ERPs for each condition.

5.2.2 LME Analysis of the Electrophysiological Results

The LME analysis for the EPN and its relationship with condition, reaction times, and peak acceleration (Table 3) revealed significant effects for all the conditions on the EPN mean amplitude. Snakes elicited the most negative amplitude, followed by spiders, butterflies, and finally birds. Peak acceleration was not found to have a significant effect (p = -0.50) on the EPN. Reaction times, on the other hand, had a negative effect (p = .001) on the mean amplitude in the 200-300 ms range, meaning that the smaller the EPN, the shorter the reaction times were.

Table 3.

Linear m	ixed effects	analysis	examining	the effect	of condition,	reaction	times and	acceleration	on the
EEG am	olitude in the	e 200-300) ms (EPN) time wind	dow. Snake o	condition	used as in	ntercept.	

Variable	Estimate	t	p	Lower 95% CI	Upper 95% CI
Snake	6.32	8.19	<.001	4.81	7.84
RT	-0.004	-4.86	<.001	-0.01	0.002
Peak acceleration	-0.01	-0.67	.50	-0.05	0.03
Spider	0.82	5.43	<.001	0.53	1.12
Bird	2.56	16.67	<.001	2.26	2.86
Butterfly	1.91	12.52	<.001	1.61	2.21

6 Discussion

This study aimed to look at the correlation between reaction times and the early posterior negativity. Three hypotheses were set before the study: 1. Reaction times and peak acceleration would be faster to snakes than to other stimuli, 2. Snakes would elicit the highest EPN amplitudes, and 3. The mean amplitude in the 200-300 ms range (the EPN) would correlate with reaction times positively (i.e., the more positive the signal, the longer the reaction times) and with peak acceleration negatively (the more positive the signal, the smaller the peak acceleration). Consistent with previous studies, results from this study supported the first two hypotheses, even though the difference for faster reaction times was not statistically significant. Previous studies have shown that people react faster to snakes than to other stimuli (LoBue & DeLoache, 2011; Penkunas & Coss, 2013), and these results were replicated by the present study. Many studies have also established that snakes elicit higher EPNs compared to other animals (Beligiannis & Van Strien, 2019, 2019; He et al., 2014; Van Strien et al., 2016; Van Strien & Van der Peijl, 2018), and this was also replicated by the current study. The third hypothesis, however, was not supported by the results, as the correlation between the EPN and reaction times was found to be opposite to the hypothesis, and no significant correlation was observed between peak acceleration and the EPN.

6.1 Behavioral Measures

6.1.1 Reaction Times

In the present study, snakes elicited nearly statistically significantly faster reaction times compared to other animal categories. Though there are many studies that have found faster reaction times to snakes and other threatening stimuli than to innocuous stimuli (Öhman et al, 2001; Penkunas and Coss, 2013), other studies have not found a significant difference between threatening and non-threatening stimuli (Demchenko et al., 2020; Tipples et al., 2002). Moreover, most studies do not appear to have compared reaction times between snakes and other threatening stimuli. Therefore, even though the reaction times elicited by snakes were not quite fast enough to be statistically significantly different, the strong trend is intriguing and warrants more investigation in the future.

It is possible that the trend toward faster reaction times to snakes might have been influenced by the experimental design of the study. The present study used a naturalistic touch screenbased paradigm that has not been used in previous studies. Most experiments in the past have used button-press tasks, which do not provide much ecological validity, as button press is not a very intuitive response to encountering a snake in nature. Thus, it looks like the experimental setting used in this study was successful in bringing out faster, more intuitive responses to snakes especially compared to visual search paradigms where reaction times tend to be slow (around 800-970ms in the experiment conducted by Öhman (2001), for example).

It is also possible that the participants of this study happened to be more snake phobic than people on average. Öhman et al. (2001) found that phobic participants were faster to detect a feared target (snake or spider) in a matrix of non-fear relevant distractors than they were to find a non-feared fear-relevant target. Though fear questionnaires for each animal were filled out by the participants before the experiment, these fear evaluations were not used in the main analyses of this study, therefore any analyses regarding the level of fear toward a specific animal and the EPNs elicited by said category were not performed. Future studies could investigate whether a similar trend towards faster detection of snakes can be replicated in different samples by using the naturalistic paradigm.

6.1.2 Peak Acceleration

The difference for peak acceleration varied significantly between categories. This shows that even though people might not be significantly faster at the initial detection of fear-relevant stimuli, there is a clear difference between categories in the acceleration of the withdrawal motion from the stimulus once it has been detected. These results indicate that acceleration speed is a good measurement for fear responses and future studies might find it useful to take more advantage of it since most studies to date have only measured simple reaction times, which do not offer a full understanding of people's reactions.

People showed the fastest peak acceleration times to snakes followed by spiders. These results show that people withdraw faster from threatening stimuli than they do from non-threatening stimuli, and that snakes elicit the highest peak acceleration, providing more evidence for the snake detection theory. However, as there was no correlation between reaction times and peak acceleration, it seems that even though a similar pattern for faster reaction to threatening stimuli was seen for both categories (reflecting the influence of the mammalian fear module), these are still at least partially distinct processes with different neural origins.

6.2 Early Posterior Negativity

The second hypothesis of the study was that snakes would elicit the highest EPNs. This hypothesis was supported by the results, as snakes elicited the strongest EPN by giving rise to

the most negative EEG mean amplitude during the 200-300ms time window after stimulus onset. Spiders elicited the second largest EPNs, followed by butterflies, and finally birds, which elicited the least EPN activity. This EPN pattern is consistent with previous studies, where snakes have also elicited the strongest EPNs followed by other threatening animal stimuli. Moreover, the EPN pattern observed in the study was consistent with the results from behavioral measurements, as snakes and spiders also elicited the fastest reaction times as well as the highest peak acceleration, even though the differences were not statistically significant for reaction times.

The third, and main hypothesis of the study concerned the EPN's correlation with behavioral measurements. The LME analysis revealed significant correlations between the EPN and reaction times, however, contrary to the hypothesis, this correlation between the EEG mean amplitude and reaction times was negative, meaning that the larger the EPN, the slower the reaction times were. This finding was rather surprising, as previous studies have linked both the EPN and shorter reaction times with the snake detection theory, making it seem logical that the EPN would correlate with the fast reaction times to snakes argued in the snake detection theory. Therefore, the results from this study shed some new light on the EPN, inviting further investigations to understand its role and function better.

Unlike reaction times, peak acceleration was not found to have a significant correlation with the EPN amplitude, which was also rather surprising, given that it seems likely that the mammalian fear module would affect both reaction times and peak acceleration. However, given that peak acceleration was not correlated with reaction times either, it seems that peak acceleration is determined by other factors.

There are many possible explanations for the surprising correlation found between the EPN and reaction times. The fact that snakes elicit the shortest reaction times out of all the categories and the highest EPN, yet larger EPNs correlate with slower reaction times, suggests other cognitive processes besides the EPN are responsible for the faster reaction times to snakes. And while both the EPN as well as fast reaction times are likely influenced by the mammalian fear module, reaction times are determined by a complex process in the brain, and the EPN is only one component influencing this process. One important factor to notice, is that while there was a significant correlation between the EPN and slower reaction times, this slowing was very small, only a 0.004 μ V decrease in the EPN amplitude per 1 ms increase in reaction times. Given that ERPs are very small fluctuations in the signal, this change is

virtually imperceptible by human senses. It is hard to think that this kind of slowing would affect escaping from a snake in nature.

Attentional capture might be one factor explaining EPN's correlation with slower reaction times, as attentional capture by a distractor is known to slow reaction times (Anderson et al., 2011; Schmidt et al., 2015) when attending to a task. As the EPN is known to be sensitive to emotionally arousing stimuli, it could be that the emotionally salient pictures that elicited strong EPNs worked as a "distractor" from the task, resulting in slightly slowed reaction times, even if the participants were supposed to pay attention to the target stimuli. Though the task required the participants to attend and react to the stimuli by withdrawing their arm from the monitor as fast as possible, it is possible that something in the pictures eliciting the highest EPNs still "distracted" the participants from the experiment briefly.

Perhaps the best explanation is that the EPN reflects some kind of evaluative process taking place. As the EPN is sensitive to both pleasant as well as unpleasant stimuli (Schupp et al., 2004), and is thought to index early attention to these emotionally arousing stimuli, in light of the results of this study, it seems intuitive that the slower responses caused by the EPN are indicative of some cognitive process assessing the emotionally arousing stimuli. If thought about this way, it makes sense that the more EPN activation there is, the slower the reaction time become, as the cognitive process the EPN reflects is assessing the emotional stimulus's meaning and proper way to respond. While fast reactions to threatening stimuli are important, it is also important to assess the emotionally arousing stimuli to come up with a correct response. As this process is slightly more involved, it makes sense that more consideration by the brain would lead to slightly slower reaction times. This makes sense especially in the case of evolutionarily important stimuli, to which the EPN is thought to be especially sensitive to, as these stimuli are potentially crucial to the survival of the species. Thus, an accurate evaluation of the stimuli is important for the continuation of the evolutionarily line. Perhaps EPN reflects this process.

What further speaks for this idea is that despite its name, the EPN is a middle-latency potential, unlikely to be completely unconscious and "automatic" in nature. As mentioned, there are earlier components such as the VAN that are known to index awareness (Koivisto & Revonsuo, 2010; Railo et al., 2011; Koivisto & Grassini, 2016; Koivisto et al., 2016). Thus, it might be that earlier potentials, such as the P100, which is also evoked in response to visual stimuli, might better predict the fast reaction times seen in response to snakes, for example.

6.3 Future Work and Limitations

The experimental stimuli used in this study consisted of threatening target stimuli, and more neutrally experienced animal stimuli as controls. As the EPN is known to be sensitive to both pleasant and unpleasant stimuli, it would be interesting to see whether the same effect of the EPN causing slower reaction times would take place in the case of differently valenced stimuli, such as pleasant or disgusting stimuli. It would also be interesting to use other threatening stimuli besides animal images. This would give further insight into whether larger EPNs have a general slowing effect on the reaction times, or whether this effect is limited to negatively experienced or threatening stimuli. Even though the control stimuli included more neutral animals, i.e., birds and butterflies, these are not likely to generate a very strong positive emotion either and many participants reported some level of fear towards these animals as well. Because of this, future research might want to include other types of stimuli.

To better understand the EPN's effect on reaction times, it would also be a good idea to take a better look at the individual stimuli that caused the highest EPNs and compare it to those that elicited less EPN. Though the target stimuli used in this experiment was emotionally arousing and threatening in nature, it is possible that the EPN might have been modulated by other factors such as figure-ground composition, which has been shown to have a modulatory effect on the EPN. The EPN is also modulated by visual features such as figure-ground composition (Nordström & Wiens, 2012), so a look at the stimuli that elicited the strongest EPNs might be useful. This might give better insight about whether there are any other factors besides "emotional salience" that were responsible for the highest EPNs in this study, and potentially provide a better understanding of the results. It is possible that the highest EPNs were not elicited solely due to emotional salience, but image complexity, for example.

7 Conclusions

The results obtained from this study indicate that snakes cause different reactions both behaviorally as well neurophysically compared to other animal stimuli, even though the relationships between these reactions are not as clear as previously assumed. As Öhman and Mineka suggest in their paper, the fear responses generated by the mammalian fear module are manifested at different levels, including cognitively, behaviorally, as well as physiologically. The EPN reflects a physiological (and perhaps cognitive) manifestation, while peak acceleration and simple reaction times are behavioral manifestations. Responding to a threatening stimulus is a complex process, involving many different neural circuits and responses, of which the EPN is only one. One important thing to remember is that withdrawal is not the only response to a threatening stimulus – in some cases fighting, or even freezing is more beneficial. Perhaps the EPN reflects this evaluation of the emotionally arousing stimuli and the subsequent response, and more activation naturally slows the reaction times. If encountering a snake in the wild, one would first have to assess the situation before moving.

Given the results from the study, it might be a good idea to rethink EPN's role when it comes to the EPN snake effect. What does the EPN even represent? The EPN is thought to reflect motivated attention that is evoked by emotionally arousing stimuli (Schupp et al., 2006). While snakes certainly do elicit a stronger EPN response, indicating emotional capture, the EPN alone does not account for people's reactions to snakes, making its role in the detection and subsequent reaction to snakes more complicated. As with any behavioral response, the response to snakes is a complicated one, involving many different brain regions and networks. The EPN is not the only component determining how fast people react to snakes, as can be seen with the results of this study. Future studies might find it useful to investigate the relationship between other ERP components and reactions to snakes, such as the P1 or N1 components, which also reflect early attention.

Though partially surprising, the results from this study provide many new insights. First, the naturalistic paradigm used in the study was useful in studying people's reactions to threatening animal pictures, and future studies might benefit from utilizing similar touchscreen based experimental designs to increase the ecological validity of the results. In addition, the accelerometer results show that peak acceleration is a useful measure in investigating reactions to threatening stimuli. Finally, the correlation between the EPN and reaction times provides new understanding about the EPN's role in the processing of snake

and other emotional stimuli, as well as raises new questions about its function. These are significant findings that provide new insights and material for future research.

References

- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011). Learned Value Magnifies Salience-Based Attentional Capture. *PLoS ONE*, 6(11), e27926. https://doi.org/10.1371/journal.pone.0027926
- Beligiannis, N., & Van Strien, J. W. (2019). Blurring attenuates the early posterior negativity in response to snake stimuli. *International Journal of Psychophysiology*, 146, 201– 207. https://doi.org/10.1016/j.ijpsycho.2019.09.002
- Beligiannis, N., & Van Strien, J. W. (2020). Early posterior negativity in humans to pictures of snakes and spiders: Effects of proximity. *Experimental Brain Research*, 238(12), 2795–2804. https://doi.org/10.1007/s00221-020-05925-5
- Biasiucci, A., Franceschiello, B., & Murray, M. M. (2019). Electroencephalography. Current Biology, 29(3), R80–R85. https://doi.org/10.1016/j.cub.2018.11.052
- Blackwood, D. H. R., & Muir, W. J. (1990). Cognitive Brain Potentials and their Application. British Journal of Psychiatry, 157(S9), 96–101. https://doi.org/10.1192/S0007125000291897
- 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
- Bloch, J. I., & Boyer, D. M. (2002). Grasping primate origins. *Science (New York, N.Y.)*, 298(5598), 1606–1610. https://doi.org/10.1126/science.1078249
- Bo, Z., Zhi-Gang, Z., Yin, Z., & Yong-Chang, C. (2020). Increased attention to snake images in cynomolgus monkeys: An eye-tracking study. *Zool. Res.*, *41*(1), 32–38. https://doi.org/10.24272/j.issn.2095-8137.2020.005
- Bradley, M. M., Hamby, S., Löw, A., & Lang, P. J. (2007). Brain potentials in perception: Picture complexity and emotional arousal. *Psychophysiology*, 44(3), 364–373. https://doi.org/10.1111/j.1469-8986.2007.00520.x
- Calder, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience*, *2*(5), 352–363. https://doi.org/10.1038/35072584
- Cartmill, M. (1974). Rethinking Primate Origins. *Science*, *184*(4135), 436–443. https://doi.org/10.1126/science.184.4135.436
- Csathó, Á., Tey, F., & Davis, G. (2008). Threat perception and targeting: The brainstem– amygdala–cortex alarm system in action? *Cognitive Neuropsychology*, 25(7–8), 1039– 1064. https://doi.org/10.1080/02643290801996360
- DeLoache, J. S., & LoBue, V. (2009). The narrow fellow in the grass: Human infants associate snakes and fear. *Developmental Science*, *12*(1), 201–207. https://doi.org/10.1111/j.1467-7687.2008.00753.x
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of singletrial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009
- Demchenko, I., Debruille, J. B., Sinha, S., Carboni-Jiménez, A., Hwang, P., Maduro, A., Mady, N., Tounkara, F., Sapkota, R. P., & Brunet, A. (2020). Letter to the editor: Can early posterior negativity and late posterior potential reduction be state biomarkers of emotional scene processing in bipolar disorder? *Journal of Psychiatric Research*, 130, 41–42. https://doi.org/10.1016/j.jpsychires.2020.07.031
- Desimone, R. (1991). Face-selective cells in the temporal cortex of monkeys. *Journal of Cognitive Neuroscience*, 3(1), 1–8. https://doi.org/10.1162/jocn.1991.3.1.1

- Farkas, A. H., Oliver, K. I., & Sabatinelli, D. (2020). Emotional and feature-based modulation of the early posterior negativity. *Psychophysiology*, 57(2). https://doi.org/10.1111/psyp.13484
- 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*, 53–61. https://doi.org/10.1016/j.biopsycho.2016.10.007
- He, H., Kubo, K., & Kawai, N. (2014). Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. *NeuroReport: For Rapid Communication of Neuroscience Research*, 25(13), 1049–1053. https://doi.org/10.1097/WNR.0000000000227
- Headland, T. N., & Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, 108(52). https://doi.org/10.1073/pnas.1115116108
- Hedger, N., Gray, K. L. H., Garner, M., & Adams, W. J. (2016). Are visual threats prioritized without awareness? A critical review and meta-analysis involving 3 behavioral paradigms and 2696 observers. *Psychological Bulletin*, 142(9), 934–968. https://doi.org/10.1037/bul0000054
- Im, C.-H. (Ed.). (2018). Computational EEG Analysis: Methods and Applications. Springer Singapore. https://doi.org/10.1007/978-981-13-0908-3
- Isbell, L. (2009). The Fruit, the Tree, and the Serpent: Why We See so Well. https://doi.org/10.2307/j.ctvjnrvj0
- 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
- Jaspers-Fayer, F., Ertl, M., Leicht, G., Leupelt, A., & Mulert, C. (2012). Single-trial EEG– fMRI coupling of the emotional auditory early posterior negativity. *NeuroImage*, 62(3), 1807–1814. https://doi.org/10.1016/j.neuroimage.2012.05.018
- 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*, 130(3), 299–303. https://doi.org/10.1037/com0000032
- King, G. (2013). The Attentional Basis for Primate Responses to Snakes.
- Koivisto, M., & Grassini, S. (2016). Neural processing around 200 ms after stimulus-onset correlates with subjective visual awareness. *Neuropsychologia*, 84, 235–243. https://doi.org/10.1016/j.neuropsychologia.2016.02.024
- Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience & Biobehavioral Reviews*, 34(6), 922–934. https://doi.org/10.1016/j.neubiorev.2009.12.002
- Koivisto, M., Salminen-Vaparanta, N., Grassini, S., & Revonsuo, A. (2016). Subjective visual awareness emerges prior to P3. *European Journal of Neuroscience*, 43(12), 1601– 1611. https://doi.org/10.1111/ejn.13264
- 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. (2010a). Superior detection of threat-relevant stimuli in infancy: Threat detection in infancy. *Developmental Science*, *13*(1), 221–228. https://doi.org/10.1111/j.1467-7687.2009.00872.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

- Löw, A., Bradley, M. M., & Lang, P. J. (2013). Perceptual processing of natural scenes at rapid rates: Effects of complexity, content, and emotional arousal. *Cognitive, Affective,* & *Behavioral Neuroscience*, 13(4), 860–868. https://doi.org/10.3758/s13415-013-0179-1
- Luck, S. J. (2005). An introduction to the event-related potential technique. MIT Press.
- 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
- Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences*, 96(4), 1680–1685. https://doi.org/10.1073/pnas.96.4.1680
- Napier, J. R., & Walker, A. C. (1967). Vertical clinging and leaping—A newly recognized category of locomotor behaviour of primates. *Folia Primatologica; International Journal of Primatology*, 6(3), 204–219. https://doi.org/10.1159/000155079
- Nordström, H., & Wiens, S. (2012). Emotional event-related potentials are larger to figures than scenes but are similarly reduced by inattention. *BMC Neuroscience*, *13*(1), 49. https://doi.org/10.1186/1471-2202-13-49
- Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG* (2nd ed). Oxford University Press.
- 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
- Penkunas, M. J., & Coss, R. G. (2013). A comparison of rural and urban Indian children's visual detection of threatening and nonthreatening animals. *Developmental Science*, 16(3), 463–475. https://doi.org/10.1111/desc.12043
- Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition*, 20(3), 972–983. https://doi.org/10.1016/j.concog.2011.03.019
- Rolls, E. T. (1992). Neurophysiology and functions of the primate amygdala. In *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction*. (pp. 143–165). Wiley-Liss.
- Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2015). Attentional capture by signals of threat. *Cognition and Emotion*, 29(4), 687–694. https://doi.org/10.1080/02699931.2014.924484
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: Event-related brain potential studies. *Progress in Brain Research*, 156, 31–51. https://doi.org/10.1016/S0079-6123(06)56002-9
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis: Selective emotional processing. *Psychophysiology*, 41(3), 441–449. https://doi.org/10.1111/j.1469-8986.2004.00174.x

- Schupp, H. T., & Kirmse, U. M. (n.d.). *Case-by-case: Emotional stimulus significance and the modulation of the EPN and LPP.* 13.
- Schupp, H. T., Markus, J., Weike, A. I., & Hamm, A. O. (2003). Emotional Facilitation of Sensory Processing in the Visual Cortex. *Psychological Science*, 14(1), 7–13. https://doi.org/10.1111/1467-9280.01411
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghofer, M., Weike, A. I., & Hamm, A. O. (2007). Selective Visual Attention to Emotion. *Journal of Neuroscience*, 27(5), 1082– 1089. https://doi.org/10.1523/JNEUROSCI.3223-06.2007
- Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. *Journal of Comparative Psychology*, 123(2), 131–135. https://doi.org/10.1037/a0015095
- Soares, S. C. (2012). The Lurking Snake in the Grass: Interference of Snake Stimuli in Visually Taxing Conditions. *Evolutionary Psychology*, 10(2), 147470491201000. https://doi.org/10.1177/147470491201000202
- Strien, J. W. V., & Beligiannis, N. (n.d.). *High spatial frequencies drive the early posterior negativity in response to snake pictures*. 2.
- Tamietto, M., & de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, 11(10), 697–709. https://doi.org/10.1038/nrn2889
- Tipples, J., Young, A. W., Quinlan, P., Broks, P., & Ellis, A. W. (2002). Searching for threat. *The Quarterly Journal of Experimental Psychology Section A*, 55(3), 1007–1026. https://doi.org/10.1080/02724980143000659
- Van Le, Q., 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*, 110(47), 19000–19005. https://doi.org/10.1073/pnas.1312648110
- Van Strien, J. W., Christiaans, G., Franken, I. H. A., & Huijding, J. (2016). Curvilinear shapes and the snake detection hypothesis: An ERP study: Curvilinear shapes and snake detection. *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 eventrelated brain potentials. *Biological Psychology*, 96, 150–157. https://doi.org/10.1016/j.biopsycho.2013.12.014
- Van Strien, J. W., Franken, I. H. A., Eijlers, R., & Huijding, J. (2012). Early posterior negativity is larger for snake pictures than for spider pictures in non-phobic women. *International Journal of Psychophysiology*, 85(3), 374. https://doi.org/10.1016/j.ijpsycho.2012.07.032
- Van Strien, J. W., Franken, I. H. A., & 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. https://doi.org/10.3389/fnhum.2014.00691
- Van Strien, J. W., & Isbell, L. A. (2017). Snake scales, partial exposure, and the Snake Detection Theory: A human event-related potentials study. *Scientific Reports*, 7(1), 46331. https://doi.org/10.1038/srep46331
- 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

- Weinberg, A., & Hajcak, G. (2010). Beyond good and evil: The time-course of neural activity elicited by specific picture content. *Emotion*, 10(6), 767–782. https://doi.org/10.1037/a0020242
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods*, 42(3), 671–684. https://doi.org/10.3758/BRM.42.3.671