Acta Soc. Zool. Bohem. **86**: 193–209, 2022 [2023]
ISSN 2788-1369 (on-line)
ISSN 1211-376X (print)

Eye movement patterns in response to fear- and disgust-eliciting reptiles

Barbora Vobrubová[1)], Kristýna Sedláčková[1)], Markéta Janovcová[1)], Silvie Rádlová[2,*)], Jakub Polák[1)], Šárka Peléšková[1)], Daniel Frynta[1)] & Eva Landová[1, 2)]

[1)] Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ–128 00 Praha 2, Czechia
[2)] National Institute of Mental Health, Topolová 748, CZ–250 67 Klecany, Czechia
[*)] corresponding author: silvie.radlova@nudz.cz

Received 13 April 2023; *accepted 16 June 2023*
Published 27 August 2023

Abstract. We tested the hypothesis that human reaction to snakes is very specific when compared to other reptiles. Using the eye-tracker, we measured free-gazing pattern of 61 respondents while presenting snake and other reptile images categorized as fear-eliciting, disgusting, beautiful, and neutral. We divided the respondents according to their SNAQ and DS-R scores into high/low fear and high/low disgust groups. We found that while the time watching the stimuli was equal, there were more fixations on the non-snakes due to more continuous watching of the snake stimuli. With fear-eliciting stimuli, most of the attention was directed toward the animal's head, but people focused on both the head and tail when watching the disgusting stimuli. The high-fear respondents' fixation number was overall lower. We conclude that the respondents' gaze pattern differs when watching snakes and this also applies for other fear-eliciting reptiles. We offer various explanations for these findings, supporting the hypothesis of snakes representing a specific group of fear-eliciting animals.

Key words. Eye tracker, snake, fear, disgust, emotions.

INTRODUCTION

Animals can attract human attention more than inanimate objects (New et al. 2007, Yang et al. 2012). Humans and other hominids have evolved specific attention criteria, which enabled them to distinguish animals from other objects and to react preferentially to animal stimuli (Öhman 2007). Specific predator recognition bears an evolutionary advantage, as it allows a fast behavioural response. Threat detection of fear-relevant stimuli is associated with activation of the fear module (Seligman 1971, Ohman & Mineka 2001, 2003). These traits may be fixed genetically in some animals including primates (Smith 1975, Weiss et al. 2015) and may also be enhanced by learning (Mineka et al. 1980, Cook et al. 1985, Cook & Mineka 1989), although both processes may be involved at the same time. A snake is an example of such dangerous stimulus representing a serious threat during primate evolution (Isbell 2006, Landová et al. 2018). Attentional bias to snakes associated with emotional activation and control involves specific circuits in the brain of humans and other primates most likely due to a long co-evolutionary history of snakes and human ancestors (Isbell 2006, Öhman et al. 2012, Van Le et al. 2013). In theory, this helps process the snake stimuli better and results in a quick and appropriate solution of the approach/avoidance task when confronted with a snake (but see Wheeler et al. 2011, Coelho et al. 2019, Zsido 2019).

The specificity of snake stimuli is a well-studied phenomenon (e.g., Mcnally 1987, Öhman et al. 2001, DeLoache & LoBue 2009, Penkunas & Coss 2013, Grassini et al. 2016, Fančovičová et al. 2020). Taken together, the studies show how the specific fear response increases chances of early visual detection and appropriate avoidance. First, snakes are detected faster than neutral stimuli in visual search tasks (Fox et al. 2007, Lobue & Deloache 2011). The privileged attentional processing of snakes is especially noticeable when the stimulus is presented in peripheral vision or for a very short time (less than 300 ms) or appear unexpectedly (reviewed by Öhman 2009, Öhman et al. 2012, Schaefer et al. 2014, Soares et al. 2014). Second, snakes elicit a measurable psycho-physiological response in humans (Öhman & Soares 1994, Dimberg et al. 1998, Flykt & Caldara 2006, Courtney et al. 2009, 2010, Flykt et al. 2017). Schaefer et al. (2014), for example, found that videos of snakes, especially those in an attacking posture, elicit a higher skin conductance fear response than fish. Deweese et al. (2014) demonstrated intense hypervigilance to snake pictures using electrophysiological measurements of steady-state visual evoked potentials (ssVEPs). Van Strien (2014a) recorded event-related potentials and they found that snake pictures captured more early attention than spiders or birds (Van Strien 2014a) and even crocodiles or turtles (Van Strien et al. 2014b). Third, startle reactions to snakes described by many herpetologists may present an evolutionary advantage for avoiding snakebites (Penkunas & Coss 2013, but see Coelho et al. 2019) and appear in other primates as well (Ramakrishnan et al. 2005, Zamma 2011).

The emotional saliency of reptiles, and especially snakes, was also studied in the past with fear and disgust being the most often associated emotions (e.g., Janovcová et al. 2019, Rádlová et al. 2019). Both fear and disgust are considered basic emotions (Ekman et al. 1969, Ekman & Friesen 1978, Ekman 1992, Steiner et al. 2001), with a universal distinctive facial expression and physiological response in humans and non-human primates (Steiner et al. 2001, Burrows 2008). From biological perspective, the two emotions are similar as their purpose is to induce an adaptive reaction to life-threatening stimuli, increasing the chances of survival (reviewed in Rádlová et al. 2020). However, fear allows quick decision-making in danger (such as a predation attempt), while disgust may help avoid disease-transmitting agents (e.g., some parasites or poisonous food; Curtis 2011, Curtis et al. 2011). Nonetheless, some species of reptiles are preferred on the basis of aesthetic criteria and are considered beautiful (Frynta et al. 2009, 2011, Marešová et al. 2009, Landová et al. 2012, 2018, Janovcová 2015). Beauty and positive affect may attract attention to animals in general (i.e., including the ones that are neither fear- nor disgust-relevant) in attentional visual detection tasks (Tipples et al. 2002, Lipp et al. 2004).

However, humans do not perceive reptiles as a homologous group either and the most distinctive and separate category are snakes. Janovcová et al. (2019) showed that there was a negative correlation between perceived beauty and disgust in reptiles, i.e., the least beautiful species were the same as the most disgusting ones. Additionally, the correlation between fear and disgust was negative in all reptiles; the most fear-eliciting species at the same time evoked only little disgust. In snakes but not in other non-snake reptiles (see also Landová et al. 2018), a positive correlation between fear and beauty of snakes was revealed, i.e., the most feared species also tended to be perceived as beautiful (Janovcová et al. 2019). However, there are many animals with a similar body shape as snakes (e.g., legless lizards) and there are also many snake species that do not resemble the general representation of snakes, e.g., fossorial snakes resembling worms (Rádlová et al. 2019). The question remains how specific snakes really are within the scope of other reptiles and whether a specific feature for identifying a specific animal as a snake can be determined.

Visual attention is frequently tested using various experimental settings, either using an eye-tracking device (e.g., LoBue et al. 2014, Haberkamp et al. 2018) or measuring the reaction time, which is usually done by pressing a button (Waters & Lipp 2008) or touching a touchscreen (e.g., LoBue & Matthews 2014, Zsido et al. 2019). However, visual attention is affected by many stimulus traits that are usually not the focus of the experiment, e.g., low-level visual features (Le Meur et al. 2006, Judd et al. 2009) such as colour (Frey et al. 2008, 2011), shape (Turatto & Galfano 2000), complexity (Pilelienė & Grigaliūnaitė 2016), or pattern and luminance contrast

(Einhäuser & König 2003). Whenever there are more than one stimulus presented at once, other factors influencing visual attention need to be considered, including (but not limited to) eccentricity (Bindemann 2010), lateralization (Kovic et al. 2009, Hairol & Waugh 2010), or visual similarity/dissimilarity (Arun 2012) with other presented objects. Even the given task or context within which the stimuli are presented may influence the overt attention. For example, Flowe et al. (2013) found that guns did not attract more attention than other unexpected objects and argue that the reason why guns were found as preferentially attended in other studies may be simply because they were unexpected within the given context (see also Loftus & Mackworth 1978). Thus, it is very important to heed a large number of factors that may influence the results when designing an experiment measuring visual attention.

In our eye-tracking experiment, we chose to measure a simple spontaneous visual reaction (during a free-viewing task) to individually presented reptile (snake/non-snake) stimuli. This simple method is exempt from a majority of the pitfalls mentioned above, excluding the low-level visual features (which were controlled for in our study) and provides relatively consistent results regardless of the given task (Kovic et al. 2009. The dwell time has been already found to be correlated with human preference towards depicted faces (Glaholt et al. 2009) and, in our study, it can reveal whether the respondents dodge their gaze away from the aesthetically unpreferred (i.e., rated as the least beautiful or "ugly"), feared, or disgusting animals. It should be noted that for the purpose of this study, we follow Janovcová et al (2019) and use reptiles in the traditional sense. More precisely, we use the term "reptiles" as a paraphyletic group of Reptilia excluding birds and extinct species since birds represent a separate category in research of human relationship to animals (Berlin 2014).

We hypothesize that snakes represent a separate category and are perceived differently from other reptiles; therefore, our first aim is to test whether eye movement patterns differ between snakes and non-snake reptiles. The second goal focuses on characteristics of the emotionally salient stimuli and its aim is to determine whether there are differences in eye movement patterns in response to snakes or other reptiles eliciting different emotions. The third goal is focused on variability among respondents and whether there are differences in reactions between respondents with different levels of snake fear and general disgust propensity.

MATERIAL AND METHODS

Respondents

Snake fear seems to be a crucial variable affecting a range of the measured psychophysiological parameters (Klorman et al. 1974, Dimberg et al. 1998, Lueken et al. 2011). Additionally, specific snake morphotypes evoke not only fear, but also disgust (Rádlová et al. 2019). Propensity of the respondents to animal fear or disgust might influence results of the experiment, hence it is necessary to examine the interindividual differences in snake fear (and disgust propensity) in more detail. Each respondent (n=61, 9 men, 52 women) completed the Snake Questionnaire (SNAQ: Klorman et al. 1974, Czech translation: Polák et al. 2016) and Disgust Scale-Revised (DS-R: Haidt et al. 1994, modified by Olatunji et al. 2007, Czech translation: Polák et al. 2019). Those who scored 8 or higher (the 75th percentile in the screening study Polák et al. 2016) on the SNAQ were classified as "high-fear" respondents (n=25). Similarly, those scoring 52 or above (the 75th percentile in Polák et al. 2019) on the DS-R were classified as "high-disgust" respondents (n=23). The rest of the participants were classified as "low-fear" (n=36) and/or "low-disgust" (n=38) respondents, respectively. Fourteen respondents qualified as both high-fear and high-disgust (for an overview, see Table 1). Mean age was 27.36, age range was 18–63 years.

The sample size was based on previous studies (e.g., Wang et al. 2012, Rosa et al. 2014, 2015) and a statistical a *priori* power analysis computed in G*Power 3 (Faul et al. 2007). This analysis was conducted to test the difference in eye movement patterns in response to eight categories of stimuli (fear-eliciting, disgust-eliciting, beautiful, neutral, with and without legs, snakes and non-snakes) using a repeated measures within factor ANOVA (6 repeats, correlation between repeated measures = 0.5), a medium effect size (f=0.25) and an alpha of 0.05. The result showed a total sample of 32 participants. Because we wanted to have comparable samples of high/low fear and high/low disgust participants, we doubled the number of participants, resulting in the final n=61.

Table 1. Overview of the number of respondents in each category. The respondents who scored at the 75th percentile (score 8) or higher on the SNAQ were classified as "high-fear" respondents (n=25), those scoring at the 75th percentile (score 52 or above) on the DS-R were classified as "high-disgust" respondents (n=23). The rest of the participants were classified as "low-fear" (n=36) and/or "low-disgust" (n=38) respondents, respectively

	high fear	low fear	total
high disgust	14	9	23
low disgust	11	27	38
total	25	36	61

Stimuli

We used 24 standardized photographs of reptiles as the stimuli (see Table 2). We chose three snakes and three non-snakes from four categories: animals perceived as (1) fear-eliciting, (2) disgust-eliciting, (3) neutral, and (4) beautiful. The stimuli were chosen from the sets used in Janovcová et al. (2019). In this study, we asked 70 respondents to pick five stimuli they would be afraid of, then five stimuli they find disgusting, and finally five stimuli they find beautiful. Fear- and disgust-eliciting stimuli for this experiment were chosen from the top 10% of stimuli most often picked as eliciting the respective emotion, however we excluded stimuli that also elicited the other emotion (i.e., those that had been picked more than five times also for the other emotion). Beautiful stimuli were those that had not been among 10% of the most often picked as fear- and disgust-eliciting. From these, we chose 10% of the most often picked as beautiful and selected three snakes and three non-snakes for this experiment. Neutral stimuli were those that had never been picked for either of the three emotions. In all cases, we aimed to choose those species that also well represented the taxonomical variability within the category specified by the above-mentioned criteria. The rating of each stimulus on a Likert scale according to beauty, disgust, and fear as assessed in Janovcová et al. (2019) is shown in Table 2.

Low-level visual features

To ensure that the results we sought were not affected by low-level features, we performed the following pre-analysis: the picture stimuli were analysed using Barvocuc, a picture analysis software (Rádlová et al. 2016), which extracted information about colour, lightness, and pattern properties of the stimuli (for a detailed description of the processed variables, see Lišková et al. 2015). Then, we performed general linear model analyses, which included opacity (the total number of pixels minus the pixels covering the background, i.e., "robustness" or "silhouette" of the animal), mean and StD lightness (L), mean and StD saturation (S), pattern, and the proportion of white, black, grey, brown, yellow, green, blue, and pink colours as explanatory variables.

An analysis of the total dwell time resulted in a reduced model that was not significant, i.e., no low-level visual features affected the resulting total dwell time on the picture stimuli. Analysis of the total fixation count resulted in

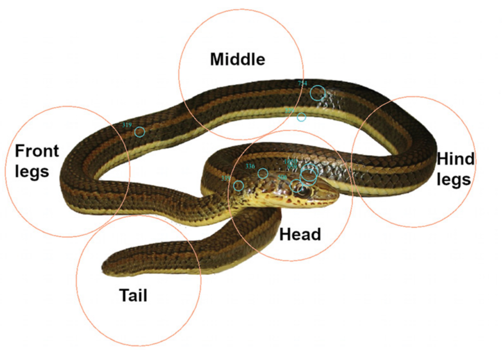

Fig. 1. The interest areas (IAs) on a spotted grass snake (*Psammophylax rhombeatus*; original picture is in Public Domain). The IAs are delineated by orange circles, fixations of a participant are marked as blue circles (their diameter is proportional to the duration of fixation). In snakes, the IA labelled as "front legs" was situated approximately in one third of the body length, the IA labelled as "hind legs" was situated in two thirds of the body length.

Table 2. Overview of the stimuli used in the experiment. The species were selected based on the emotion they elicited in respondents in a previous study (beauty, disgust, fear, neutral; Likert scores are from Janovcová et al. 2019) and whether they have legs or not

species	subfamily	snake / non-snake	legs?	category	Likert fear	Likert disgust	Likert beauty
Uracentron azureum	Tropidurinae	non-snake	yes	beauty	1.92	1.63	6.21
Chelonia mydas	Cheloniinae	non-snake	yes	beauty	1.32	1.15	6.44
Anolis punctatus	Dactyloinae	non-snake	yes	beauty	1.76	1.70	6.03
Epicrates crassus	Boinae	snake	no	beauty	4.67	3.45	4.78
Psammophylax rhombeatus	Psammophiinae	snake	no	beauty	4.09	3.43	4.6
Blythia reticulata	Colubridae	snake	no	beauty	4.65	3.68	4.43
Anelytropsis papillosus	Dibamidae	non-snake	no	disgust	3.93	5.16	2.05
Bipes biporus	Bipedinae	non-snake	no	disgust	3.53	5.43	1.98
Rhineura floridana	Rhineurinae	non-snake	no	disgust	3.73	5.44	1.78
Xenotyphlops mocquardi	Xenotyphlopinae	snake	no	disgust	3.51	5.17	2.21
Austrotyphlops pinguis	Typhlopinae	snake	no	disgust	3.91	4.79	2.47
Helminthophis frontalis	Anomalepinae	snake	no	disgust	4.25	4.77	2.71
Macrochelys temminckii	Chelydrinae	non-snake	yes	fear	3.36	3.30	4.21
Varanus komodoensis	Varaninae	non-snake	yes	fear	3.77	2.13	5.16
Crocodylus moreletii	Crocodylinae	non-snake	yes	fear	5.10	2.28	5.16
Protobothrops jerdonii	Crotalinae	snake	no	fear	5.48	3.52	5.74
Azemiops feae	Azemiopinae	snake	no	fear	4.95	3.51	5.34
Pseudocerastes persicus	Viperinae	snake	no	fear	5.54	3.65	4.38
Anniella geronimensis	Anniellidae	non-snake	no	neutral	3.90	4.28	3.15
Tetradactylus ellenbergeri	Gerrhosaurinae	non-snake	no	neutral	3.91	3.69	3.83
Pletholax gracilis	Pygopodinae	non-snake	no	neutral	4.28	3.83	3.96
Prosymna stuhlmannii	Prosymninae	snake	no	neutral	4.20	3.98	3.17
Macrocalamus lateralis	Calamariinae	snake	no	neutral	4.35	3.93	3.14
Buhoma vauerocegae	Pseudaspidinae	snake	no	neutral	4.66	3.80	3.48

a reduced model (r^2 adj.=44.42%, p=0.016, df=1, residuals = 16) that included mean L, mean S, white, grey, green, and pink, but only the effect of grey (F=12.670, p=0.003) and green (F=5.514, p=0.0321) were significant. Tukey post-hoc test showed that the pre-defined groups do not differ among each other in distribution of the grey nor green colour with two exceptions: non-snake reptiles in our picture set are greyer than snakes, p=0.027; and animals with legs are more green than legless animals (p=0.015). This pre-analysis shows that the categories of the stimuli used in our study differ from each other only marginally.

Eyetracking experiment

The stimuli were presented in 300 DPI resolution on a 19-inch monitor (full HD resolution, refresh rate 60 Hz), which was situated 70 cm from the respondent. The location of the respondent's head was fixed using a chinrest. The stimuli were presented to each respondent one by one in a random order. Eye movements were recorded with the EyeLink1000 eye-tracking device, the experimental setup was designed using the SR-Research Experiment Builder. At the beginning of each presentation, the respondent answered four questions: age, gender, whether he/she was right- or left-handed and his/her country of origin. The device was calibrated for each respondent, using the manufacturer's procedure, and the calibration was subsequently validated. The maximal allowed error was 1° of the visual angle and average allowed error was 0.5°. If the error during validation was higher than allowed, the device was adjusted, and calibration and validation were repeated. Once the validation was completed, the stimuli were presented for 5 seconds each (trial) in a randomized order. A drift check was performed before each stimulus. The respondents were instructed to watch the stimuli as they appeared on the screen, without any specific task. Using the DataViewer (SR-Research), we extracted the total number of fixations during the trial (fixation count), the total time the respondent was watching the area of the stimulus (dwell time). We also recorded the fixation count and dwell time for five interest areas (IAs) – head, tail, front legs, hind legs, and the centre of the body. In case of snakes/legless reptiles, "front/hind legs" were measured as the first third/last third of the body. All the IAs were circular, had the same area size, and did not overlap in any of the stimuli (see Fig. 1).

Table 3. Geeglm models for individual interest areas; upper values = X^2, lower values = p. Trial = trial order; legs = presence/absence of legs; type = snake / non-snake; HF/LF = high- / low-fear respondents; HD/LD = high- / low-disgust respondents; stimulus = beautiful / fear-eliciting / disgust-eliciting / neutral. Results significant at p=0.05 are marked in bold

	head	tail	front legs	hind legs	middle
trial	0.27	1.30	1.40	**8.30**	**6.00**
	0.605	0.250	0.236	**0.004**	**0.018**
legs	**18.10**	**102.70**	**11.10**	**166.00**	**352.00**
	0.001	**0.001**	**0.001**	**0.001**	**0.001**
type	**18.45**	**98.40**	**80.80**	3.60	**43.00**
	0.001	**0.001**	**0.001**	0.058	**0.001**
HF / LF	**4.41**	2.20	0.30	2.70	2.00
	0.036	0.140	0.596	0.097	0.121
HD / LD	1.06	0	0	0.20	0
	0.304	0.980	0.901	0.642	0.838
stimulus	**28.27**	**287.20**	**186.70**	**77.40**	**70.00**
	0.001	**0.001**	**0.001**	**0.001**	**0.001**

Statistical analysis

We employed a generalized estimating equations model for Poisson distribution (geeglm command in R, package geepack) for the total fixation count with the stimulus order in the presentation (trial order), presence or absence of visible legs, whether the reptile was a snake or not, whether the respondent was high- or low-fear and high- or low-disgust, and the

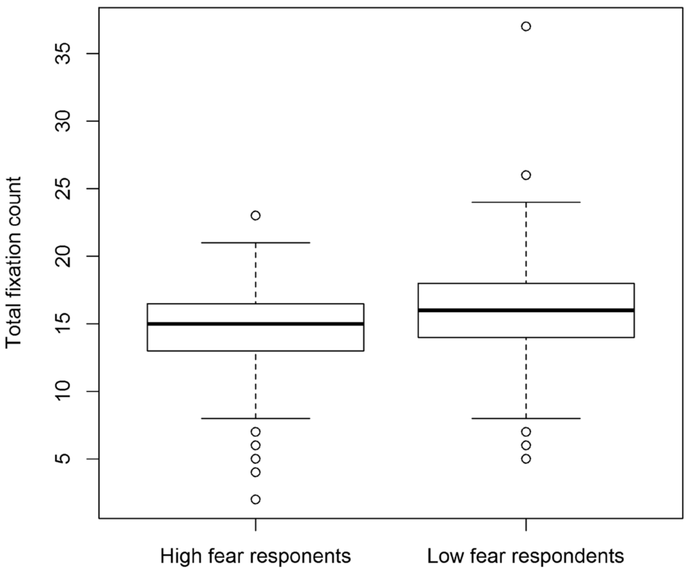

Fig. 2. Boxplot of total fixation counts for high-fear and low-fear respondents. Quartiles, medians, and outliers are indicated. High-fear respondents had less fixations to the stimuli (see geeglm model for overall fixation count). A possible explanation is that high-fear respondents want to keep an eye contact with the fearsome animals to avoid possible unexpected movement or a risk of bite.

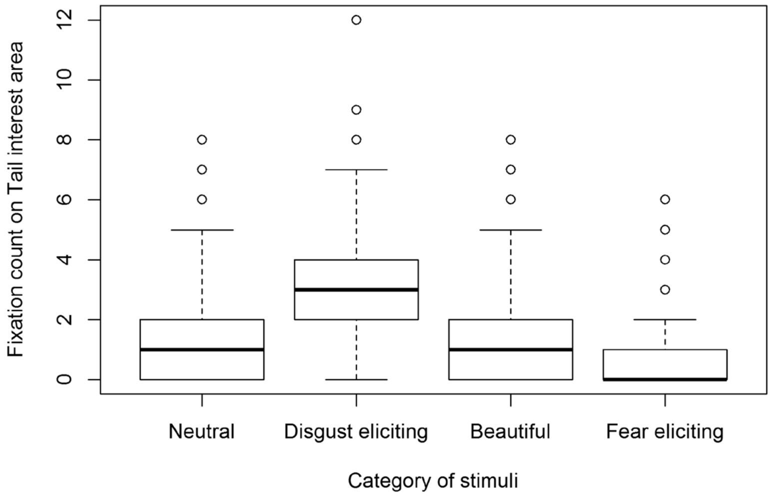

Fig. 3. Boxplot of fixation counts on the "tail" interest area for different stimuli categories. Quartiles, medians, and outliers are indicated. Fear-eliciting stimuli attract most of the attention on the head; therefore, the participants paid little attention to the tail area. In disgust-eliciting stimuli, attention is divided between the head and the tail area.

type of stimulus (neutral, fear-evoking, disgust-evoking, beautiful) as fixed factors and the participant's ID as a random factor. We also used the same fixed and random factors for a geeglm model explaining the fixation count for the individual IAs (head, front legs, hind legs, middle of the body, tail) and for a generalized least square (GLS) model (as implemented in the package nlme in R, command gls) for the total dwell time on the stimulus (not transformed) and the proportion of fixation count concentrated on the head IA (arcsin transformed), computed as the number of fixations on the head divided by the total number of fixations for the whole trial. The non-significant fixed factors were removed from the full GLS models, and the reduced and full models were compared with ANOVA to ensure that the reduced model equals the full one. After Bonferroni correction, the alpha level was set to 0.00625.

RESULTS

The gls analysis of the trial dwell time resulted in a model that contained only two variables – order of the stimulus in the presentation (trial order; $F=20.288$, $p<0.001$) and disgust propensity of the respondent ($F=4.625$, $p=0.032$). The stimuli presented later had shorter dwell time.

The geeglm model for the overall fixation count yielded three significant variables – the reptilian type (snake/non-snake, df=1, $X^2=19.36$, $p<0.001$), respondent's fear (high/low fear, df=1, $X^2=6.98$, $p=0.008$), and the stimulus type (neutral/fear evoking/disgust evoking/ beautiful, df=3, $X^2=31.24$, $p<0.001$). The participants had more fixations when looking at non-snake stimuli (estimate = 0.032, $p<0.001$) and high-fear respondents had less fixations than the low-fear ones (estimate = –0.094, $p=0.008$; Fig. 2). Compared to the neutral stimuli, beautiful stimuli did not differ significantly in the number of fixations (estimate = 0.007, $p=0.570$), but disgust-evoking stimuli had significantly more fixations (estimate = 0.024, $p=0.028$) and fear-evoking stimuli had significantly less fixations (estimate = –0.033, $p=0.002$).

In the models for individual IAs, the stimulus type and presence/absence of legs was significant for all the IAS, while the respondent's disgust propensity were not significant for any of the

Table 4. Coefficients of the geeglm models. For the overview of the variables, see Table 2. Reference levels for the factors, to which the other levels are compared, are as follows: legs = legs present; type = snake; HF/LF = high fear respondents; stimulus = neutral. Disgust propensity of the respondent was excluded, as it was not significant for any of the models. Results significant at p=0.05 are marked in bold (lower values)

	level of factor	head	tail	front legs	hind legs	middle
trial		–0.001 0.643	0.005 0.157	0.004 0.318	0.014 **0.003**	–0.011 **0.002**
legs	legs absent	0.101 **0.001**	0.731 **0.001**	–0.506 **0.001**	–1.196 **0.001**	–1.055 **0.001**
type	non-snake	–0.055 **0.010**	0.303 **0.001**	0.293 **0.001**	–0.046 0.591	–0.265 **0.001**
HF / LF	low fear	0.109 **0.019**	0.126 0.133	0.050 0.591	0.133 0.138	0.127 0.129
stimulus	disgust-eliciting	0.091 **0.001**	0.826 **0.001**	–0.805 **0.001**	–0.41 **0.001**	0.116 0.177
	beautiful	0.082 **0.002**	0.119 0.140	–0.856 **0.001**	–0.43 **0.001**	0.064 0.403
	fear-eliciting	0.125 **0.001**	–0.164 0.041	–1.018 **0.001**	–0.769 **0.001**	0.486 **0.001**

IAs. The fear level of the respondent was significant only for the head interest area. The reptilian type (snake/non-snake) was significant for all IAs except the "hind legs" IA. The trial order was significant only for the middle of the body and the "hind legs" IA. For an overview of the results, see Table 3.

Respondents had more fixations in the head and tail IAs (Fig. 3) and less fixations in the front legs, hind legs, and middle IAs, when watching the legless animals, compared to animals with legs. When watching snakes, they had more fixations on the head and middle area and less fixations on the tail and front legs area than when watching non-snakes (Fig. 4). High- and low-fear respondents differed only in their fixation count on the head interest area, where low-fear

Fig. 4. Heat map of fixations on a fear-eliciting black-headed Burmese viper (*Azemiops feae*; photo by Tom Charlton, used with a permission). The red colour indicates the area with most fixations. In fear-eliciting snakes, most fixations are concentrated on the head area, while the tail area receives almost no fixations.

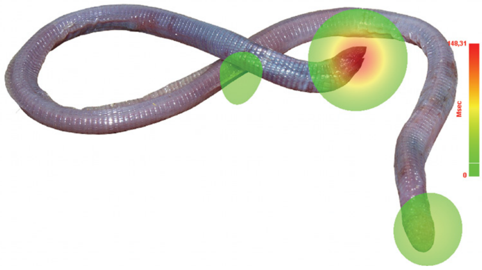

Fig. 5. Heat map of fixations on a disgust eliciting non-snake reptile, the Florida worm lizard (*Rhineura floridana*; photo by Jacob Scott, used with permission). The red colour indicates the area with most fixations. In disgusting stimuli, the fixations are mostly distributed between the head and tail area.

respondents had more fixations. In disgusting stimuli, respondents had more fixations on the head and tail areas and fewer fixations on the front legs and hind legs IAs than in neutral stimuli (see Fig. 5 for illustration of fixation pattern in disgust-evoking stimuli). Beautiful stimuli resulted in more fixations on the head area and less fixations on the front legs and hind legs interest areas compared to neutral stimuli. When watching the fear-eliciting stimuli, respondents had more fixations on the head and middle interest areas and less fixations on the tail, front legs and hind legs interest areas. For the coefficients and their p values, see Table 4.

The model analysing proportion of fixations concentrated on the head area yielded similar results (Table 5). In concordance with previous analyses, it showed a significant effect of presence/absence of legs ($F=23.032$, $p<0.001$), reptilian type ($F=35.722$, $p<0.001$), and the stimulus type ($F=8.541$, $p<0.001$). We did not find a significant effect of either fear or disgust of the respondent ($p>0.05$). More specifically, the legless animals had a larger proportion of fixations on the head area (t-value = 2.883, $p=0.004$). Non-snakes had less fixations on the head than snakes (t-value = –3.388, $p=0.001$). All emotionally salient stimuli had more fixations on the head area than neutral animals (disgust-eliciting: t-value = 2.597, $p=0.001$; beautiful: t-value = 3.047, $p=0.002$, fear-eliciting: t-value = 4.996, $p<0.001$).

Table 5. Gls model of proportion of fixation on the head area (arcsin transformed). Trial = trial order; legs = presence / absence of legs; type = snake / non-snake; HF/LF = high- / low-fear respondents; HD/LD = high- / low-disgust respondents; stimulus = beautiful / fear-eliciting / disgust-eliciting / neutral. Significant results are marked in bold

	DF	F	p
(intercept)	1	6000.205	**<0.001**
trial	1	2.466	0.117
legs	1	23.032	**<0.001**
type	1	35.722	**<0.001**
fear	1	0.083	0.773
disgust	1	0.012	0.914
stimulus	3	8.541	**<0.001**

DISCUSSION

Snakes seem to represent very special threatening stimuli that primarily attract attention in situations where a number of objects compete for visual attention (Soares et al. 2009, LoBue & DeLoache 2011, Van Strien et al. 2014). But do the snakes also attract a specific pattern of visual saccades when being watched alone during a spontaneous visual task? And if so, does this pattern differ among fear-eliciting, disgust-eliciting, and beautiful snakes?

We found multiple factors that influenced the number of fixations, but not the dwell time, when respondents watched reptile images: snakes, leglessness, and emotion affected the continual attention devoted to some parts of the reptile body. The snakes represent a very specific group differing from other legless reptiles by fixation pattern concentrated to the head and middle body. The emotion of the stimulus also played a role, as human respondents fixated more often on head when watching emotionally-salient animals compared to the neutral ones. We discuss possible explanations of these findings further in the text.

The specificity of snakes among reptiles

In this study, we explored the hypothesis that humans perceive snakes as a distinct category within reptiles, which selectively attract visual attention. Previously, Janovcová et al. (2019) has analysed self-reported fear and disgust and shown that snakes elicit specific emotional and aesthetical preferences and are subjectively evaluated differently than other reptiles. Moreover, the same pattern expanded onto other species resembling snakes, like the worm lizards (Amphisbaenia) and legless lizards. Here we took a rather different approach and focused on spontaneous visual attention patterns to snake and non-snake reptiles or visual preferences of specific features of these stimuli (head, legs, other parts of the body).

An interesting result of this study is that the respondents had overall fewer fixations to the snake stimuli, while the dwell time was no different from the non-snake stimuli. This observation can be interpreted in several ways. For example, Pertzov et al. (2009) concluded that a higher number of fixations within an object leads to the accumulation of information about that object and thus to better memory performance. Moreover, Jacob & Hochstein (2010) showed a link between a higher number of fixations and object identification (also see Loftus 1981, reviewed in Duchowski 2007). It is thus possible that snakes, receiving fewer fixations, are identified more quickly than other non-snake reptiles. This would be in agreement with other works that found a faster identification of snakes when compared to non-snake reptiles, e.g., Kawai & Qiu (2020). To further explore the gazing pattern, we performed analyses of particular features present on the reptile body.

However, to better understand the results, it is useful to review the general pattern of gaze as measured by the eye tracking method used in the study. During free picture viewing, focus is affected either using "bottom–up" processes, i.e., by physically salient visual features (features that are distinct from background/stand out in terms of lightness, saturation, colour, structure, complexity, etc.; Yantis 2005, Harel et al. 2007, Dupont et al. 2014), or using "top–down processes", i.e., affected by the goal of exploration (the given task; Humphrey & Underwood 2009, Villani et al. 2015, Dupont et al. 2016). In our study, the respondents were not given any specific task. However, as already discussed, snakes represent evolutionarily threat-relevant stimuli that have been reported to be visually detected faster than similar objects. When watching snake stimuli, it is thus reasonable to assume that unconscious processes may lead to preferential attention to informationally salient key features that might help the viewer with identification of the animal and quick assessment of the actual threat (Prokop et al. 2018), e.g., leglessness (Lobue & Deloache 2011) or protruding snake scales (Van Strien & Isbell 2017). In other words, it is possible that even without any specific given task, the respondent's attention may be unconsciously led by the "top-down" processes towards specific life-threatening animal features.

The legless reptiles possess a long and usually visually homogenous body that contains low physical salience of visual features. Only the tips of the animal – the head and the tail – provide enough salience to catch attention, and it is thus reasonable to expect that these body parts will receive the highest number of fixations (the "visual salience" hypothesis). However, if the "top–down processes" played role, other features such as missing legs should be searched for by the viewer. Thus, we hypothesized that in legless lizards and snakes, the number of fixations on missing legs will be comparable to the number of fixations to the corresponding interest areas of the animals with legs present (the "evolutionary salience" hypothesis).

Our results regarding the animal leglessness showed no support for the "evolutionary salience" hypothesis. Instead, the respondents fixated significantly more on the head and tail areas of the legless animals, which fully supported the "visual salience" hypothesis. However, when analyzing the stimuli divided into taxonomically defined snakes and non-snakes, the data showed very interesting results: the respondents fixated more on the head and middle body areas of the animals, while the tail was fixated less. These results cannot be explained by the "visual salience" hypothesis alone and rather suggest that snakes are somewhat special – they differ categorically from other legless reptiles included within the non-snake group and attract specific attention processed "top-down".

It was indeed described that human respondents heed particular snake features when assessing the level of self-perceived fear from a given snake morphotype, and these features were mainly located on the head: a larger, protruding head with a thin neck (as compared to thick necks and indistinguishable heads of some mainly disgusting, fossorial snakes, which are also present in legless lizards; Ptáčková et al. 2017) and protruding scales (which are located on the whole snake including the head; Rádlová et al. 2019). Snakes also have fused and transparent eyelids, which makes their eyes very different from other legless lizards (Walls 1940). Moreover, some snakes possess even more specific features, such as the viperids and similar snakes, which are cross-culturally perceived as the most fear-evoking snakes (Landová et al. 2018). Many of these species possess distinctive scale pattern above their eyes and narrow pupils (Dullemeijer 1968). In comparison, the blind fossorial snakes (with small, featureless heads and little eyes) from the family Typhlopoidea elicit mainly disgust (Rádlová et al. 2019, 2020) and present virtually no danger to humans (Uetz & Hošek 2020). It is thus possible that human respondents first quickly assess whether the species is a snake or not and then their attention lasts longer shifting around the snake head and body to effectively assess the actual dangerousness of the species, because the head and body region of snakes contains all the necessary information. Our results are consistent with this theory. In any case, it would be interesting to further test this hypothesis, e.g., by using a manipulative experiment (i.e., one that would use artificially modified and standardized pictures of reptiles).

Fear, disgust, and beauty

We detected a lower number of fixations when the participants were watching fear-eliciting stimuli compared to neutral stimuli eliciting no specific emotion which we already discussed above. The results also showed that all the emotionally relevant stimulus categories (disgust-eliciting, fear-eliciting, beautiful) had more fixations on the head and less on the front and hind legs compared with the neutral ones (for typical pattern, see Figs. 3–5). These results suggest that the animal's head is a crucial part of the body for our attention, which might determine the elicited emotion (Kano et al. 2008, Kovic et al. 2009). Additionally, in disgust-eliciting stimuli, the and the respondents also fixated more often on the tail area, which might be caused by the worm-like body shape of the disgust-eliciting reptiles, where it is not obvious at the first glance which part of the body is the head and which is the tail. Thus, the respondents probably needed more fixations to identify the head of the animal and/or assess the dangerousness of the animal. Interestingly, non-snake reptiles had more fixations on the tail area than snakes.

Comparison with previous studies

A substantial amount of research is devoted to snakes and their ability to attach preferential attention among other stimuli. The results usually vary, and some authors argue that there is a preferential reaction to animal stimuli in general when searched for among other non-animate stimuli such as flowers and mushrooms (Lipp et al. 2004, but see LoBue 2010) and that snakes are no more special than other predatory or attractive animals (Tipples et al. 2002). In our previous study, we studied some aspects of the attentional, behavioural and emotional response to snake and invertebrate stimuli like scorpion, spider and crab stimuli used as task irrelevant distractors in the centre of the screen (Landová et al. in prep.). We found that participants with normative fear of spiders were distracted most by snakes and scorpions, but those with high fear of spiders were distracted more by spiders and similar crabs.

Snake specificity was confirmed with regards to their distractor properties or when detection took place under challenging set ups (Flykt 2006, Soares et al. 2014, Gomez et al. 2018, reviewed in Kawai 2019). However, when put together (see Rádlová et al. 2018, for a more detailed review on this), it seems that the effect is rather continuous than binary, i.e., human respondents process predatory animals such as snakes and lions faster than reptiles (Yorzinski et al. 2014) since they belong to the most fear-evoking animals (Staňková et al 2021), reptiles faster than birds (Van Strien & Isbell 2017), and birds faster than other, non-animate objects. These results also conclude that visual attention is very sensitive to the context in which the stimuli are presented, although it may affect threatening stimuli less than neutral ones (Zsido et al. 2019).

Because of this, the results of the present study may not be fully comparable to the results from similar field. We employed different experimental methods. In this case, we explored the gazing pattern to single objects, i.e., we removed the effect of context and focused on the base attention devoted to each animal and/or their particular bodily parts. Due to these differences, we are able to present novel insight into the complex knowledge of snake fear and related attentional processes.

Although using a different approach, our results are in agreement with previous literature. Our analyses showed that snakes receive a very specific gazing pattern that differs from other legless reptiles, suggesting they may be perceived as a separate category. Additionally, we found similar pattern for fear-relevant reptiles, which included non-snakes such as the crocodile or Komodo dragon.

Limitations of the study

Because the stimuli set was primarily balanced according to the emotions elicited by the stimuli and taxonomy (snake / non-snake), we could not balance it properly for the presence or absence of the legs. Therefore, the analysis of the effect of the presence of legs is not the focus of the study. Rather, we tried to eliminate the effect during the statistical analysis; however, this is possible only to a certain extent. For the same reason (i.e., the study was performed on naturally occurring stimuli without specific computer manipulations), we were unable to properly balance the colours. Therefore, non-snakes were greyer and animals with legs were greener. This fact made it more difficult to provide clear interpretation of the data, however, as the results are in agreement with widely accepted view of snakes as special and threatening stimuli, we believe that our interpretation is valid. Moreover, during the selection of the respondents, the primary criterion was the level of fear and disgust. Because women are generally more prone to disgust and snake fear, we were unable to achieve a sample balanced by gender.

Ethical note and data availability statement

This study was carried out in accordance with the recommendations of Institutional Review Board (IRB), Faculty of Sciences, Charles University, approval n. 2013/7, and approval of the Ethical Committee of the National Institute of Mental Health n. 55/16, with the written informed consent from all subjects in accordance with the Declaration of Helsinki. The protocol was approved by the Institutional Review Board (IRB).

The data that support the findings of this study are available from the corresponding author, S.R., upon reasonable request.

Acknowledgements

We are thankful to David Nácar for his help with the collection of initial data. We thank all the photographers who kindly provided us with the images to use in our research, and all our respondents who agreed to take part in the study. This work was supported by the Czech Science Foundation under grant nr. 17-15991S and participation of MJ and SP on finalization of the manuscript was partially covered by the SVV project n. 260684/2023.

REFERENCES

Arun S. P. 2012: Turning visual search time on its head. *Vision Research* **74**: 86–92.

Berlin B. 2014: *Ethnobiological Classification*: *Principles of Categorization of Plants and Animals in Traditional Societies*. Princeton: Princeton University Press, 335 pp.

Bindemann M. 2010: Scene and screen center bias early eye movements in scene viewing. *Vision Research* **50**: 2577–2587.

Burrows A. M. 2008: The facial expression musculature in primates and its evolutionary significance. *Bioessays* **30**: 212–225.

Chiari Y., Cahais V., Galtier N. & Delsuc F. 2012: Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). *BioMedCentral Biology* **10**(65): 1–14.

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): 1–10.

Cook M. & Mineka S. 1989: Observational conditioning of fear to fear-relevant versus fear-irrelevant stimuli in rhesus monkeys. *Journal of Abnormal Psychology*, **98**: 448–459.

Cook M., Mineka S., Wolkenstein B. & Laitsch K. 1985: Observational conditioning of snake fear in unrelated rhesus monkeys. *Journal of Abnormal Psychology* **94**: 591–610.

Courtney C. G., Dawson M. E., Schell A. M. & Parsons T. D. 2009: Affective computer-generated stimulus exposure: psychophysiological support for increased elicitation of negative emotions in high and low fear subjects. Pp. 459–468. In: Nandi A., Sujatha N., Menaka R. & Alex J. (eds): *International Conference on Foundations of Augmented Cognition*. Berlin & Heidelberg: Springer, 884 pp.

Courtney C. G., Dawson M. E., Schell A. M., Iyer A. & Parsons T. D. 2010: Better than the real thing: Eliciting fear with moving and static computer-generated stimuli. *International Journal of Psychophysiology* **78**: 107–114.

Curtis V. 2011: Why disgust matters. *Philosophical Transactions of the Royal Society B*: *Biological Sciences* **366**: 3478–3490.

Curtis V., De Barra M. & Aunger R. 2011: Disgust as an adaptive system for disease avoidance behaviour. *Philosophical Transactions of the Royal Society B*: *Biological Sciences* **366**: 389–401.

DeLoache J. S. & LoBue V. 2009: The narrow fellow in the grass: Human infants associate snakes and fear. *Developmental Science* **12**: 201–207.

Deweese M. M., Bradley M. M., Lang P. J., Andersen S. K., Müller M. M. & Keil A. 2014: Snake fearfulness is associated with sustained competitive biases to visual snake features: hypervigilance without avoidance. *Psychiatry Research* **219**: 329–335.

Dimberg U., Hansson G. Ö. & Thunberg M. 1998: Fear of snakes and facial reactions: A case of rapid emotional responding. *Scandinavian Journal of Psychology* **39**: 75–80.

Duchowski A. T. 2007: Eye tracking methodology. *Theory and Practice* **328**: 2–3.

Dullemeijer P. 1968: Growth and size of the eye in viperid snakes. *Netherlands Journal of Zoology* **19**: 249–276.

Dupont L., Antrop M. & Van Eetvelde V. 2014: Eye-tracking analysis in landscape perception research: Influence of photograph properties and landscape characteristics. *Landscape Research* **39**: 417–432.

Dupont L., Ooms K., Antrop M. & Van Eetvelde V. 2016: Comparing saliency maps and eye-tracking focus maps: The potential use in visual impact assessment based on landscape photographs. *Landscape and Urban Planning* **148**: 17–26.

Einhäuser W. & König P. 2003: Does luminance□contrast contribute to a saliency map for overt visual attention? *European Journal of Neuroscience* **17**: 1089–1097.

Ekman P. 1992: An argument for basic emotions. *Cognition & Emotion* **6**: 169–200.

Ekman P. & Friesen W. V. 1978: *Facial Action Coding System*: *Investigator*'*s Guide*. Palo Alto: Consulting Psychologists Press, 197 pp.
Ekman P., Sorenson E. R. & Friesen W. V. 1969: Pan-cultural elements in facial displays of emotion. *Science* **164**: 86–88.
Fančovičová J., Prokop P., Szikhart M. & Pazda A. 2020: Snake coloration does not influence children's detection time. *Human Dimensions of Wildlife* **25**: 1–9.
Faul F., Erdfelder E., Lang A. G. & Buchner A. 2007: G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods* **39**: 175–191.
Flowe H. D., Hope L. & Hillstrom A. P. 2013: Oculomotor examination of the weapon focus effect: does a gun automatically engage visual attention? *Public Library of Science One* **8**(12; e81011): 1–7.
Flykt A. 2006: Preparedness for action: Responding to the snake in the grass. *American Journal of Psychology* **119**: 29–43.
Flykt A. & Caldara R. 2006: Tracking fear in snake and spider fearful participants during visual search: A multi-response domain study. *Cognition and Emotion* **20**: 1075–1091.
Flykt A., Bänziger T. & Lindeberg S. 2017: Intensity of vocal responses to spider and snake pictures in fearful individuals. *Australian Journal of Psychology* **69**: 184–191.
Fox E., Griggs L. & Mouchlianitis E. 2007: The detection of fear-relevant stimuli: Are guns noticed as quickly as snakes? *Emotion* **7**: 691–696.
Frey H. P., Honey C. & König P. 2008: What's color got to do with it? The influence of color on visual attention in different categories. *Journal of Vision* **8**(14; 6): 1–17.
Frey H. P., Wirz K. T., Willenbockel V., Betz T., Schreiber C., Troscianko T. & Konig P. 2011: Beyond correlation: do color features influence attention in rainforest? *Frontiers in Human Neuroscience* **5**(36): 1–13.
Frynta D., Marešová E., Landová E., Lišková S., Šimková O., Tichá I., Zelenková M. & Fuchs R. 2009: Are animals in zoos rather conspicuous than endangered? Pp. 299–341. In: Columbus A. M. & Kuznetsov L. (eds.): *Endangered Species – New Research*. New York: Nova Science Publishers, Inc., 380 pp.
Frynta D., Marešová J., Řeháková-Petrů M., Šklíba J., Šumbera R. & Krása A. 2011: Cross-cultural agreement in perception of animal beauty: boid snakes viewed by people from five continents. *Human Ecology* **39**: 829–834.
Frynta D., Peléšková Š., Rádlová S., Janovcová M. & Landová E. 2019: Human evaluation of amphibian species: a comparison of disgust and beauty. *Science of Nature* **106**: 1–19.
Glaholt M. G., Wu M. C. & Reingold E. M. 2009: Predicting preference from fixations. *PsychNology Journal* **7**: 141–158.
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.
Gomes N., Soares S. C., Silva S. & Silva C. F. 2018: Mind the snake: Fear detection relies on low spatial frequencies. *Emotion* **18**: 886–892.
Haberkamp A., Biafora M., Schmidt T. & Weiß K. 2018: We prefer what we fear: A response preference bias mimics attentional capture in spider fear. *Journal of Anxiety Disorders* **53**: 30–38.
Haidt J., McCauley C. & Rozin P. 1994: Individual differences in sensitivity to disgust: A scale sampling seven domains of disgust elicitors. *Personality and Individual Differences* **16**: 701–713.
Hairol M. I. & Waugh S. J. 2010: Lateral facilitation revealed dichoptically for luminance-modulated and contrast-modulated stimuli. *Vision Research* **50**: 2530–2542.
Harel J., Koch C. & Perona P. 2007: Graph-based visual saliency. Pp. 545–552. In: Jordan M. I., LeCun Y. & Solla S. A. (eds): *Advances in Neural Information Processing Systems*. Cambridge: MIT Press (CD ROM).
Hermans D., Vansteenwegen D. & Eelen P. 1999: Eye movement registration as a continuous index of attention deployment: Data from a group of spider anxious students. *Cognition & Emotion* **13**: 419–434.
Humphrey K. & Underwood G. 2009: Domain knowledge moderates the influence of visual saliency in scene recognition. *British Journal of Psychology* **100**: 377–398.
Isbell L. A. 2006: Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution* **51**: 1–35.
Jacob M. & Hochstein S. 2010: Graded recognition as a function of the number of target fixations. *Vision Research* **50**: 107–117.
Janovcová M. 2015: [*Factors Influencing Worldwide Zoo Collections of Lizards*, *Snakes*, *Turtles and Crocodiles*: *Effect of Conservation Status*, *Body Size and Their Attractiveness to Humans*]. Master's thesis, Charles University in Prague, 133 pp (in Czech)
Janovcová M., Rádlová S., Polák J., Sedláčková K., Peléšková Š., Žampachová B., Frynta D. & Landová E. 2019: Human attitude toward reptiles: A relationship between fear, disgust, and aesthetic preferences. *Animals* **9**(5; 238): 1–17.
Judd T., Ehinger K., Durand F. & Torralba A. 2009: Learning to predict where humans look. Pp. 2106–2113. In: Anonymous (ed.): *2009 Institute of Electrical and Electronics Engineers 12th International Conference on Computer Vision*. Lisboa: Institute of Electrical and Electronics Engineers, 2396 pp.
Kano F., Tanaka M. & Tomonaga M. 2008: Enhanced recognition of emotional stimuli in the chimpanzee (Pan troglodytes). *Animal Cognition* **11**: 517–524.

Kawai N. 2019: Do snakes draw attention more strongly than spiders or other animals? Pp. 73–94. In: Kawai N. (ed.): *The Fear of Snakes*: *Evolutionary and Psychobiological Perspectives on Our Innate Fear.* Singapore: Springer Singapore, 187 pp.

Kawai N. & Qiu H. 2020: Humans detect snakes more accurately and quickly than other animals under natural visual scenes: a flicker paradigm study. *Cognition and Emotion* **34**: 614–620.

Kovic V., Plunkett K. & Westermann G. 2009: Eye-tracking study of animate objects. *Psihologija* **42**: 307–327.

Klorman R., Weerts T. C., Hastings J. E., Melamed B. G. & Lang P. J. 1974: Psychometric description of some specific-fear questionnaires. *Behavior Therapy* **5**: 401–409.

Landová E., Marešová J., Šimková O., Cikánová V. & Frynta D. 2012: Human responses to live snakes and their photographs: evaluation of beauty and fear of the king snakes. *Journal of Environmental Psychology* **32**: 69–77.

Landová E., Bakhshaliyeva N., Janovcová M., Peléšková Š., Suleymanova M., Polák J., Guliev A. & Frynta D. 2018: Association between fear and beauty evaluation of snakes: cross-cultural findings. *Frontiers in Psychology* **9**(333): 1–15.

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. *Public Library of Science One* **15**(8; e0236999): 1–31.

Landová E., Štolhoferová I., Vobrubová B., Polák J., Sedláčková K., Janovcová M., Rádlová S. & Frynta D. submitted: Attentional, emotional, and behavioral response toward spiders, scorpions, crabs, and snakes: Do they all scare us?

Le Meur O., Le Callet P., Barba D. & Thoreau D. 2006: A coherent computational approach to model bottom-up visual attention. *Institute of Electrical and Electronics Engineers Transactions on Pattern Analysis and Machine Intelligence* **28**: 802–817.

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* **4**: 233–250.

Lišková S., Landová E. & Frynta D. 2015: Human preferences for colorful birds: Vivid colors or pattern? *Evolutionary Psychology* **13**: 339–359.

LoBue V. 2010: And along came a spider: An attentional bias for the detection of spiders in young children and adults. *Journal of Experimental Child Psychology* **107**: 59–66.

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**: 129–143.

LoBue V. & Matthews K. 2014: The snake in the grass revisited: An experimental comparison of threat detection paradigms. *Cognition & Emotion* **28**: 22–35.

LoBue V., Matthews K., Harvey T. & Stark S. L. 2014: What accounts for the rapid detection of threat? Evidence for an advantage in perceptual and behavioral responding from eye movements. *Emotion* **14**: 816.

Loftus G. R. 1981: Tachistoscopic simulations of eye fixations on pictures. *Journal of Experimental Psychology*: *Human Learning and Memory* **7**: 369–376.

Loftus G. R. & Mackworth N. H. 1978: Cognitive determinants of fixation location during picture viewing. *Journal of Experimental Psychology*: *Human Perception and Performance* **4**: 565–572.

Lueken U., Kruschwitz J. D., Muehlhan M., Siegert J., Hoyer J. & Wittchen H. U. 2011: How specific is specific phobia? Different neural response patterns in two subtypes of specific phobia. *Neuroimage* **56**: 363–372.

Lyson T. R., Sperling E. A., Heimberg A. M., Gauthier J. A., King B. L. & Peterson K. J. 2012: MicroRNAs support a turtle+lizard clade. *Biology Letters* **8**: 104–107.

Marešová J., Landová E. & Frynta D. 2009: What makes some species of milk snakes more attractive to humans than others? *Theory in Biosciences* **128**: 227–235.

Mayer B., Muris P., Vogel L., Nojoredjo I. & Merckelbach H. 2006: Fear-relevant change detection in spider-fearful and non-fearful participants. *Journal of Anxiety Disorders* **20**: 510–519.

McGlynn F. D., Wheeler S. A., Wilamowska Z. A. & Katz J. S. 2008. Detection of change in threat-related and innocuous scenes among snake-fearful and snake-tolerant participants: Data from the flicker task. *Journal of Anxiety Disorders* **22**: 515–523.

McNally R. J. 1987: Preparedness and phobias: a review. *Psychological Bulletin* **101**: 283–303.

Mineka S., Keir R. & Price V. 1980: Fear of snakes in wild-and laboratory-reared rhesus monkeys (Macaca mulatta). *Animal Learning & Behavior* **8**: 653–663.

New J., Cosmides L. & Tooby J. 2007: Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 16598–16603.

Öhman A. 2007: Has evolution primed humans to "beware the beast"? *Proceedings of the National Academy of Sciences of the United States of America* **104**: 16396–16397.

Öhman A. 2009: Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology* **50**: 543–552.

Öhman A. & Mineka S. 2001: Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychological Review* **108**: 483–522.
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**: 5–9.
Öhman A. & Soares J. J. 1994: "Unconscious anxiety": phobic responses to masked stimuli. *Journal of Abnormal Psychology* **103**: 231–240.
Öhman A., Flykt A. & Esteves F. 2001: Emotion drives attention: detecting the snake in the grass. *Journal of Experimental Psychology: General* **130**: 466–478.
Öhman A., Soares S. C., Juth P., Lindström B. & Esteves F. 2012: Evolutionary derived modulations of attention to two common fear stimuli: Serpents and hostile humans. *Journal of Cognitive Psychology* **24**: 17–32.
Olatunji B. O., Williams N. L., Tolin D. F., Abramowitz J. S., Sawchuk C. N., Lohr J. M. & Elwood L. S. 2007: The disgust scale: item analysis, factor structure, and suggestions for refinement. *Psychological Assessment* **19**: 281–297.
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**: 463–475.
Pertzov Y., Avidan G. & Zohary E. 2009: Accumulation of visual information across multiple fixations. *Journal of Vision* **9**(10; 2): 1–12.
Pflugshaupt T., Mosimann U. P., von Wartburg R., Schmitt W., Nyffeler T. & Müri R. M. 2005: Hypervigilance – avoidance pattern in spider phobia. *Journal of Anxiety Disorders* **19**: 105–116.
Pilelienė L. & Grigaliūnaitė V. 2016: Influence of print advertising layout complexity on visual attention. *Eurasian Business Review* **6**: 237–251.
Polák J., Sedláčková K., Nácar D., Landová E. & Frynta D. 2016: Fear the serpent: A psychometric study of snake phobia. *Psychiatry Research* **242**: 163–168.
Polák J., Landová E. & Frynta D. 2019: Undisguised disgust: a psychometric evaluation of a disgust propensity measure. *Current Psychology* **38**: 608–617.
Prokop P., Fančovičová J. & Kučerová A. 2018: Aposematic colouration does not explain fear of snakes in humans. *Journal of Ethology* **36**: 35–41.
Ptáčková J., Landová E., Lišková S., Kuběna A. & Frynta D. 2017: Are the aesthetic preferences towards snake species already formed in pre-school aged children? *European Journal of Developmental Psychology* **14**: 16–31.
Ramakrishnan U., Coss R. G., Schank J., Dharawat A. & Kim S. 2005: Snake species discrimination by wild bonnet macaques (Macaca radiata). *Ethology* **111**: 337–356.
Rádlová S., Viktorin P. & Frynta D. 2016: *Barvocuc 2.0. Software for Color Image Analysis*. URL: https://github.com/encukou/barvocuc/releases.
Rádlová S., Peléšková Š., Polák J., Landová E. & Frynta D. 2018: [Emotions trigerred by animals II: fear and disgust]. *e-Psychologie* **12**: 61–77 (in Czech).
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**(1085): 1–18.
Rádlová S., Polák J., Janovcová M., Sedláčková K., Peléšková Š., Landová E. & Frynta D. 2020: Emotional reaction to fear- and disgust-evoking snakes: Sensitivity and propensity in snake-fearful respondents. *Frontiers in Psychology* **11**(31): 1–13.
Rieppel O. & DeBraga M. 1996: Turtles as diapsid reptiles. *Nature* **384**: 453–455.
Rinck M. & Becker E. S. 2006: Spider fearful individuals attend to threat, then quickly avoid it: evidence from eye movements. *Journal of Abnormal Psychology* **115**: 231–238.
Rosa P. J., Esteves F. & Arriaga P. 2014: Effects of fear-relevant stimuli on attention: integrating gaze data with subliminal exposure. Pp. 1–6. In: Anonymous (ed.): *2014 Institute of Electrical and Electronics Engineers International Symposium on Medical Measurements and Applications* (*MeMeA*). Lisboa: Institute of Electrical and Electronics Engineers, 715 pp.
Rosa P. J., Esteves F. & Arriaga P. 2015: Beyond traditional clinical measurements for screening fears and phobias. *Institute of Electrical and Electronics Engineers Transactions on Instrumentation and Measurement* **64**: 3396–3404.
Schaefer H. S., Larson C. L., Davidson R. J. & Coan J. A. 2014: Brain, body, and cognition: Neural, physiological and self-report correlates of phobic and normative fear. *Biological Psychology* **98**: 59–69.
Seligman M. E. 1971: Phobias and preparedness. *Behavior Therapy* **2**: 307–320.
Smith S. M. 1975: Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**: 759–760.
Soares S. C., Esteves F. & Flykt A. 2009: Fear, but not fear-relevance, modulates reaction times in visual search with animal distractors. *Journal of Anxiety Disorders* **23**: 136–144.
Soares S. C., Lindström B., Esteves F. & Öhman A. 2014: The hidden snake in the grass: superior detection of snakes in challenging attentional conditions. *Public Library of Science One* **9**(12; e114724): 1–26.
Staňková H., Janovcová M., Peléšková Š., Sedláčková K., Landová E. & Frynta D. 2021: The ultimate list of the most frightening and disgusting animals: Negative emotions elicited by animals in central European respondents. *Animals* **11**(3; 747): 1–21.

Steiner J. E., Glaser D., Hawilo M. E. & Berridge K. C. 2001: Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. *Neuroscience & Biobehavioral Reviews* **25**: 53–74.
Tipples J., Young A. W., Quinlan P., Broks P. & Ellis A. W. 2002: Searching for threat. *Quarterly Journal of Experimental Psychology Section A* **55**: 1007–1026.
Turatto M. & Galfano G. 2000: Color, form and luminance capture attention in visual search. *Vision Research* **40**: 1639–1643.
Uetz P., Freed P. & Hošek J. (eds.) 2020: *The Reptile Database*. URL: http://www.reptile-database.org. Accessed on 25 May 2020.
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 of the United States of America* **110**: 19000–19005.
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**(46331): 1–9.
Van Strien J. W., Eijlers R., Franken I. H. A. & Huijding J. 2014a: Snake pictures draw more early attention than spider pictures in non-phobic women: evidence from event-related brain potentials. *Biological Psychology* **96**: 150–157.
Van Strien J. W., Franken I. H. & Huijding J. 2014b: 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): 1–9.
Villani D., Morganti F., Cipresso P., Ruggi S., Riva G. & Gilli G. 2015: Visual exploration patterns of human figures in action: An eye tracker study with art paintings. *Frontiers in Psychology* **6**(1636): 1–10.
Walls G. L. 1940: Ophthalmological implications for the early history of the snakes. *Copeia* **1940**(1): 1–8.
Wang J., Le Callet P., Tourancheau S., Ricordel V. & Da Silva M. P. 2012: Study of depth bias of observers in free viewing of still stereoscopic synthetic stimuli. *Journal of Eye Movement Research* **5**(5; 1): 1–11.
Waters A. M. & Lipp O. V. 2008: The influence of animal fear on attentional capture by fear-relevant animal stimuli in children. *Behaviour Research and Therapy* **46**: 114–121.
Weiss L., Brandl P. & Frynta D. 2015: Fear reactions to snakes in naïve mouse lemurs and pig-tailed macaques. *Primates* **56**: 279–284.
Wheeler B. C., Bradley B. J. & Kamilar J. M. 2011: Predictors of orbital convergence in primates: a test of the snake detection hypothesis of primate evolution. *Journal of Human Evolution* **61:** 233–242.
Yang J., Wang A., Yan M., Zhu Z., Chen C. & Wang Y. 2012: Distinct processing for pictures of animals and objects: Evidence from eye movements. *Emotion* **12**: 540–551.
Yantis S. 2005: How visual salience wins the battle for awareness. *Nature Neuroscience* **8**: 975–977.
Yorzinski J. L., Penkunas M. J., Platt M. L. & Coss R. G. 2014: Dangerous animals capture and maintain attention in humans. *Evolutionary Psychology* **12**: 534–548.
Zamma K. 2011: Responses of chimpanzees to a python. *Pan Africa News* **18**: 13–15.
Zsido A. N., Csatho A., Matuz A., Stecina D. T., Arato A., Inhof O. & Darnai G. 2019: Does threat have an advantage after all? Proposing a novel experimental design to investigate the advantages of threat-relevant cues in visual processing. *Frontiers in Psychology* **10**(2217): 1–11.