



Research



Cite this article: Biondi L, Silva F, Gomes N, Maior RS, Silva S, Soares SC. 2026 From fascination to fear and disgust: cross-cultural assessment of emotional and aesthetic responses to snake imagery. *Proc. R. Soc. B* **293**: 20261328. <https://doi.org/10.1098/rspb.2026.1328>

Received: 17 November 2025

Accepted: 7 July 2026

Subject Category:

Behaviour

Subject Areas:

behaviour, cognition, evolution

Keywords:

snake detection theory, fear, cross-cultural study, morphological heuristics, threat assessment, emotional clusters

Author for correspondence:

Sandra C. Soares

e-mail: sandra.soares@ua.pt

From fascination to fear and disgust: cross-cultural assessment of emotional and aesthetic responses to snake imagery

Luiz Biondi¹, Fábio Silva¹, Nuno Gomes², Rafael S. Maior³, Samuel Silva⁴ and Sandra C. Soares¹

¹William James Centre for Research, Department of Education and Psychology, Universidade de Aveiro, Aveiro, 3810-193, Portugal

²William James Centre for Research, ISPA – Instituto Universitário, ISPA, Lisbon, 1149-041, Portugal

³Institute of Biology, Department of Physiological Sciences, Laboratory of Neurosciences Metabolism and Behavior, Universidade de Brasília, Brasília, DF, 70910-900, Brazil

⁴Department of Electronics, Telecommunication and Informatics (DETI)/Institute of Electronics and Informatics Engineering (IEETA), Universidade de Aveiro, Aveiro, 3810-193, Portugal

LB, 0000-0002-4568-7315

The primate visual system is thought to have evolved under selective pressures favouring rapid detection of snakes, ancestral predators that shaped perceptual and attentional mechanisms. Yet, the transition from visual detection to subjective fear remains poorly understood and may depend on specific morphological cues. Here, we examined how snake morphology modulates human emotional and aesthetic responses across ecological and cultural contexts. A total of 377 participants from Portugal (low snake biodiversity) and Brazil (high snake biodiversity) rated images of 92 snake species on fear, disgust, beauty, valence, arousal and perceived size. Cluster analyses revealed three consistent emotional profiles across populations: a *High-Fear* cluster (mainly viperids, boids and mimics with threatening traits), a *High-Valence* cluster (mostly harmless colubrids and dipsadids), and a smaller *High-Disgust* cluster (fossorial or limbless reptiles). Cluster membership was unaffected by country, indicating cross-cultural consistency in emotional evaluations of snake morphology. Species in the High-Fear cluster exhibited higher edge density. By contrast, greater exposure to snakes, particularly in natural environments, was associated with lower Snake Fear Questionnaire scores. These results support the view that humans rely on evolutionarily conserved morphological heuristics (e.g. triangular heads, keeled scales and disruptive patterns) to assess potential threats, while individual predispositions and experience modulate response intensity.

1. Introduction

Snakes (suborder Serpentes, order Squamata, class Reptilia) exhibit remarkable diversity in morphology, ecology, behaviour and physiology, reflecting complex evolutionary trajectories shaped by interactions with both biotic and abiotic factors [1]. Although invariably limbless and elongated predators, snake species differ substantially in colouration, body proportions, scalation, head morphology and pigmentation patterns [2,3]. These phenotypic traits are often linked to deeper functional characteristics, such as venom composition, dentition and trophic roles, that structure ecological interactions and position snakes as both predators and prey within food webs. Such dynamics have long fuelled coevolutionary processes consistent with Darwin's *struggle for existence*

[4], later conceptualized as *evolutionary arms races* [5], involving adaptations such as venom specialization and toxin resistance [6,7], mimicry [8,9], aposematism [10], caudal luring [11] and camouflage [12,13].

Building on this framework, Isbell [14,15] proposed the *Snake Detection Theory* (SDT), integrating Darwin's perspective with Seligman's *Preparedness Theory* [16] and Öhman and Mineka's *Fear Module* [17]. SDT posits that recurrent predation pressure from snakes, particularly ancestral constricting snakes (e.g. Boidae) and venomous snakes (e.g. Viperidae and Elapidae), shaped the visual systems of anthropoid primates, enhancing rapid snake detection and identification and increasing survival. Supporting evidence indicates that both humans and non-human primates are anatomically and physiologically adapted for efficient snake detection and preferential attention [14,15,18–21]. Despite the effectiveness of cryptic strategies [12], snake stimuli gain privileged access to human awareness [22,23] and elicit stronger and faster neural responses than other categories of visual stimuli [24–26].

This body of evidence suggests that snakes represent a universal stimulus for rapid and automatic visual detection, largely owing to their elongated and curvilinear body shape [27–32]. However, the transition from detection to subjective fear appears to involve different processes [27]. Whereas initial detection may be triggered by general shape features, subjective fear seems to arise after species-level recognition and is more sensitive to morphological cues such as head shape, scalation, body proportions or colouration [33–35]. Crucially, these responses occur even when observers lack explicit knowledge about the species' danger, as cross-cultural studies demonstrate [35,36], suggesting that detection and fear, although related, rely on partly distinct morphological mechanisms [19,37].

This functional dissociation aligns with the notion that detection biases constitute the entry point to the broader psychophysiological cascade described by the fear module [38,39]. For instance, after visual detection, capuchin monkeys (*Sapajus* spp.) modify their behaviour depending on whether they encounter venomous snakes (or mimics thereof) or harmless species, and this apparently determines the ecological relationship that may subsequently develop, with monkeys and snakes assuming the roles of predator or prey [40]. Similarly, in humans, the conscious recognition of species-specific features modulates the intensity of emotional responses [33,35]. However, these responses are not limited to fear. In many cultures, snakes are not only associated with fear and death but may also be venerated as gods, revered as symbols of healing and knowledge, or simply admired for their beauty (e.g. [41]), underscoring the importance of studying the emotional impacts that snakes exert on humans, which extend well beyond fear.

Taken together, these considerations suggest that the morphological diversity of snakes must be carefully considered in studies where the subjective evaluation of snake stimuli represents a key variable influencing behavioural and emotional outcomes. Such diversity may be less relevant in research focusing on rapid and automatic detection of snakes presented outside the foveal field of vision, but it becomes crucial in paradigms involving foveally presented snakes and in studies assessing subjective fear (for a review on differences between subjective fear and automatic defensive responses, see [32]). Previous findings indicating that morphological traits, such as triangular heads, pronounced scalation or aposematic colouration, modulate subjective responses [33,35] highlight the importance of examining emotional and perceptual reactions across multiple species rather than relying on generic snake stimuli.

The present study expands on this idea by examining how images of different snake species are associated with subjective ratings of fear, disgust, valence, arousal, perceived beauty and estimated size in two populations, in Portugal and Brazil. This cross-cultural design contrasts responses in a region with exceptionally high snake biodiversity (Brazil) and one with comparatively low diversity (Portugal). Specifically, we test whether emotional and aesthetic responses cluster according to snake morphology, and whether these patterns generalize across distinct ecological and cultural contexts. In addition, we examined whether participant characteristics, such as environmental exposure, previous encounters with snakes and individual differences in snake-related imagery, contribute to variation in self-reported snake fear.

We hypothesize that (1) morphological traits characteristic of venomous species or large constrictors (e.g. Viperidae, Elapidae and Boidae) will be associated with higher fear ratings; (2) non-venomous mimics will also elicit elevated fear and arousal; and (3) harmless species lacking such traits will receive higher ratings of beauty and positive valence. Despite ecological and cultural differences, we expect overall response patterns to be consistent across populations, in line with evidence that morphological features can trigger subjective fear even when the species is unfamiliar [35]. In addition, with respect to participant characteristics potentially associated with snake fear questionnaire (SNAQ) [42] scores, we expect variations that may reflect snake-related imagery across cultural contexts. By directly linking morphological diversity to subjective evaluations in distinct ecological and cultural settings, this study advances a more comprehensive understanding of the evolutionary, perceptual and cultural bases of the complex and multifaceted relationship between humans and snakes.

2. Methods

(a) Participants

A total of 377 participants (257 females and 1 non-binary) aged 18–74 years (mean = 32.8, s.d. = 12.9) were recruited in Brazil and Portugal to complete an online questionnaire and image evaluation task. The Brazilian subsample included 186 participants (118 females; age range = 18–65 years, mean = 31.8, s.d. = 12.0) and the Portuguese subsample included 191 participants (133 females, 1 non-binary; age range = 18–74 years, mean = 33.7, s.d. = 13.8). Recruitment was conducted through social media platforms and institutional mailing lists. All participants provided informed consent, and the study was approved by the University of Aveiro Research Ethics Committee (7-CE/2025).



Figure 1. Examples of standardized stimuli. (A) *Trachyboa boulengeri* (Tropidophiidae). (B) *Incaspis simonsii* (Dipsadidae), source: [2].

(b) Stimuli

A total of 92 colour photographs of snake species were obtained from the *Reptiles of Ecuador* project [2]. Permission for use was granted by the project coordinator. Although the dataset primarily comprised snake species, a small number of limbless or elongate squamates (e.g. Amphisbaenidae and Gymnophthalmidae) were also included owing to their strong morphological resemblance to snakes. This allowed us to assess whether emotional responses are primarily associated with phylogenetic identity or with visual morphology. All images were standardized to a resolution of 300 × 300 pixels. Additional taxonomic and ecological information was obtained from different sources [43,44]. We selected a maximum of two species randomly per taxonomic genus, when available. Because some families and subfamilies (e.g. Dipsadinae, Xenodontinae and Colubrinae) contain substantially more genera than others (e.g. Boinae and Elapinae), the number of species per family was allowed to vary to preserve taxonomic representativeness. All images depicted the animals in highly similar postures against a completely white background (figure 1).

Following image selection, we employed custom Python scripts to batch-process all images to quantify a set of low-level visual variables computed from the foreground (i.e. the snake body) after background segmentation. The use of a uniform white background allowed reliable foreground extraction and minimized contextual confounds. These variables, previously associated with affective and aesthetic evaluations (see e.g. [45–50]), served as predictors in our statistical model. The operational definitions for each variable were as follows:

- Mean luminance: overall brightness of the image, with higher values indicating lighter scenes.
- Edge density is calculated by applying a Sobel filter to grayscale images; the average edge strength quantifies the amount of fine structural detail.
- Foreground ratio: proportion of non-background pixels, estimated via brightness thresholding, indexing the proportion of the image occupied by the snake.
- Saturation: mean saturation value from the hue, saturation and value (HSV) colour space, with higher values indicating more vivid colouration.

(c) Procedure

After providing informed consent, participants completed a sociodemographic questionnaire. They reported their lifetime exposure to urban, rural and forested/natural environments, as well as their frequency of encounters with snakes across different contexts (media, captivity and natural settings). In addition, participants rated the valence of these encounters, irrespective of context. All responses were provided using 7-point Likert scales (1 = never, 7 = very frequently). These measures reflect subjective self-reports rather than objective quantifications of time spent in each environment. Participants then completed the SNAQ before proceeding to the main experimental task.

Each participant was randomly presented with 30 images sampled without replacement from the full set of 92 stimuli. For each image, participants provided ratings on six dimensions using 7-point Likert scales:

1. Fear: 1 = very weak, 7 = very strong
2. Disgust: 1 = very weak, 7 = very strong
3. Beauty: 1 = very ugly, 7 = very beautiful
4. Valence: 1 = very negative, 7 = very positive
5. Arousal: 1 = low arousal, 7 = high arousal
6. Size estimation: 1 = <0.5 m; 4 = 1.5–2 m; 7 = >3 m

Each image remained on screen until all six ratings were provided. Following the image-rating task, participants answered additional questions regarding their mental representation of a ‘typical snake’ (e.g. when responding to the SNAQ). Specifically, they rated a set of imagined morphological and ecological characteristics using 7-point Likert scales. These included imagined head–neck differentiation, imagined scale salience, imagined body length, imagined width-to-length ratio, imagined distinction between fangs and other teeth, imagined vertical habitat position (below ground = 1; ground = 4; top of the trees = 7) and imagined venom potency (no poison = 1; fatal poison = 7). Participants were instructed to base their responses on their own mental image

of a generic snake, rather than on any specific species. These variables therefore capture subjective representations rather than objective biological traits.

Finally, a debriefing message explained the study's objectives. The procedure lasted approximately 30–40 minutes.

The study was designed to obtain at least 50 independent ratings per image and per country [50]. This threshold was exceeded, with a mean of 60.54 ratings per image in the Brazilian sample (s.d. = 5.72, range = 51–73) and 62.15 in the Portuguese sample (s.d. = 5.00, range = 52–75).

3. Statistical analysis

All statistical analyses were performed using R [51]. For the cluster analysis, six subjective measures (Fear, Disgust, Valence, Arousal, Beauty and Size) were z-score standardized and assessed for clusterability using the Hopkins package [52]. The optimal cluster number was determined using NbClust [53] with both *k*-means and hierarchical clustering (Ward's D2 method) across *k* = 2–10 solutions.

Silhouette analysis, using the cluster package [54], was subsequently performed to compare cluster quality between methods, which supported the selection of *k*-means clustering. Based on these previous analyses, the final cluster analysis used *k*-means clustering with *k* = 3 clusters. Final cluster sizes were 34, 51 and 7. When exploring possible significant differences between variables across clusters, using independent sample Welch *t*-tests (with Bonferroni correction), cluster three (*n* = 7) was excluded given its low representation.

To investigate which image features were associated with cluster membership, again excluding cluster three because of its low representation, we fitted a generalized linear model (binomial family) with cluster type as the dependent variable. Predictors derived from the image analysis were first screened for multicollinearity. Based on this procedure, edge density, saturation, mean luminance, contrast and texture were entered as initial predictors. The final model, selected through backward stepwise reduction, retained edge density, saturation and mean luminance.

To assess whether *Portuguese* or *Brazilian* participants differed in cluster composition, two independent clustering analyses were performed using the same procedures and number of clusters described above. A chi-square test of independence was then conducted after verifying that its assumptions were met.

Spearman correlation analyses were conducted to assess the association between SNAQ values and both sociodemographic variables (time spent in urban, rural and forested areas, previous encounters with snakes in captivity, in nature, or through media, emotional valence of those encounters) and imagery/habitat/venom-related variables derived from participants' subjective mental representation of snakes (imagined head–neck differentiation, imagined scale salience, imagined body length, imagined width-to-length ratio, imagined distinction between fangs and other teeth, imagined vertical habitat position and imagined venom potency). This analysis was performed individually for Portuguese and Brazilian participants. To evaluate whether correlation coefficients between these two samples are statistically significant, a Fisher's *z*-transformation was performed on the coefficients using the package cocor [55]. All *p*-values in these analyses were adjusted for multiple comparisons using Bonferroni's correction.

Redundancy analysis (RDA) was used to examine how visual and individual predictors jointly explain variation in the multivariate outcome set (fear, disgust and beauty). Model significance was assessed using permutation-based ANOVA (999 permutations), including a global test of the full model and marginal tests for each predictor. The results for the permutation-based ANOVA are shown visually through a variance-partitioning plot depicting the unique variance explained by each statistically significant predictor relative to the total constrained variance.

Descriptive statistics for all species, including emotional ratings and image-derived features, as well as the full species list, are provided in the supplementary materials.

4. Results

(a) Cluster analysis

Cluster analyses were conducted separately for Portuguese and Brazilian participants using the 92 species. Three consistent clusters emerged in both national cohorts: a High-Fear cluster (HF), characterized by elevated fear ratings; a High-Valence cluster (HV), associated with more positively emotional evaluations; and a High-Disgust cluster (HD), defined by elevated disgust ratings. A chi-square test of independence revealed that the country in which participants had lived for most of their lives (Brazil vs. Portugal) was not significantly associated with cluster membership ($\chi^2(2) = 2.43$, $p = 0.297$; Cramer's $V = 0.12$; $n = 184$). Consequently, data were merged to construct a unified cluster solution, resulting in a final distribution of 34 species in the HF cluster, 51 in the HV cluster and 7 in the HD cluster (figure 2). Z-score centroids defining each cluster profile are shown in figure 3.

Given its low representativeness, the HD cluster (*n* = 7) was excluded from further comparisons, which were therefore restricted to HF versus HV clusters.

Species in the HF cluster elicited higher ratings of fear, disgust, arousal and perceived size when compared with those in the HV cluster. Conversely, species in the HV cluster were rated higher in valence, reflecting more positive emotional appraisals. Beauty ratings were lower for HF species ($p = 0.042$), although this difference did not remain significant after Bonferroni correction ($p = 0.255$; table 1).



Figure 2. Density distributions of emotional responses (fear, disgust, valence and arousal) and aesthetic judgments (beauty and size estimate) across three identified clusters: HF (high fear, red), HV (high valence, green) and HD (high disgust, orange). The x-axis represents rating scores for each variable, and the y-axis shows probability density (area under each curve = 1).

Table 1. Pairwise comparisons between the High-fear (HF) and High-valence (HV) clusters across the evaluated variables (independent samples *t*-tests with Bonferroni-corrected *p*-values).

variable	<i>t</i>	<i>df</i>	<i>p</i>	<i>p</i> (corr.)
fear	13.17	74.22	<0.001	<0.001
disgust	7.00	51.53	<0.001	<0.001
valence	−8.08	59.69	<0.001	<0.001
arousal	11.64	69.21	<0.001	<0.001
beauty	−2.07	63.03	0.042	0.255
size estimate	3.76	55.18	<0.001	0.002

(b) Taxonomic composition

Cluster membership broadly reflected phylogenetic relationships among snake taxa. The HF cluster contained all Viperidae, both Tropidophiidae, most Boidae, two Elapidae and subsets of Colubridae and Dipsadidae. The HV cluster was primarily composed of Colubridae and Dipsadidae species. The HD cluster consistently included fossorial taxa and limbless or elongate squamates, including non-snake species such as amphisbaenians and a gymnophthalmid.

(c) Low-level visual features

Concerning image features and cluster membership, the overall model was statistically significant ($\chi^2(3) = 18.09, p < 0.001$). Edge density was a strong predictor ($\beta = -37.333, \text{s.e.} = 11.412, z = -3.27, p = 0.001$), indicating that higher edge density was associated with lower odds of belonging to the HV cluster. Mean luminance approached statistical significance ($\beta = 6.965, \text{s.e.} = 3.557,$



Figure 3. Z-score centroids characterizing cluster profiles. Values represent standardized deviations from the overall mean, highlighting each cluster's distinctive response pattern.

Table 2. Spearman's correlations between SNAQ and sociodemographic variables for Portuguese and Brazilian participants, including Fisher's z-tests comparing correlation coefficients between groups (*p*-values corrected for multiple comparisons).

variable	PT r_s	PT <i>p</i> -value	BR r_s	BR <i>p</i> -value	Fisher's <i>z</i>	<i>p</i> -value
lifetime forest exposure	-0.06	1.000	-0.28	0.001	2.15	0.224
lifetime rural exposure	0.08	1.000	-0.19	0.072	2.63	0.063
lifetime urban exposure	-0.04	1.000	0.13	0.620	-1.56	0.840
snake media exposure	-0.32	<0.001	-0.18	0.097	-1.42	1.000
snake observation in captivity	-0.21	0.020	-0.25	0.004	0.41	1.000
snake encounters in natural settings	-0.24	0.006	-0.25	0.004	0.14	1.000
valence of snake encounters	-0.71	<0.001	-0.56	<0.001	-2.41	0.112

$z = 1.96$, $p = 0.050$), with higher values suggesting greater odds of being in the HV cluster. Lastly, saturation narrowly failed to reach statistical significance ($\beta = -0.017$, *s.e.* = 0.009, $z = -1.94$, $p = 0.053$).

(d) SNAQ and sociodemographic variables

Spearman correlation analyses were conducted to examine the association between SNAQ scores and self-reported lifetime exposure to different environments, as well as frequency and affective valence of previous encounters with snakes (table 2). Time spent in forested areas correlated negatively with SNAQ scores in the Brazilian sample ($r_s = -0.28$, $p = 0.001$), though not in the Portuguese sample. No significant relationships were found between time spent in rural or urban areas and SNAQ scores.

For Portuguese participants, higher contact with snakes was associated with lower SNAQ scores, particularly for exposure on screens ($r_s = -0.32$, $p < 0.001$), in captivity ($r_s = -0.21$, $p = 0.020$) and in natural settings ($r_s = -0.24$, $p = 0.006$). A similar pattern was found for Brazilians, with negative correlations between SNAQ scores and contact in natural settings ($r_s = -0.25$, $p = 0.004$) and in captivity ($r_s = -0.25$, $p = 0.004$), but not through screen exposure ($r_s = -0.18$, $p = 0.097$).

As expected, the perceived valence of previous encounters correlated strongly and inversely with SNAQ scores in both Portuguese ($r_s = -0.71$, $p < 0.001$) and Brazilian participants ($r_s = -0.56$, $p < 0.001$).

Fisher's *z*-tests revealed no significant differences between correlation coefficients across countries after Bonferroni correction, indicating that, despite minor differences in effect sizes, the overall pattern was consistent: greater exposure to snakes across contexts was associated with lower SNAQ scores.

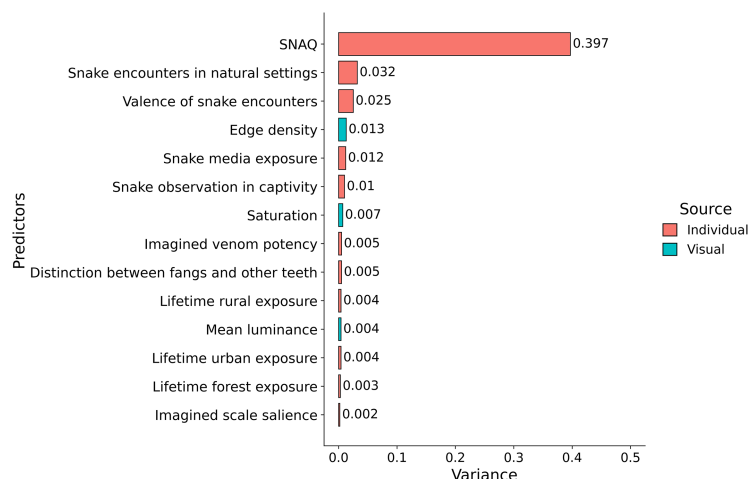


Figure 4. Permutation-based ANOVA marginal tests from the RDA model showing the unique (semi-partial) variance explained by each statistically significant predictor.

Table 3. Spearman's correlations between SNAQ and subjective imagery-, habitat- and venom-related variables for Portuguese and Brazilian participants, including Fisher's z-tests comparing correlation coefficients between groups (p -values corrected for multiple comparisons).

variable	PT r_s	PT p	BR r_s	BR p	Fisher's z	p -value
imagined head–neck differentiation	−0.200	0.034	−0.28	0.001	0.74	1.000
imagined scale salience	0.040	1.000	−0.03	1.000	0.73	1.000
imagined distinction between fangs and other teeth	0.090	1.000	0.11	0.865	−0.24	1.000
imagined vertical habitat position	−0.030	1.000	−0.05	1.000	0.26	1.000
imagined body length	0.220	0.015	0.11	0.942	1.09	1.000
imagined width-to-length ratio	0.003	1.000	0.05	1.000	−0.49	1.000
imagined venom potency	0.490	<0.001	0.19	0.074	3.28	0.007

(e) SNAQ and imagery-/habitat-/venom-related variables

Spearman correlations between SNAQ scores and variables related to participants' mental representations of snakes (i.e. subjective imagery-, habitat- and venom-related characteristics) are presented in table 3. Among Portuguese participants, higher SNAQ scores were associated with lower imagined head-neck differentiation ($r_s = -0.20$, $p = 0.034$), greater imagined body length ($r_s = 0.22$, $p = 0.015$), and particularly with higher imagined venom potency ($r_s = 0.49$, $p < .001$). Among Brazilians, SNAQ scores were similarly related to imagined head-neck differentiation ($r_s = -0.28$, $p = 0.001$), but the correlation with imagined venom potency and imagined body length did not reach statistical significance ($r_s = 0.19$, $p = 0.074$ and $r_s = 0.11$, $p = 0.942$, respectively). No significant associations were found for imagined scale salience, imagined fang distinctiveness, imagined vertical habitat position, or imagined body width-to-length ratio.

(f) Redundancy analysis and predictor-explained variances

The RDA indicated that the full set of predictors explained a substantial proportion of variance in the multivariate outcome space (constrained inertia = 1.18, 39.4% of total variance), with the remaining variance being unconstrained (60.6%). The first constrained axis accounted for the majority of explained variation (RDA1 = 1.11), whereas subsequent axes contributed minimally (RDA2 = 0.043; RDA3 = 0.023), as shown in figure 4.

5. Discussion

Extensive evidence suggests that the sinuous, elongated body of snakes constitutes the primary visual feature enabling their early and automatic detection, a process supported by subcortical pathways [27–32]. By contrast, subjective fear emerges later, following a more detailed identification of features that confirm the threat [37]. It is therefore crucial to distinguish detection and identification processes from subsequent emotional and behavioural reactions, processes that, although interconnected, rely on

distinct neural mechanisms and unfold across different temporal scales, as evidenced by the dissociation between very early (P1) and late (LPP) event-related potentials in response to snakes [19,27]. The present study examined the subjective emotions elicited after this initial detection and during sustained attentional engagement, considering both the visual properties of snake stimuli and participant characteristics.

Cluster analyses revealed three consistent profiles across Brazilian and Portuguese samples: (i) species eliciting high fear and arousal, (ii) species associated with positive valence, and (iii) species predominantly linked to disgust. This convergence occurred despite pronounced ecological differences in snake diversity and familiarity, indicating robust perceptual–emotional patterns across populations, consistent with previous cross-cultural findings [35,36].

As expected, all viperids and most boids clustered in the fear group, consistent with their salient morphology (triangular heads, large body size in both taxa and keeled scales in viperids) and their evolutionary role as major selective pressures [14,15]. Conversely, fossorial snakes and limbless non-snake reptiles, characterized by smooth or ring-like scales, small size, reduced head–neck differentiation and a worm-like appearance, were placed in the disgust cluster. Most colubrids and dipsadids, particularly slender species with smooth morphology [2,3], were included in the high-valence cluster, although several exceptions emerged. This pattern closely replicates previous findings identifying viperids as prototypical fear-evoking snakes and fossorial or limbless taxa as predominantly disgust-eliciting stimuli [33,35,36,56].

The concentration of fossorial species in the disgust cluster is consistent with the Pathogen Avoidance Theory, which posits that disgust evolved as a mechanism to minimize pathogen exposure [57]. Within this framework, smooth, vermiform morphologies constitute plausible cues of pathogen risk and may therefore activate evolved avoidance mechanisms. Empirical evidence supports this interpretation: fossorial snakes are often rated by humans as disgust-eliciting rather than fear-eliciting, with traits such as small eyes and minimal patterning contributing to higher disgust ratings [33,56]. At the same time, this pattern may not be uniform across individuals. In particular, snake-fearful respondents may show co-activation of fear and disgust even for stimuli that are generally associated with disgust, suggesting that disgust can also be integrated into a broader defensive response [58]. By contrast, snakes with salient features, such as triangular heads, strong contrast or aposematic colouration, tend to elicit fear responses [36,58].

A notable finding was the inclusion of numerous harmless species, such as Tropidophiidae, Aniliidae and several colubrids and xenodontines, within the high-fear cluster. In these cases, morphological resemblance to genuinely dangerous snakes (e.g. robust bodies, keeled scales, triangular heads or red-black-white/yellow colour patterns resembling *Micrurus* spp.) appeared sufficient to evoke fear. Tropidophiids, for example, although small and harmless, share conspicuous traits with boids (large constrictors) and viperids (highly venomous), probably explaining their unexpected clustering. Similarly, some species, such as *Erythrolamprus mimus* (mimetic false-coralsnake) or *Hydrops triangularis* (triangle watersnake), clearly mimic the aposematic colouration pattern of venomous *Micrurus* spp. Such findings highlight the apparent reliance of the human perceptual system on salient morphological heuristics rather than ecological accuracy, consistent with preparedness theory [16], the fear module framework [38] and the Snake Detection Theory [14,15]. The clustering of harmless mimics with genuinely dangerous taxa may reflect an adaptive trade-off consistent with the Error Management Theory [59,60], in which rapid identification based on perceptual heuristics (e.g. [61]) is favoured over the potentially lethal cost of false negatives. This prioritization underscores the evolutionary preparedness of the human visual system to respond to threat-relevant morphological cues.

The triangular or broad head of snakes appears to serve as a biologically relevant visual cue of danger, despite functional differences across families. In viperids, wide heads accommodate large venom glands and musculature for efficient toxin delivery [62,63], whereas in boids, robust mandibular musculature and cranial structures facilitate the capture and ingestion of large prey [64]. In macrostomatan species, head width correlates positively with maximum prey mass [65], highlighting the adaptive significance of cranial morphology.

Colour patterns in elapids and their mimics are well documented in the literature, with *Micrurus* spp. (elapids) exemplifying aposematism, as their distinctive colouration functions as an evolved warning signal to predators [66]. Plasticine models with conspicuous patterns, either through head shape or colouration, suffer fewer attacks from avian predators [67–69]. Although vipers are typically cryptic, their contrasting patterns also appear to deter predators [10,70]. Collectively, these findings suggest that both colour and pattern function independently as salient cues for predators and humans alike, with snakes displaying such traits perceived as more threatening [36,58,71, 72]. Experimental evidence further indicates that banded patterns (e.g. black-white or red-black-yellow) are associated with higher perceived fear, while fear and beauty can vary independently [72]. Studies on milk snakes show that such patterns also influence aesthetic preferences and spontaneous categorization, with respondents clustering species according to the relative proportions of red and black colouration and the presence of banded patterns [73]. However, aposematic colouration alone does not fully explain fear responses, indicating that colour pattern interacts with broader morphological and structural cues when shaping perceived threat [74]. Indeed, cross-cultural evidence shows that body width, rather than colouration or pattern, most strongly predicts fear of snakes [75]. This interspecific sensitivity may reflect evolutionary calibration, consistent with the notion of a prepared fear of visually salient danger signals [14,38].

Visual feature analyses further supported this interpretation: species with higher edge density were less likely to be included in the high-valence cluster, suggesting that structural complexity acts as a fear-relevant cue. This aligns with broader evidence that low- and mid-level visual features, including angularity, curvilinearity and colour pattern, affect affective evaluations [76]. In this context, salient scales and complex angular contrast patterns may contribute to higher edge density and more negative valence. Humans and great apes generally prefer smoothly curved shapes over sharp-angled ones [77,78], with angular features perceived as more threatening [79]. Such associations probably stem from their resemblance to naturally threatening stimuli, including teeth, horns, angry facial expressions [80] and snake scales [72], supported by evidence that sharp-angled images increase amygdala activity [81].

Moreover, the aforementioned colour pattern of *Micrurus* spp. and their mimics appeared relevant to the inclusion of these species in the high-fear cluster. Although saturation was not a significant predictor in this study, the spatial arrangement of colours, with abrupt transitions between hues, probably increases edge density, suggesting that structural pattern complexity, rather than colour vividness *per se*, plays a more critical role in modulating threat perception.

Regarding this topic (edge density, structural complexity and angularity), it is important to distinguish subtle aspects of early visual detection from those involved in subsequent emotional appraisal. Early snake detection is often assumed to be intrinsically tied to fear, yet evidence suggests otherwise [23,39]. Early snake detection is more pronounced in the visual periphery and relies on low spatial frequency features [23] processed via direct subcortical pathways, ensuring rapidity but not necessarily subjective fear [61]. When stimuli enter foveal vision, high spatial frequency features gain prominence, engaging cortico-amygdalar interactions that contribute to conscious emotional evaluations. Smoothly curved lines predominantly capture and sustain attention, as shown in humans and great apes [75,76]. Within the SDT framework, the general sinuous shape and posture of snakes act as efficient attentional cues without being intrinsically fear-inducing. By contrast, sharp-angled features, such as salient scales, fangs, and the triangular heads of viperids and boids, depend on foveal vision and high spatial frequency processing, exerting stronger influence on subjective fear and negative valence, as corroborated by our findings.

Interestingly, in the mental imagery questionnaire, participants with higher SNAQ scores described lower differentiation between head and neck in their imagined snake. At first glance, this appears inconsistent with the cluster results, in which species with triangular heads (e.g. viperids) elicited the strongest fear responses. However, this apparent discrepancy probably reflects a distinction between the prototypical mental representation of a 'snake' and the specific morphological features that maximize perceived threat. Whereas imagined snake prototypes may be shaped by familiarity or generic category representations, fear responses appear to rely on evolutionarily salient cues such as head shape, body robustness, and pattern complexity.

At the same time, many snakes that mimic venomous *Micrurus* species were also grouped in the high-fear cluster. Both *Micrurus* and their mimics typically exhibit narrow, rounded heads with little distinction from the rest of the body, differing anatomically and functionally from viperids and boids. This pattern further indicates that head–neck differentiation alone does not determine fear responses, reinforcing the idea that multiple, partially independent morphological cues contribute to perceived threat. Taken together, these findings suggest that imagined snake prototypes do not necessarily correspond to the features that most strongly drive fear, and that fear elicitation is supported by a flexible set of perceptual heuristics rather than a single prototypical configuration.

This distinction between shared perceptual structure and individual variability is further supported by the redundancy analysis (RDA), which examined the joint contribution of visual features and participant-level variables to multivariate emotional responses. Although low-level visual properties such as edge density contributed to explaining variation, individual differences, particularly SNAQ scores, accounted for a substantially larger proportion of the total variance. This pattern indicates that while morphological features reliably structure which snakes are perceived as more threatening, individual predispositions primarily modulate the intensity of these responses. In other words, participants tend to agree on the relative threat value of different snake morphotypes, but differ in how strongly they experience these emotional reactions.

Notably, the high-fear cluster coincided with high arousal scores, showing that visual features not only elicit fear but also enhance physiological and attentional activation. These findings converge with evidence from studies on low-level visual properties and affective perception. It has been demonstrated that both contrast and colour independently modulate subjective fear ratings, with colour primarily influencing decision criteria and overall perceived fear [82]. Evaluations of visual complexity, which capture formal properties such as edge density and feature congestion, are strongly associated with arousal, reflecting both perceptual processing and affective engagement [83]. Colour saturation and brightness have also been shown to systematically increase arousal and physiological responses, including skin conductance amplitude, with hue effects modulated by saturation–brightness interactions [84]. Together, these findings suggest that vivid colouration, high contrast and structural complexity in certain snakes may synergistically amplify both fear and arousal, reinforcing preparatory behavioural responses. This interpretation is also consistent with psychophysiological evidence showing stronger autonomic responses to venomous and viper-like snakes than to fossorial disgust-eliciting species [71].

A particularly relevant case concerns the elapid species included in this study. Although represented by only three species owing to limited taxonomic availability, one of them (*Micrurus ornatissimus*) was not included in the fear cluster but in the valence cluster instead. This finding is intriguing, as most harmless species that clearly mimic *Micrurus* spp. were classified within the fear cluster. While the small number of elapids precludes definitive conclusions, the aposematic colouration of *Micrurus* species, the absence of significant differences in beauty ratings between the HF and HV clusters, and even the Latin epithet of this venomous species (*ornatissimus*, meaning 'very decorated'), together suggest fruitful avenues for future research on the interplay between beauty and fear. More broadly, this pattern is consistent with previous work showing that fear and aesthetic evaluation of snakes are at least partially independent dimensions [56,72].

Cross-national comparisons revealed no direct differences between Brazil and Portugal, but within-country patterns pointed to contextual influences. In Brazil, greater forest exposure was associated with reduced SNAQ scores, while media representations were unrelated to SNAQ scores, a pattern that contrasted with the Portuguese sample. At the same time, Portuguese participants significantly associated higher imagined snake length and greater imagined venom potency with increased SNAQ scores, associations absent among Brazilian participants. These findings underscore that biodiversity alone does not shape attitudes; rather, access to natural habitats and the frequency and quality of encounters, even when screen-mediated, may play a critical role, with implications for conservation strategies across cultural and ecological contexts.

Our findings, in line with the Snake Detection Theory [14,15], suggest that some characteristics of snakes may facilitate the emergence of fear and arousal in a relatively universal way, consistent with the notion of an evolutionarily prepared module

[17,38]. At the same time, other classes of stimuli appear to depend more heavily on cultural and contextual influences. As shown by Gomes and collaborators [50], certain images less directly relevant in evolutionary terms elicited distinct emotional patterns across populations, with cultural context shaping whether they were primarily associated with fear, disgust, or even positive emotions such as happiness. This contrast supports the view that while snakes constitute a privileged stimulus category with strong cross-cultural consistency [35,36], broader affective responses to other animals and objects may be more malleable and culturally grounded.

These interpretations, however, should be weighed against the study's methodological limitations. Although cross-cultural, the samples from Portugal and Brazil share a Western background, limiting generalization. Recruitment was also conducted online, which may have biased the sample. Our reliance on static images, with only one photograph per species, excluded important ecological cues such as posture, habitat and perceived distance, which are known to influence threat perception (e.g. [25,28,82–84]). Future studies employing dynamic or virtual-reality stimuli could address this gap. Finally, while validated measures such as the SNAQ were employed, all participants' emotional data were self-reported, precluding causal inference, particularly regarding the relationship between fear intensity and environmental exposure, and highlighting the value of incorporating psychophysiological or behavioural indices, as well as integrating snake morphometric and physiological data to disentangle the relative contributions of snake features and individual differences to emotional responses in future research.

In conclusion, our results demonstrate that human perception of snakes is driven by the interaction of salient visual features and individual predispositions, with morphological cues structuring perceived threat and individual differences modulating response intensity. Morphological heuristics that predict danger, such as triangular heads, keeled scales, robust body forms and patterns with high edge density, strongly bias fear responses, even towards harmless species. The convergence of structural complexity and colour salience with arousal further indicates that visual properties act synergistically to enhance emotional engagement. Such heuristics may reflect coevolutionary dynamics between snakes and primates that contributed to shaping human perceptual systems, favouring rapid identification over taxonomic precision.

Ethics. All participants provided informed consent, and the study was approved by the Research Ethics Committee of the University of Aveiro (7-CE/2025).

Data accessibility. Data, supplementary materials and analysis scripts supporting this study are publicly available through the Open Science Framework (OSF) repository (see [85]). The repository includes species-level datasets, participant-level aggregated data, image-derived visual features, supplementary figures, questionnaires and analysis scripts supporting the analyses reported in this study.

Declaration of AI use. AI-assisted technologies were used exclusively to improve the readability, grammar and fluency of the manuscript. No AI tools were used for study design, data analysis, interpretation of results or generation of scientific conclusions. All scientific content was developed, verified and approved by the authors.

Authors' contributions. L.B.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, validation, visualization, writing—original draft, writing—review and editing; F.S.: data curation, formal analysis, software, writing—review and editing; N.G.: conceptualization, validation, writing—review and editing; R.S.M.: supervision, validation, writing—review and editing; S.S.: formal analysis, writing—review and editing; S.C.S.: supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by Portuguese national funds through FCT – Fundação para a Ciência e a Tecnologia, I.P., under the project UID/04810/2020. L.B. was supported by an FCT grant (2021.05287.BD). N.G. was supported by an individual grant from Fundação para a Ciência e a Tecnologia, I.P. (2022.06494.CEECIND). R.S.M. was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant 308291/2020-4).

Acknowledgements. We are grateful to Alejandro Arteaga and the Reptiles of Ecuador project for generously granting permission to use snake images in this study.

References

1. Da Silva FO, Fabre AC, Savriama Y, Ollonen J, Mahlow K, Herrel A, Müller J, Di-Poi N. 2018 The ecological origins of snakes as revealed by skull evolution. *Nat. Commun.* **9**, 376. (doi:10.1038/s41467-017-02788-3)
2. Arteaga A, Bustamante L, Vieira J. 2024 *Reptiles of Ecuador: life in the middle of the world*. 1st edn. Quito, Ecuador: Khamai Foundation & Tropical Herping. (doi:10.47051/MNHT9360)
3. P Uetz, P Freed, J Hošek (eds). 2025 *The reptile database* [Internet]. <https://www.reptile-database.org/> [accessed 20 August 2025].
4. Darwin C. 2009 *The origin of species: by means of natural selection, or the preservation of favoured races in the struggle for life* [Internet]. 6th edn. Cambridge, UK: Cambridge University Press. (doi:10.1017/CB09780511694295)
5. Dawkins R, Krebs JR. 1979 Arms races between and within species. *Proc. R. Soc. B* **205**, 489–511. (doi:10.1098/rspb.1979.0081)
6. Barlow A, Pook CE, Harrison RA, Wüster W. 2009 Coevolution of diet and prey-specific venom activity supports the role of selection in snake venom evolution. *Proc. R. Soc. B* **276**, 2443–2449. (doi:10.1098/rspb.2009.0048)
7. Holding ML, Biardi JE, Gibbs HL. 2016 Coevolution of venom function and venom resistance in a rattlesnake predator and its squirrel prey. *Proc. R. Soc. B* **283**, 20152841. (doi:10.1098/rspb.2015.2841)
8. Smith SM. 1975 Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**, 759–760. (doi:10.1126/science.187.4178.759)
9. Pfennig DW, Harcombe WR, Pfennig KS. 2001 Frequency-dependent Batesian mimicry. *Nature* **410**, 323. (doi:10.1038/35066628)
10. Niskanen M, Mappes J. 20057 Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators. *J. Anim. Ecol.* **4**, 1091–1101. (doi:10.1111/j.1365-2656.2005.01008.x)

11. Hagman M, Phillips BL, Shine R. 2008 Tails of enticement: caudal luring by an ambush-foraging snake (*Acanthophis praelongus*, Elapidae). *Funct. Ecol.* **22**, 1134–1139. (doi:10.1111/j.1365-2435.2008.01466.x)
12. Stevens M, Merilaita S. 2009 Defining disruptive coloration and distinguishing its functions. *Phil. Trans. R. Soc. B* **364**, 481–488. (doi:10.1098/rstb.2008.0216)
13. Reynolds C. 2025 Camouflage from coevolution of predator and prey. *Artif. Life* **31**, 153–176. (doi:10.1162/artl_a_00473)
14. Isbell LA. 2006 Snakes as agents of evolutionary change in primate brains. *J. Hum. Evol.* **51**, 1–35. (doi:10.1016/j.jhevol.2005.12.012)
15. Isbell LA. 2011 *The fruit, the tree, and the serpent: why we see so well*. Cambridge, MA: Harvard University Press.
16. Seligman MEP. 1971 Phobias and preparedness. *Behav. Ther.* **2**, 307–320. (doi:10.1016/S0005-7894(71)80064-3)
17. Öhman A, Mineka S. 2001 Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* **108**, 483–522. (doi:10.1037/0033-295x.108.3.483)
18. Öhman A, Flykt A, Esteves F. 2001 Emotion drives attention: detecting the snake in the grass. *J. Exp. Psychol. Gen.* **130**, 466–478. (doi:10.1037/0096-3445.130.3.466)
19. Soares SC, Kessel D, Hernández-Lorca M, García-Rubio MJ, Rodrigues P, Gomes N, Carretié L. 2017 Exogenous attention to fear: differential behavioral and neural responses to snakes and spiders. *Neuropsychologia* **99**, 139–147. (doi:10.1016/j.neuropsychologia.2017.03.007)
20. Soares SC, Lindström B, Esteves F, Öhman A. 2014 The hidden snake in the grass: superior detection of snakes in challenging attentional conditions. *PLoS ONE* **9**, e114724. (doi:10.1371/journal.pone.0114724)
21. Soares SC, Maior RS, Isbell LA, Tomaz C, Nishijo H. 2017 Fast detector/first responder: interactions between the superior colliculus-pulvinar pathway and stimuli relevant to primates. *Front. Neurosci.* **11**, 67. (doi:10.3389/fnins.2017.00067)
22. Gomes N, Silva S, Silva CF, Soares SC. 2017 Beware the serpent: the advantage of ecologically-relevant stimuli in accessing visual awareness. *Evol. Hum. Behav.* **38**, 227–234. (doi:10.1016/j.evolhumbehav.2016.10.004)
23. Gomes N, Soares SC, Silva S, Silva CF. 2018 Mind the snake: fear detection relies on low spatial frequencies. *Emotion* **18**, 886–895. (doi:10.1037/emo0000391)
24. Van Le Q *et al.* 2013 Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. *Proc. Natl Acad. Sci. USA* **110**, 19000–19005. (doi:10.1073/pnas.1312648110)
25. Le QV *et al.* 2014 Monkey pulvinar neurons fire differentially to snake postures. *PLoS ONE* **9**, e114258. (doi:10.1371/journal.pone.0114258)
26. Le QV *et al.* 2016 Snakes elicit earlier, and monkey faces, later, gamma oscillations in macaque pulvinar neurons. *Sci. Rep.* **6**, 20595. (doi:10.1038/srep20595)
27. Van Strien JW, Christiaans G, Franken IHA, Huijding J. 2015 Curvilinear shapes and the snake detection hypothesis: an ERP study. *Psychophysiology* **53**, 252–257. (doi:10.1111/psyp.12564)
28. Grassini S, Railo H, Valli K, Revonsuo A, Koivisto M. 2019 Visual features and perceptual context modulate attention towards evolutionarily relevant threatening stimuli: electrophysiological evidence. *Emotion* **19**, 348–364. (doi:10.1037/emo0000434)
29. Bertels J, Bourguignon M, de Heering A, Chetail F, De Tiège X, Cleeremans A, Destrebecqz A. 2020 Snakes elicit specific neural responses in the human infant brain. *Sci. Rep.* **10**, 7443. (doi:10.1038/s41598-020-63619-y)
30. Bertels J, de Heering A, Bourguignon M, Cleeremans A, Destrebecqz A. 2023 What determines the neural response to snakes in the infant brain? A systematic comparison of color and grayscale stimuli. *Front. Psychol.* **14**, 1027872. (doi:10.3389/fpsyg.2023.1027872)
31. Lobue V, Deloache JS. 2011 What's so special about slithering serpents? Children and adults rapidly detect snakes based on their simple features. *Vis. Cogn.* **19**, 129–143. (doi:10.1080/13506285.2010.522216)
32. Biondi L, Gomes N, Maior RS, Soares SC. 2025 Revisiting “the malicious serpent”: phylogenetically threatening stimulus marked in the human brain. *Emot. Rev.* **17**, 81–91. (doi:10.1177/17540739241277942)
33. 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. *Front. Psychol.* **10**, 1085. (doi:10.3389/fpsyg.2019.01085)
34. Grassini S, Valli K, Souchet J, Aubret F, Segurini GV, Revonsuo A, Koivisto M. 2019 Pattern matters: snakes exhibiting triangular and diamond-shaped skin patterns modulate electrophysiological activity in human visual cortex. *Neuropsychologia* **131**, 62–72. (doi:10.1016/j.neuropsychologia.2019.05.024)
35. Frynta D *et al.* 2023 Are vipers prototypic fear-evoking snakes? A cross-cultural comparison of Somalis and Czechs. *Front. Psychol.* **14**, 1233667. (doi:10.3389/fpsyg.2023.1233667)
36. 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. *Front. Psychol.* **9**, 333. (doi:10.3389/fpsyg.2018.00333)
37. Van Strien JW, Isbell LA. 2017 Snake scales, partial exposure, and the snake detection theory: a human event-related potentials study. *Sci. Rep.* **7**, 46331. (doi:10.1038/srep46331)
38. Öhman A, Mineka S. 2003 The malicious serpent: snakes as a prototypical stimulus for an evolved module of fear. *Curr. Dir. Psychol. Sci.* **12**, 5–9. (doi:10.1111/1467-8721.01211)
39. Gomes N, Silva S, Soares SC. 2019 “Threat-unrelated” properties: an ill-defined concept. A reply to “The danger of interpreting detection differences between image categories” (Gayet, Stein, & Peelen, 2019). *Emotion* **19**, 933–937. (doi:10.1037/emo0000632)
40. Falótico T, Verderane MP, Mendonça-Furtado O, Spagnoletti N, Ottoni EB, Visalberghi E, Izar P. 2018 Food or threat? Wild capuchin monkeys (*Sapajus libidinosus*) as both predators and prey of snakes. *Primates* **59**, 99–106. (doi:10.1007/s10329-017-0631-x)
41. Zengiaro N, Jaramillo TJ. 2025 Mythology and zoosemiotics: exploring snake narratives in Greek, Aztec, and Amazonian cultures. *Biosemiotics* **18**, 469–483. (doi:10.1007/s12304-025-09598-x)
42. Klorman R, Weerts TC, Hastings JE, Melamed BG, Lang PJ. 1974 Psychometric description of some specific-fear questionnaires. *Behav. Ther.* **5**, 401–409. (doi:10.1016/S0005-7894(74)80008-0)
43. Grazziotin FG, Zaher H, Murphy RW, Scrocchi G, Benavides MA, Zhang Y-P, Bonatto SL. 2012 Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics* **28**, 437–459. (doi:10.1111/j.1096-0031.2012.00393.x)
44. Zaher H *et al.* 2019 Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE* **14**, e0216148. (doi:10.1371/journal.pone.0216148)
45. Valdez P, Mehrabian A. 1994 Effects of color on emotions. *J. Exp. Psychol. Gen.* **123**, 394–409. (doi:10.1037/0096-3445.123.4.394)
46. Forsythe A, Nadal M, Sheehy N, Cela-Conde CJ, Sawey M. 2011 Predicting beauty: fractal dimension and visual complexity in art. *Br. J. Psychol.* **102**, 49–70. (doi:10.1348/000712610X498958)

47. Lakens D, Fockenberg DA, Lemmens KPH, Ham J, Midden CJH. 2013 Brightness differences influence the evaluation of affective pictures. *Cogn. Emot.* **27**, 1225–1246. (doi:10.1080/02699931.2013.781501)
48. Redies C. 2015 Combining universal beauty and cultural context in a unifying model of visual aesthetic experience. *Front. Hum. Neurosci.* **9**, 218. (doi:10.3389/fnhum.2015.00218)
49. Redies C, Grebenkina M, Mohseni M, Kaduhm A, Döbel C. 2020 Global image properties predict ratings of affective pictures. *Front. Psychol.* **11**, 953. (doi:10.3389/fpsyg.2020.00953)
50. Gomes N, Benrós MF, Semin GR. 2024 Validation of the open biological negative image set for a Portuguese population: comparing Japanese and Portuguese samples and an exploration of low-order visual properties of the stimuli. *Behav. Res. Methods* **56**, 860–880. (doi:10.3758/s13428-023-02090-9)
51. R Core Team. 2025 R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>.
52. Wright K. 2023 Hopkins: calculate Hopkins statistic for clustering [Internet]. <https://CRAN.R-project.org/package=hopkins> [accessed 20 August 2025].
53. Charrad M, Ghazzali N, Boiteau V, Niknafs A. 2014 NbClust: an R package for determining the relevant number of clusters in a data set. *J. Stat. Softw.* **61**, 1–36. <https://www.jstatsoft.org/v61/i06/>.
54. Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2022 Cluster: cluster analysis basics and extensions [Internet]. <https://cran.r-project.org/web/packages/cluster/index.html>.
55. Diedenhofen B, Musch J. 2015 cocor: a comprehensive solution for the statistical comparison of correlations. *PLoS ONE* **10**, e0121945. (doi:10.1371/journal.pone.0121945)
56. 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**, 238. (doi:10.3390/ani9050238)
57. Curtis V, de Barra M, Auger R. 2011 Disgust as an adaptive system for disease avoidance behaviour. *Phil. Trans. R. Soc. B* **366**, 389–401. (doi:10.1098/rstb.2010.0117)
58. 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. *Front. Psychol.* **11**, 31. (doi:10.3389/fpsyg.2020.00031)
59. Haselton MG, Buss DM. 2000 Error management theory: a new perspective on biases in cross-sex mind reading. *J. Pers. Soc. Psychol.* **78**, 81–91. (doi:10.1037/0022-3514.78.1.81)
60. Haselton MG, Nettle D. 2006 The paranoid optimist: an integrative evolutionary model of cognitive biases. *Personal Soc. Psychol. Rev.* **10**, 47–66. (doi:10.1207/s15327957pspr1001_3)
61. LoBue V, Matthews K, Harvey T, Stark SL. 2014 What accounts for the rapid detection of threat? Evidence for an advantage in perceptual and behavioral responding from eye movements. *Emotion* **14**, 816–823. (doi:10.1037/a0035869)
62. Savitzky AH. 1980 The role of venom delivery strategies in snake evolution. *Evolution* **34**, 1194–1204. (doi:10.1111/j.1558-5646.1980.tb04065.x)
63. Kardong KV, Bels VL. 1998 Rattlesnake strike behavior: kinematics. *J. Exp. Biol.* **201**, 837–850. (doi:10.1242/jeb.201.6.837)
64. Frazzetta TH. 1966 Studies on the morphology and function of the skull in the Boidae (Serpentes). Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. *J. Morphol.* **118**, 217–295. (doi:10.1002/jmor.1051180206)
65. Vincent SE, Dang PD, Herrel A, Kley NJ. 2006 Morphological integration and adaptation in the snake feeding system: a comparative phylogenetic study. *J. Evol. Biol.* **19**, 1545–1554. (doi:10.1111/j.1420-9101.2006.01126.x)
66. Davis Rabosky AR, Cox CL, Rabosky DL, Title PO, Holmes IA, Feldman A, McGuire JA. 2016 Coral snakes predict the evolution of mimicry across New World snakes. *Nat. Commun.* **7**, 11484. (doi:10.1038/ncomms11484)
67. Brodie ED. 1993 Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**, 227–235. (doi:10.1111/j.1558-5646.1993.tb01212.x)
68. Valkonen JK, Nokelainen O, Mappes J. 2011 Antipredatory function of head shape for vipers and their mimics. *PLoS ONE* **6**, e22272. (doi:10.1371/journal.pone.0022272)
69. Valkonen JK, Vakkila A, Pesari S, Tuominen L, Mappes J. 2020 Protective coloration of European vipers throughout the predation sequence. *Anim. Behav.* **164**, 99–104. (doi:10.1016/j.anbehav.2020.04.005)
70. Wüster W. 2004 Do aposematism and Batesian mimicry require bright colours? A test, using European viper markings. *Proc. R. Soc. B* **271**, 2495–2499. (doi:10.1098/rspb.2004.2894)
71. Landová E, Peléšková Š, Sedláčková K, Janovcová M, Polák J, Rádlová S, Vobrubová B, Frynta D. 2020 Venomous snakes elicit stronger fear than nonvenomous ones: psychophysiological response to snake images. *PLoS ONE* **15**, e0236999. (doi:10.1371/journal.pone.0236999)
72. 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. *J. Environ. Psychol.* **32**, 69–77. (doi:10.1016/j.jenvp.2011.10.005)
73. Marešová J, Landová E, Frynta D. 2009 What makes some species of milk snakes more attractive to humans than others? *Theory Biosci.* **128**, 227–235. (doi:10.1007/s12064-009-0075-y)
74. Prokop P, Fančovičová J, Kučerová A. 2018 Aposematic colouration does not explain fear of snakes in humans. *J. Ethol.* **36**, 35–41. (doi:10.1007/s10164-017-0533-9)
75. Frynta D *et al.* 2025 Why are some snakes more terrifying and what is behind the fear? *Animals* **15**, 731. (doi:10.3390/ani15050731)
76. Damiano C, Walther DB, Cunningham WA. 2021 Contour features predict valence and threat judgements in scenes. *Sci. Rep.* **11**, 19405. (doi:10.1038/s41598-021-99044-y)
77. Munar E, Gómez-Puerto G, Call J, Nadal M. 2015 Common visual preference for curved contours in humans and great apes. *PLoS ONE* **10**, e0141106. (doi:10.1371/journal.pone.0141106)
78. Bar M, Neta M. 2006 Humans prefer curved visual objects. *Psychol. Sci.* **17**, 645–648. (doi:10.1111/j.1467-9280.2006.01759.x)
79. Larson CL, Aronoff J, Sarinopoulos IC, Zhu DC. 2009 Recognizing threat: a simple geometric shape activates neural circuitry for threat detection. *J. Cogn. Neurosci.* **21**, 1523–1535. (doi:10.1162/jocn.2009.21111)
80. Aronoff J, Barclay AM, Stevenson LA. 1988 The recognition of threatening facial stimuli. *J. Pers. Soc. Psychol.* **54**, 647–655. (doi:10.1037/0022-3514.54.4.647)
81. Bar M, Neta M. 2007 Visual elements of subjective preference modulate amygdala activation. *Neuropsychologia* **45**, 2191–2200. (doi:10.1016/j.neuropsychologia.2007.03.008)
82. Lu Z, Guo B, Boguslavsky A, Cappiello M, Zhang W, Meng M. 2015 Distinct effects of contrast and color on subjective rating of fearfulness. *Front. Psychol.* **6**, 1521. <https://journal.frontiersin.org/Article/10.3389/fpsyg.2015.01521/abstract>. (doi:10.3389/fpsyg.2015.01521)
83. Madan CR, Bayer J, Gamer M, Lonsdorf TB, Sommer T. 2018 Visual complexity and affect: ratings reflect more than meets the eye. *Front. Psychol.* **8**, 2368. (doi:10.3389/fpsyg.2017.02368)
84. Wilms L, Oberfeld D. 2018 Color and emotion: effects of hue, saturation, and brightness. *Psychol. Res.* **82**, 896–914. (doi:10.1007/s00426-017-0880-8)
85. Biondi L, Silva F, Gomes N, Maior RS, Silva S, Soares SC. 2026 Data and code for: From fascination to fear and disgust: cross-cultural assessment of emotional and aesthetic responses to snake imagery. Open Science Framework. (doi:10.17605/OSF.IO/JMA87)