scientific reports

OPEN

# Japanese monkeys rapidly noticed snake-scale cladded salamanders, similar to detecting snakes

Nobuyuki Kawai[1,2]✉

**The ability to detect threats quickly is crucial for survival. Primates, including humans, have been shown to identify snakes quickly and accurately due to their evolutionary history. However, it is unclear which visual features humans and primates detect as threat targets. Several studies have suggested that snake scales possess potent visual features. My previous study demonstrated that removing snake scales through digital image processing reduces attention directed toward snakes. Here, I conducted a visual search task using luminance- and contrast-adjusted photographs of snakes and salamanders in monkeys that had never seen these real reptiles and amphibians. This study demonstrates that the presence or absence of snake scales is responsible for the rapid detection of target animals. The monkeys quickly detected one snake photograph from the eight salamander photographs than vice versa. However, when the same salamanders were clothed with snake scales using image processing, the difference in detection speed between snakes and salamanders disappeared. These results are consistent with the snake-detection theory that snakes were a strong selective pressure favoring modifications in the primate visual system that allow them to detect snakes more quickly or reliably. This strongly suggests that primates' snake detection depends on the snake-scale shapes, which are both snake-specific and common to all snakes.**

**Keywords** Snakes, Visual search task, Snake detection theory, Snake scale, Monkeys

Snakes pose the greatest threat by animals to humans today[1]. Medical research has shown that venomous snakebites cause a significant number of deaths globally (up to 94,000 per year), making snakes a crucial threat to humans[2]. Therefore, many humans fear snakes. In 2019, 63,400 people died from snakebites worldwide, corresponding to an age-standardized mortality rate of 0.8 deaths per 100,000[3]. Threats from snakes manifest as attention paid to snakes. Many studies have shown that adults, young children, and monkeys who have never seen snakes can quickly and accurately detect snake pictures[4]. As even 8–14-month-old infants responded more rapidly to snake images than to those of flowers[5], and snake pictures elicited specific neural responses in 7–10-month-old infants[6,7], it is conceivable that rapid detection is not the consequence of learning that snakes have a negative valence, but rather that humans and primates are equipped with perceptual systems tuned to detect them quickly and accurately as defensive behaviors. Rapid detection also occurs when snakes are presented in the peripheral visual field[8]. Humans and primates have an innate visual system for detecting snakes[4,9,10], and there has been strong interest in determining the key visual features primates use to detect snakes so quickly.

Snakes have several unusual visual characteristics. The visible characteristics of snakes include a curvilinear shape[11], absence of limbs[12], triangular-shaped heads (especially vipers), coloration[13–16],poses and postures[17,18], and scales[19–21]. Any of these, individually or in combination, could serve as a trigger to indicate a "snake." Caterpillars, snails, eels, and other limbless animals are also widespread. Some caterpillars are even toxic and can harm humans. Therefore, humans must pay as much attention to caterpillars as to snakes. However, when children aged 3–5 years were given a visual search task comparing the time taken to detect snakes and caterpillars, they detected snakes more quickly than caterpillars[12]. This suggests that the physical characteristics of an elongated, limbless body are ineffective visual cues for snake recognition.

LoBue investigated whether a low-level feature, a curvilinear shape, elicited rapid detection in visual-search tasks[11]. In Experiment 1, the detection times for curvilinear serrated lines were compared to those for straight serrated lines when the stimulus (eight horizontal lines) was presented. The results showed that curved or curvilinear lines among the straight or rectilinear lines were detected faster than vice versa. In Experiment 2, half of the participants were asked to detect curvilinear targets labeled "snakes" and rectilinear targets labeled "caterpillars." This relationship was reversed for the remaining participants. The curved lines labeled "snakes"

[1]Department of Cognitive and Psychological Sciences, Nagoya University, Nagoya 464-8601, Japan. [2]Academy of Emerging Science, Chubu University, Kasugai City 487-8501, Japan. ✉email: kawai@is.nagoya-u.ac.jp

were detected faster than the straight lines labeled "caterpillars." Although "curved" caterpillars were detected faster than "straight" snakes, no significant difference was observed. This clearly determines that low-level stimulus properties "per se" are not responsible for curvilinear detection. However, a series of experiments propose that the rapid detection of curvilinear stimuli is not simply dependent on low-level visual features but is influenced by higher-level attitudinal, cognitive, and emotional factors that cannot be applied to the rapid detection of snakes by primates[11].

Although plain-colored snakes exist, there are more than a few species of brightly-colored snakes[13]. Sometimes, these colors form a characteristic, conspicuous pattern. An animal attacked by a brightly colored snake might develop a stronger memory that allows it to avoid a similar occurrence in the future. Therefore, bright colors may enable humans to detect snakes. We performed a visual-search task for 4–6-year-old infants, asking them to find a single picture containing a snake from among eight flower pictures or vice versa[16]. We observed that the children found the snake more rapidly in color pictures than in grayscale ones. In both conditions, the children detected snakes faster than flowers.

However, for monkeys[22] and human adults[23], snake detection was faster on grayscale than on a color image. As both children and adults detected snakes faster than flowers, it is conceived that color alone is not a cue for snake detection. In fact, in the visual tasks performed by LoBue and DeLoache, both 3-year-old children and adults were able to find snakes faster in grayscale pictures containing many flowers than in the opposite case[12]. Thus, these findings suggest that color is not important for rapid snake detection. In multiple studies of early posterior negativity (EPN) in event-related brain potentials (ERPs), the amplitude of EPN in response to snakes was shown to be larger than that evoked by other animals, including spiders, even when the stimuli were on a grayscale[24,25]. The colors of snakes are not critical visual cues for primates. Although trichromatic platyrrhines and catarrhines may be better able to distinguish between reds and greens[26], dichromatic platyrrhines may be better able to break through snake camouflage[10,27,28].

Recent research has established that snake-threat detection is highly sensitive, with humans and monkeys reacting strongly even to partial exposure to a snake's body. Although other prominent visual features of snakes exist, two types of evidence demonstrate that humans and primates recognize snake scales as essential features: one is based on behavioral studies in monkeys, and the other on EEG studies in humans. In a behavioral study, Etting and Isbell presented to captive rhesus monkeys models of snakes in three postures: striking, coiling, and sinusoidal[17]. Each model had a mixed olive green and brown color and a body length of approximately 90 cm. A partially exposed snake-body model, showing only 15 cm of the trunk with the head and tail obscured by a cloth, was also used in the sinusoidal snake model. The four types of snake models were displayed 1.5 m away from the monkey group enclosure. The fence-clinging reaction—a fear response—was observed more frequently in the striking-snake model than in the coiled-snake model. The partially exposed model exhibited significantly more fence-clinging reactions than the original sinusoidal model. These findings suggest that monkeys become vigilant even when only a portion of the snake's body is visible, indicating that the posture of the entire body is not of great significance.

Furthermore, Isbell and Etting investigated whether wild vervet monkeys exhibited vigilance in response to partially visible snakeskin[20]. The study began with a baseline condition in which only towels were present. Subsequently, cylindrical snakeskin, a natural form of snake, was introduced in the gap ($\leq 2.7$ cm) between the towels. After the towels were presented again, a flat snakeskin was placed in the gap between the towels. The study established that monkeys exhibited greater vigilance in response to cylindrical and flat snakeskin. The monkeys displayed vigilance by standing on both feet and examining the exposed snakeskin, even though it was an unnatural-looking flat snakeskin. These findings demonstrate that one portion of the body is sufficient to trigger vigilance among the monkeys, whereas a cylindrical shape does not serve as a cue for the presence of snakes. Therefore, this study suggests that monkeys use snakeskin (scales) as a cue to detect and recognize snakes.

An EEG study has investigated human reactions to the skin of snakes and other reptiles[19]. In the second task, the stimuli were close-up images of snake scales, bird feathers, and lizard skin. The heads of the animals were not included in the photographs. The findings revealed that the EPN was significantly larger in the negative direction (greater attention) for photos of snake bodies than for those of lizard or bird bodies. This research suggests that snake bodies elicit a stronger reaction than those of other animals, according to the ERP index.

As mentioned above, several studies indicate that humans and primates rely on snake scales as crucial visual cues for rapid snake detection. If the presence of snake scales increases detection efficiency. To further examine whether snake scales are important cues for the rapid detection of snakes, I manipulated images of scaleless animals (salamanders) to appear as if they had scales. I then compared the detection times of salamanders with and without scales with that of snakes in a visual search task with monkeys that had never seen real amphibians and reptiles. Therefore, the present study investigated the detection times of snakes and salamanders, and snakes and salamanders clad in snake scales in a visual search task with monkeys that had never seen real reptiles and amphibians. Humans were not included because of their potential for top-down processing based on the categorical difference between snakes and salamanders. This study's purpose was twofold. First, it aimed to confirm that pictures of snakes were detected faster than those of other elongated animals with long tails and short limbs. Monkeys detect snakes faster than flowers and harmless mammals (koalas); however, although humans can detect snakes faster than elongated animals without long tails[29,30], it has not been confirmed that monkeys can do the same[29]. Second, it aimed to determine whether pictures of salamanders covered in scales were detected to the same extent as pictures of snakes.

## Methods
### Ethics statements
All experimental procedures were non-invasive. All data presented were collected at the Primate Research Institute (PRI) of Kyoto University through the Cooperation Research Program of the Primate Research Institute of Kyoto University. All procedures were approved by the Ethics Committee of the PRI of Kyoto University (2018-014) and performed in accordance with the Guide for the Care and Use of Laboratory Primates. This study is reported in accordance with ARRIVE guidelines.

### Participant monkeys
I used three female Japanese monkeys in compliance with the principles of the 3Rs (replacement, reduction, and refinement) in animal experimentation, as in previous studies[22,31]. Two of these monkeys were aged 9 years ("Pero" and "Ume") and one was 11 years ("Shiba") at the time of testing. All of them were born into social groups and raised to the age of 3 at the Primate Research Institute of Kyoto University. They were housed individually in cages with ad libitum access to water. Daily food requirements (biscuits and vegetables) were provided after each experimental session.

### Apparatus
The experimental tasks were performed in an operant box (700 mm × 610 mm × 700 mm) with acrylic panel walls[22,31]. A 15-inch touch-sensitive LCD screen was mounted on one side of the experimental box. A universal food dispenser was placed in the experimental box to provide the food rewards.

### Stimuli
Nine snake and nine salamander pictures were used in this study. Although the monkeys had previously been exposed to a visual-search task involving snake images, the images used in the current study differed from those used in the previous experiments[31]. Nine salamander and nine snake images from around the world were downloaded from the Internet. Five additional snake scale pictures were downloaded to dress the salamanders with snake scales, which were cut to appropriate sizes. All images have been converted to grayscale. In the "with scale" condition (Experiment 2), the cropped snake scales were attached to the body of the salamander pictures to give it the appearance of a snakeskin (Fig. 1C). The same cropped partial-scale patterns were not used for the different salamander pictures. Because the cropped scale patterns were insufficient to cover the entire body of the salamander, several pieces of the same scale pattern were combined and attached, except for the head and legs (Fig. 1C). The skin of the snake scale and the body of the homologous salamander ("without scale" condition: Fig. 1B) were then modified so that the entire picture had the same luminance as the entire picture of snake. This procedure was accomplished using the GIMP software. All initial pictures (nine snake, nine salamander, and nine scaled salamander pictures) were at least 773 × 515 pixels in size. They were resized to 600 × 450 pixels using GIMP; then, 27 of these pictures were processed using the SHINE toolbox[32] in MATLAB to minimize low-level confounding. The SHINE toolbox first adjusts the contrast of the images, and then adjusts the luminance histograms. Subsequently, each image was resized to 320 × 240 pixels, and all images were matched for luminance (Fig. 1).

In both experiments, the images were presented in a 3 × 3 matrix, with one snake image embedded within eight salamander images, or vice versa. In Experiment 1, nine snake and nine salamander pictures were presented. In Experiment 2, nine snake and nine scaled salamander pictures were presented. The same snake pictures were used in both experiments.

### Procedure
The three monkeys performed a visual search task. They had previously undergone a visual-search task with conspecific faces[33] and snakes[31]. The basic procedure was similar to that of previous studies that used visual search tasks with snake pictures[22,31,33]. The monkeys initiated the trial by touching the "start" button (a gray rectangle) at the center of the screen. On touching, this rectangle disappeared, and after 1 s, a nine-image matrix appeared. In both experiments, the monkeys had to touch one deviant picture (e.g. snake) on the touch-sensitive monitor from among eight pictures (e.g. salamanders) to receive a reward. The images were presented as a nine-image matrix in blocks of fear-relevant or -irrelevant targets. The block consisted of 72 trials in a quasi-random order that changed daily. The first was the training phase, with 63 blocks for Ume, 72 blocks for Pero, and 128 blocks for Shiba. The criterion was a performance rate of > 95% in three consecutive blocks for each target condition (i.e. six consecutive sessions). After reaching the criterion, data were collected for six consecutive days (432 trials per subject). During the test period, a correction procedure was applied to match the number of trials. If a monkey made an error during a trial, the trial was repeated until the error was corrected.

### Data analyses
As monkeys occasionally suspended their reactions and significantly slowed down the mean reaction times, I compared the reaction times of detecting snakes and salamanders for each monkey using the Mann–Whitney *U* test, similar to my previous studies[22,31,33]. The 95% confidence interval (CI) and effect size (rank-biserial correlation) are reported. When a monkey made an error, the reaction time for the correct trial was recorded.

## Results
### Experiment 1: snakes vs. salamanders
The monkeys made few errors. The error proportions were 0.5% (Ume), 3.9% (Pero), and 4.6% (Shiba). The left panel of Fig. 2 illustrates a boxplot of the reaction times taken by these monkeys to detect deviant pictures.

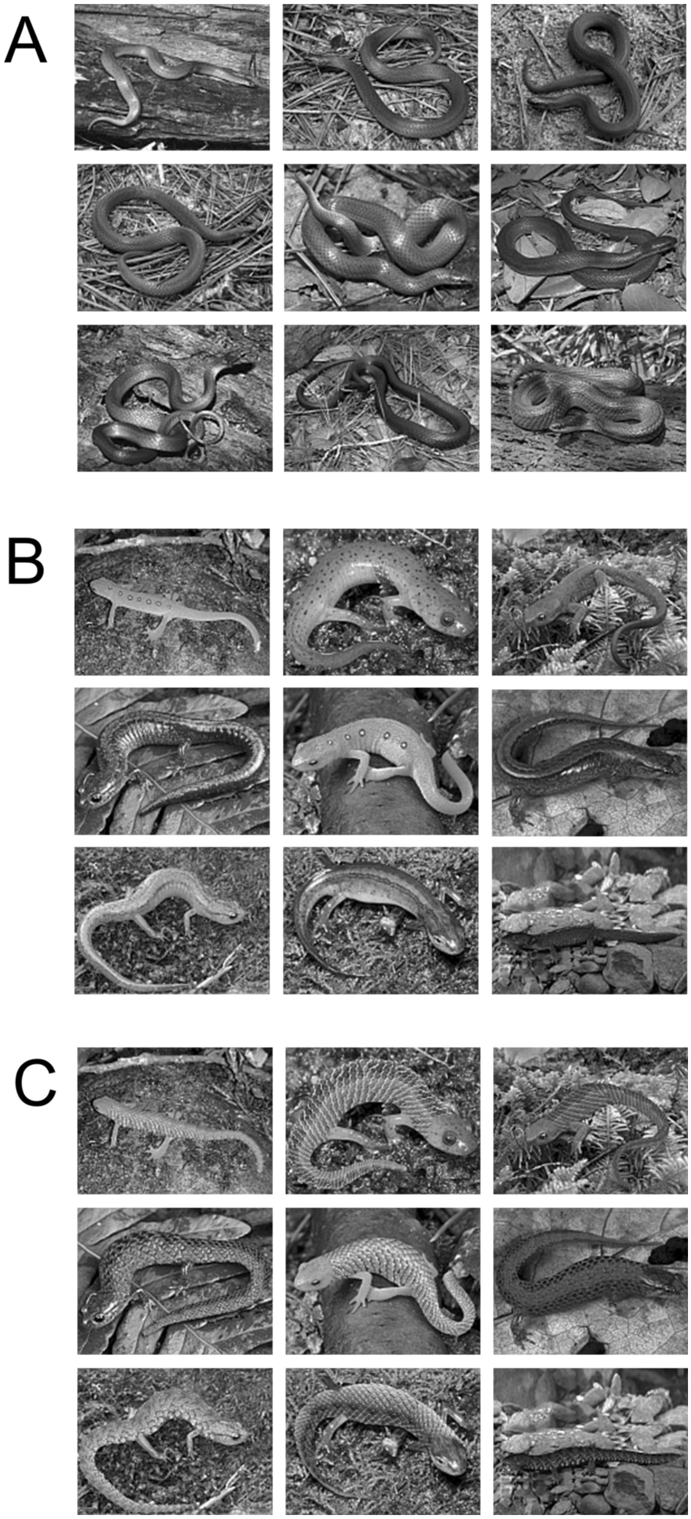


**Fig. 1**. The stimuli used in this study: (**A**) snakes, (**B**) salamanders, and (**C**) salamanders with snake scales. Stimuli were presented as a 3 × 3 matrix with one animal from a different category and eight animals from the same category.

The median reaction times (the central horizontal line of the boxplot) to detect the deviant pictures of snakes (Shiba, 1055 ms, 95% CI for means [1129, 1250]; Ume, 1007 ms, 95% CI [1029, 1113]; Pero 896 ms, 95% CI [898, 1082]) were faster than those to detect the deviant pictures of lizards (Shiba, 1095 ms, 95% CI [1266, 1432]; Ume, 1058.5 ms, 95% CI [1138, 1357]; Pero 936 ms, 95% CI [1006, 1143]) in the monkeys (Mann–Whitney *U* tests:

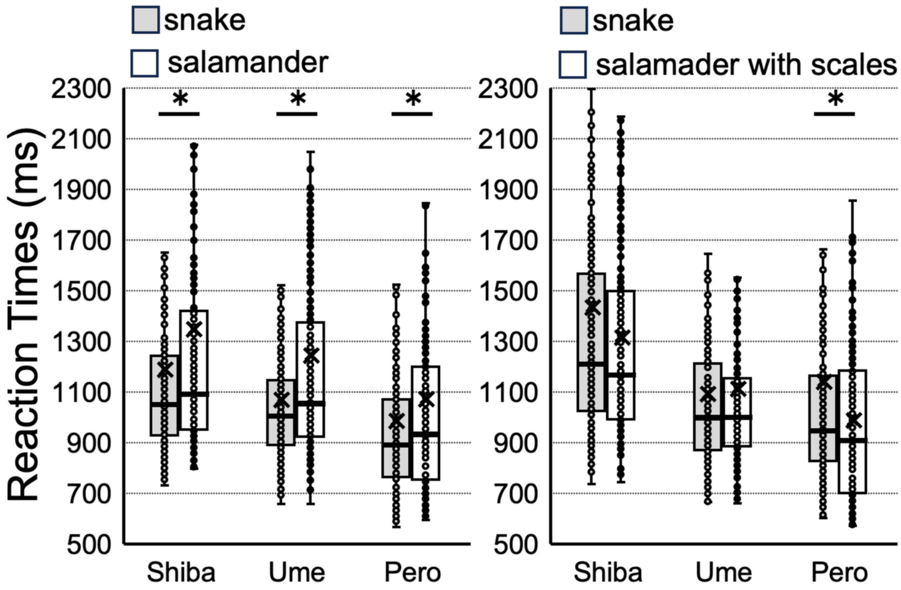


**Fig. 2**. The boxplot of the reaction times to detect the deviant pictures by three monkeys. The left panel presents the results of Experiment 1 (snake vs. salamanders), and the right panel presents the results of Experiment 2 (snake vs. salamanders with snake scale). The center line of the box plot displays the median reaction times, while the top and bottom of the box display the third and first quartiles. The vertical bars represent the largest and smallest values within 1.5 times the interquartile range above the third quartile and below the first quartile. The crosses denote the mean reaction times.

Shiba, $Z = 2.50$, $p = 0.0012$, rank biserial correlation $r = 0.139$; Ume, $Z = 3.34$, $p = 0.0008$, $r = 0.186$; Pero, $Z = 2.07$, $p = 0.038$, $r = 0.115$).

## Experiment 2: snakes vs. scaled salamanders

Similar to Experiment 1, the monkeys made few errors. The proportions of the errors were 0.5% (Ume), 1.2% (Pero), and 1.9% (Shiba). The right panel of Fig. 2 illustrates a boxplot of the reaction times taken by the monkeys to detect deviant pictures. The pattern of the results differed from Experiment 1. The median reaction times to detect the deviant pictures of snakes were slower than (Shiba, 1214.5 ms, 95% CI [1334, 1540]; Pero 950.5 ms, 95% CI [1063, 1224]) or same (Ume, 1003.5 ms, 95% CI [1040, 1151]) as those to detect the deviant pictures of salamanders (Shiba, 1172 ms, 95% CI [1258, 1384]; Ume, 1003.5 ms, 95% CI [1046, 1185]; Pero 912.5 ms, 95% CI [934, 1046]) (Mann–Whitney $U$ tests: Shiba, $Z = 1.13$, $p = 0.2589$ $r = -0.06$; Ume, $Z = 0.49$, $p = 0.6221$, $r = 0.03$; Pero, $Z = 3.16$, $p = 0.0016$, $r = -0.18$).

## Discussion

In this study, I manipulated only scales while controlling body shape, color, posture, and spatial frequency by using grayscale static images that were balanced for luminance and contrast. I found that the monkeys detected snake pictures more quickly than salamander pictures, and when the salamanders were clothed in snake scales, detection of salamander pictures was as fast as, or faster than, that of snake pictures. The first finding is consistent with previous results; however, in several respects, it provides further evidence that primates are sensitive to snakes. In previous visual search studies, monkeys quickly differentiated pictures of snakes from those of flowers[22] or innocuous mammals with rounded body shapes (e.g. koalas)[31]. However, in this study, monkeys detected snakes more rapidly than salamanders, which have a similar elongated body shape. This suggests that snakes are not detected quickly because of their elongated bodies[12,17,20]. This also shows that snakes are not detected by body color, as in previous studies[6,14,22,23].

More importantly, the same salamanders were detected as quickly as or even faster than the snakes when they were clothed in snake scales. Thus, this strongly suggests that snake scales are the factor most responsible for the rapid detection of snakes. One might think that novelty might explain their faster detection since the monkeys were used to seeing salamanders without scales. Suddenly, salamanders with scales might attract their attention more quickly; however, novelty alone cannot explain the faster detection. The monkeys had plenty of experience looking at pictures of snakes. When they saw the salamanders for the first time in this study, they should have recognized them more quickly in Experiment 1 because they were novel. However, they did not. Therefore, novelty alone cannot explain the results of this experiment. In Experiment 1, snakes were detected more quickly than salamanders because only the snakes were covered with snake scales, whereas in Experiment 2, both snakes and salamanders were covered with snake scales, which reduced differences in the detection speed between reptiles and amphibians. This is consistent with previous studies showing that both humans and nonhuman primates are drawn to snake scales[17,20]. As noted earlier, the EPN—an ERP that reflects early attention in visual information processing—responded more significantly to close-up images of snake scales, bird feathers, and lizard skin[19]. This study suggests that the texture or patterning of snake bodies elicits stronger reactions than the texture of patterning of birds and lizards, even though the latter also have scales. In another visual search study, the same monkeys detected pictures of snakes more quickly than those of koalas[31]. However, when the scales of the snakes were smoothed out by image processing, the pictures of snakes without those scales were detected more slowly than koala pictures[21] Both studies clearly determined that the detection speed of animals varied depending on the presence of snake scales.

Furthermore, snakes in the threatening posture were detected faster than those in the nonthreatening posture[18]. The rhesus monkeys in the primate center showed the strongest fear reaction to the snake model in a threatening posture[17]. The degree to which snakes are detected quickly and the extent of fear response may vary depending on the snake's posture. However, it is unclear whether snakes in certain postures can be found quickly or whether they elicit a fear response in monkeys. The snake's posture likely modulates its level of threat. In the present study, the detection speed of snakes varied depending on whether the salamanders were clad in snake scales. As the photographs of the snakes were identical in the two experiments, the results of this study cannot be explained by differences in snake postures.

However, the order of the two experiments was fixed in this experiment. The snake and salamander experiment was conducted first to train the monkeys in identifying snakes and salamanders. The novelty of the scales added in Experiment 2 could have reduced reaction times. However, there was no systematic effect, as one of the three monkeys (Shiba) actually had slower reaction times in Experiment 2 to scaled salamanders (and snakes).

This study established that the presence or absence of snake scales is responsible for quick detection. The results of this study are consistent with other studies employing different methods that have also found primates to be highly sensitive to the visual cue of snake scales[19,20,34]. Such sensitivity allows them to detect snakes more quickly than other animals. The visual feature that primates use to detect snakes is likely to be the snake-scale shape, which is both specific and common to snakes. The quick detection of snakes is thought to be mediated by the pathway from the retina to the amygdala via the superior colliculus-pulvinar[4]. Neurons that respond to a checkerboard pattern that resembles snake scales are present in the pulvinar, and V2 and V4 have strong connections to it[4,10]. These neural circuits are believed to be responsible for threat detection in primates[35].

Similar to other research, this study used a visual search task to examine the threat of snakes. In visual search tasks, there are two different interpretations of the same result. The quick detection of snakes could be explained by the effective detection of threat targets, by a delay in disengagement, or by both[28,36]. In the visual search task, a dangerous target is considered particularly effective at attracting attention; therefore, participants paid more attention to dangerous targets among distractors than to other non-dangerous targets. The fast detection of snake pictures may result from snakes catching their attention more effectively than other objects. If rapid detection of snake targets is caused by delayed disengagement during a visual search task, participants will pay more attention to snake distractors and spend more time looking at them (attention capture). Thus, dangerous objects may be particularly effective in "focusing attention," "delaying disengagement," or both during visual search tasks.

In the flicker-paradigm task, in which a stimulus has only one target but no distractors, the results may provide evidence for greater attentional capture of snakes compared to other animals. Additionally, reaction time and data accuracy can be recorded in a flicker-paradigm task. We demonstrated that humans detect snakes more accurately and quickly than lizards from natural scenes in a flicker-paradigm task[37]. Nevertheless, no studies have demonstrated that monkeys can perform the flicker-paradigm task because it is challenging to train them while they are in training for this task. Future research should be conducted to determine whether snake-naïve monkeys can detect snakes more accurately and rapidly than other animals in the flicker-paradigm tasks.

## Conclusion
This study demonstrated that monkeys that had never seen real snakes could detect them more quickly in a visual-search task using luminance- and contrast-aligned photographs, in comparison to detecting salamanders. However, this advantage disappeared when the salamanders were clothed in snake scales using image processing. These findings provide compelling evidence that the previously well-documented quick detection of snakes as a primate (including humans) threat response is accomplished by recognizing the snake-scale shapes.

## Data availability
The datasets used and analysed during the current study available from the corresponding author on reasonable request.

Received: 8 July 2024; Accepted: 1 November 2024
Published online: 10 November 2024

## References
1. Headland, T. N. & Greene, H. W. Hunter-gatherers and other primates as prey, predators, and competitors of snakes. *Proc. Natl. Acad. Sci. U. S. A.* **108**, E1470–E1474 (2011).
2. Kasturiratne, A. et al. The global burden of snakebite: A literature analysis and modelling based on regional estimates of envenoming and deaths. *PLoS Med.* **5**, 1591–1604 (2008).
3. GBD 2019 Snakebite Envenomation Collaborators et al. Global mortality of snakebite envenoming between 1990 and 2019. *Nat. Commun.* **13**, 6160 (2022).
4. Kawai, N. *The Fear of Snakes: Evolutionary and Psychobiological Perspectives on our Innate Fear* (Springer, 2019). https://doi.org/10.1007/978-981-13-7530-9.
5. Lobue, V. & Deloache, J. S. Superior detection of threat-relevant stimuli in infancy. *Dev. Sci.* **13**, 221–228 (2010).

6. Bertels, J., de Heering, A., Bourguignon, M., Cleeremans, A. & Destrebecqz, A. What determines the neural response to snakes in the infant brain? A systematic comparison of color and grayscale stimuli. *Front. Psychol.* https://doi.org/10.3389/fpsyg.2023.1027872 (2023).
7. Bertels, J. et al. Snakes elicit specific neural responses in the human infant brain. *Sci. Rep.* **10**, 7443 (2020).
8. Soares, S. C., Lindströ, B., Esteves, F. & Öhman, A. The hidden snake in the grass: superior detection of snakes in challenging attentional conditions. *PLoS One* **9**, e114724 (2014).
9. Isbell, L. A. Snakes as agents of evolutionary change in primate brains. *J. Hum. Evol.* **51**, 1–35 (2006).
10. Isbell, L. A. *The Fruit, the Tree, and the Serpent: Why We See so Well* (Harvard University Press, 2009). https://doi.org/10.4159/9780674054042/HTML.
11. LoBue, V. Deconstructing the snake: the relative roles of perception, cognition, and emotion on threat detection. *Emotion* **14**, 701–711 (2014).
12. Lobue, V. & DeLoache, J. S. Detecting the snake in the grass: Attention to fear-relevant stimuli by adults and young children. *Psychol. Sci.* **19**, 284–289 (2008).
13. Rabosky, A. D. R. et al. Coral snakes predict the evolution of mimicry across New World snakes. *Nat. Commun.* **7**, 1–9 (2016).
14. Prokop, P., Fančovičová, J. & Kučerová, A. Aposematic colouration does not explain fear of snakes in humans. *J. Ethol.* **36**, 35–41 (2018).
15. Csathó, Á. et al. Snakes represent emotionally salient stimuli that may evoke both fear and disgust. *Front. Psychol.* **10**, 1085 (2019).
16. Hayakawa, S., Kawai, N. & Masataka, N. The influence of color on snake detection in visual search in human children. *Sci. Rep.* https://doi.org/10.1038/srep00080 (2011).
17. Etting, S. F., Isbell, L. A. & Grote, M. N. Factors increasing snake detection and perceived threat in captive rhesus macaques (*Macaca mulatta*). *Am. J. Primatol.* **76**, 135–145 (2014).
18. Masataka, N., Hayakawa, S. & Kawai, N. Human young children as well as adults demonstrate 'superior' rapid snake detection when typical striking posture is displayed by the snake. *PLoS One* https://doi.org/10.1371/journal.pone.0015122 (2010).
19. Van Strien, J. W. & Isbell, L. A. Snake scales, partial exposure, and the snake detection theory: A human event-related potentials study. *Sci. Rep.* **7**, 46331 (2017).
20. Isbell, L. A. & Etting, S. F. Scales drive detection, attention, and memory of snakes in wild vervet monkeys (Chlorocebus pygerythrus). *Primates* **58**, 121–129 (2017).
21. Kawai, N. Searching for the critical features of snakes. In *The Fear of Snakes: Evolutionary and Psychobiological Perspectives on Our Innate Fear* (ed. Kawai, N.) 121–153 (Springer, 2019). https://doi.org/10.1007/978-981-13-7530-9_7.
22. Shibasaki, M. & Kawai, N. Rapid detection of snakes by Japanese monkeys (*Macaca fuscata*): An evolutionarily predisposed visual system. *J. Comp. Psychol.* **123**, 131–135. https://doi.org/10.1037/a0015095 (2009).
23. Flykt, A. Visual search with biological threat stimuli: Accuracy, reaction times, and heart rate changes. *Emotion* **5**, 349–353 (2005).
24. Grassini, S., Holm, S. K., Railo, H. & Koivisto, M. Who is afraid of the invisible snake? Subjective visual awareness modulates posterior brain activity for evolutionarily threatening stimuli. *Biol. Psychol.* **121**, 53–61 (2016).
25. He, H., Kubo, K. & Kawai, N. Spiders do not evoke greater early posterior negativity in the event-related potential as snakes. *Neuroreport* **25**, 1049–1053. https://doi.org/10.1097/WNR.0000000000000227 (2014).
26. Lythgoe, J. N. & Partridge, J. C. Visual pigments and the acquisition of visual information. *J. Exp. Biol.* **146**, 1–20 (1989).
27. Morgan, M. J., Adam, A. & Mollon, J. D. Dichromats detect colour-camouflaged objects that are not detected by trichromats. *Proc. Biol. Sci.* **248**, 291–295 (1992).
28. Kawai, N. & He, H. Breaking snake camouflage: Humans detect snakes more accurately than other animals under less discernible visual conditions. *PLoS One* https://doi.org/10.1371/journal.pone.0164342 (2016).
29. Penkunas, M. J. & Coss, R. G. Rapid detection of visually provocative animals by preschool children and adults. *J. Exp. Child Psychol.* **114**, 522–536 (2013).
30. Penkunas, M. J. & Coss, R. G. A comparison of rural and urban Indian children's visual detection of threatening and nonthreatening animals. *Dev. Sci.* **16**, 463–475 (2013).
31. Kawai, N. & Koda, H. Japanese monkeys (*Macaca fuscata*) quickly detect snakes but not spiders: Evolutionary origins of fear-relevant animals. *J. Comp. Psychol.* **130**, 299–303. https://doi.org/10.1037/com0000032 (2016).
32. Willenbockel, V. et al. Controlling low-level image properties: The SHINE toolbox. *Behav. Res. Methods* **42**, 671–684 (2010).
33. Kawai, N., Kubo, K., Masataka, N. & Hayakawa, S. Conserved evolutionary history for quick detection of threatening faces. *Anim. Cogn.* **19**, 655–660. https://doi.org/10.1007/s10071-015-0949-y (2016).
34. Coss, R. G. & Charles, E. P. The saliency of snake scales and leopard rosettes to infants: Its relevance to graphical patterns portrayed in prehistoric art. *Front. Psychol.* https://doi.org/10.3389/fpsyg.2021.763436 (2021).
35. Le, Q. V. et al. Monkey pulvinar neurons fire differentially to snake postures. *PLoS One* **9**, e114258 (2014).
36. Fox, E., Russo, R. & Dutton, K. Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cogn. Emot.* **16**, 355–379 (2002).
37. Kawai, N. & Qiu, H. Humans detect snakes more accurately and quickly than other animals under natural visual scenes: a flicker paradigm study. *Cogn. Emot.* **34**, 614–620. https://doi.org/10.1080/02699931.2019.1657799 (2020).



## Acknowledgements
I would like to thank Keiko Ishida for her help in carrying out the experiments and Huachen Qiu for her help in producing the stimuli. This study was conducted by the Cooperation Research Program of the Primate Research Institute of Kyoto University, with Hiroki Koda as my counterpart.


## Author contributions
Nobuyuki Kawai: Conceptualization, Methodology, Writing-Original draft preparation, Writing-Reviewing and Editing, Supervision, Validation, Visualization, Investigation.


## Funding
This study was supported by JSPS KAKENHI Grant Numbers 21H04421 and 23K20777.


## Declarations

## Competing interests
The authors declare no competing interests.

## Additional information
**Correspondence** and requests for materials should be addressed to N.K.