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RESEARCH ARTICLE

The thermal background determines how the infrared and visual systems interact in pit vipers

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ABSTRACT

The thermal infrared (IR) sensing system of pit vipers is believed to complement vision and provide a substitute imaging system in dark environments. Theoretically, the IR system would best image a scene consisting of a homothermal target in cold surroundings as a bright spot on a dark background. To test this hypothesis, we evaluated how the pit viper (*Gloydius brevicaudus*) discriminates and strikes prey when the background temperature is either higher or lower than that of the prey (approximately 32–33°C) in different parts of the scene. Snakes were tested in a modified predation cage in which background temperatures were set to 26°C on one side and either 33 or 40°C on the opposite side when the eyes, the pit organs or neither sensory system was occluded. When the eyes were blocked, snakes preferred to strike prey on the 26°C side rather than on the 33°C side but showed no bias in the other conditions. Snakes showed no preference for 26 versus 40°C background temperature, although more missed strikes occurred when the eyes were occluded. The results thus revealed that the pit viper IR system can accomplish a ‘brightness constancy’ computation reflecting the difference between the target and background temperatures, much as the visual system compares the luminance of a figure and the background. Furthermore, the results show that the IR system performs less well for locating prey when the background is warmer than the target.

KEY WORDS: *Gloydius brevicaudus*, Infrared sense, Predation behavior, Brightness constancy, Thermoregulation

INTRODUCTION

Many behavioral and neurophysiological studies support the idea that pit vipers (Crotalinae) can sense, identify and target prey based on a thermal image constructed by a layer of infrared (IR)-sensitive neurons located subjacent to the visual layer in the midbrain tectum. The IR and visual spatiotopic tectal maps have similar but not identical axes and IR stimulation may evoke a broader pattern of neural activity than that of vision (Hartline et al., 1978). These results along with the reconstruction model (Sichert et al., 2006) imply that the heat image is not as elaborate as the visual image although the IR system works in concert with the visual system for identifying and targeting prey (Sichert et al., 2006; Chen et al., 2012). Notably, the visual image shows more detailed features while the IR image encodes more contrast profiles. Moreover, bimodal tectal neurons exist that respond to both IR and visual stimulation and which might play a role in the integration of these two inputs (Newman and Hartline, 1981). It is unknown, however, whether visual–IR interactions (synergy, compensation and interference) remain constant or exhibit adaptive plasticity with changes in the thermal environment.

The most important elements of image configuration involved in discriminating the foreground from the background are profile and contrast (Strasburger et al., 1991). Most animals including humans can easily recognize both positive and negative features of images. For example, we can recognize visually a black mouse in front of a piece of white paper or a white mouse in front of a black board. When snakes are facing prey, the foreground of the IR image normally consists of a relatively small high-temperature stimulus against a large low-temperature background. A low-temperature foreground against a high-temperature background might correspond to a ‘negative’ sense image. Consistently, recordings of midbrain neural responses have shown that a cold stimulus (e.g. ice) evokes a depression of static activity followed by a slow return to the static level. Removal of the cold object evokes a prominent burst of spikes (Goris and Terashima, 1973; de Cock Buning et al., 1981a,b).

Van Dyke and Grace (2010) proposed that thermal contrast plays an important role in IR-based defensive targeting in an experiment in which oscillating 36 and 12°C balloons were used as warm and cool objects, respectively, against a 24°C background. Blindfolded copperhead snakes were found to approach both moving warm and cool balloons against opposite temperature backgrounds, although approach responses were more robust to warm than to cool objects. Furthermore, warm objects evoked repeated following behavior in phase with target motion, while cool targets induced rhythmic behavioral movements in antiphase to target motion. It has been proposed that the oscillating cool object might reduce the background activity of the trigeminal nerve fibers that innervate the pit membrane (de Cock Buning et al., 1981a) and that snakes might respond to the warmer background when the cool object is moving away (de Cock Buning et al., 1981b; Van Dyke and Grace, 2010).

In a previous study, we found that each sensory system (two eyes and two pits) in the short-tailed pit viper (*Gloydius brevicaudus*) seemed to have the same weight (e.g. 25%) in multimodal signal integration for targeting prey. Specifically, we found that occlusion of two eyes, two pits or one eye and one pit on the same side of the head resulted in about a 75% rate of both strike attempts and strike successes compared with the control condition in which no occlusion was performed (Chen et al., 2012). We hypothesized that the relative weights of the visual system and IR system might be adjustable depending on the thermal conditions of the foreground and background. Based on this hypothesis, three predictions can be made: (1) snakes prefer to target prey under high-contrast conditions, regardless of whether the foreground stimulus is of higher or lower temperature than the background; (2) for low thermal contrast conditions, snakes will depend more on vision than

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on the IR system, while for high thermal contrast conditions, snakes will rely more on pit input than on the eyes; and (3) there will be little effect on sensory system preference of reversing thermal conditions between the foreground and background if the thermal contrast is not changed.

MATERIALS AND METHODS

Animals

The short-tailed pit viper, *G. brevicaudus* (Stejneger 1907) (Viperidae: Crotalinae), is relatively small compared with most pit viper species. This species was selected as the subject in the present study because it is an effective hunter in both light and dark conditions. The snakes rarely chase prey and typically lie in ambush, in grass or rubble, before striking at passing animals. For these reasons, the short-tailed pit viper was considered to be an ideal subject to study the effect of thermal background selection on IR system functioning (Chen et al., 2012).

The pit vipers used in this study were collected from hilly areas in central China, Hubei and Anhui provinces. All snakes were maintained and fed in an artificial environment for more than 1 year. Each was kept individually in a home cage and supplied with one mouse a week. Water was available *ad libitum* and room temperature was kept around 26°C. For the behavioral experiment, 24 healthy snakes (total length 65–83 cm, mass 69–112 g, head width 19.3±1.3 mm, male:female ratio 9:15) were chosen based on prior observations indicating they exhibited consistent prey catching. The IR target was a mouse (*Mus musculus*) of either sex. Mice, selected according to the body size of each snake (14 days old, 7–10 g), were used for both normal feeding of the snakes and experimental trials, i.e. the mice used in the targeting trials were part of the normal feeding regimen for the experimental subjects. The experiments were performed on 2 consecutive days once a week according to the snakes' normal feeding schedule. If the snake was close to completing shedding – indicated by a gray–white color of the scales on the eyes – the experiment was postponed for that snake. All animal care and experimental procedures were approved by the Chengdu Institute of Biology Animal Care and Use Committee. No animal suffered unnecessary pain in these experiments.

Experimental set-up

A drum-shaped circular arena was used for the experiments, consisting of 0.8 mm-thick stainless steel walls of 50 cm diameter and 50 cm height (Fig. 1A).

Two pieces of 1 cm-thick Styrofoam formed the base plate, of the same size as the inner diameter of the drum. Before every trial, the used base plate was replaced with a clean one. The used base plate was cleaned with odorless tableware cleaner to remove the odor of the last trial. To avoid visual distractions from the reflection of the stainless steel, the inner wall of the drum was covered with black adhesive paper, as were the base plates. In addition, each base plate was divided into four equal sections by a red tape cross to facilitate subsequent scoring of strike behavior.

One-half of the outer wall of the drum was wrapped with carbon fiber heating film, and a thermostat (precision 0.1°C, control range 1°C) was used to control the temperature of this half-wall. Thus, one-half of the drum wall surrounding the prey was of normal baseline temperature while the other half constituted a warm background (Fig. 1B). The temperature of the warm background was maintained around the set point using feedback control (Fig. 1C,D).

The temperature of the experimental laboratory was held constant at 26°C. Three fluorescent lights (30 W, Philips) were used to illuminate the room. A camera (JVC, GZ-HD300SAC) was mounted above the center of the trial arena.

Ocular and pit organ occlusion

The eyes and pits of the subject were occluded, i.e. the eyes were covered directly with black adhesive tape and the pits were covered with wet tissue balls and then covered with the tape (Chen et al., 2012). For the experimental conditions, the eyes or pits were occluded 24 h in advance according to the experimental protocol (see below) in order to adapt the snake to the sensory condition. It should be noted that swallowing was finished within minutes of prey capture, but the occlusive materials were not removed until 24 h after the experiments in order to avoid disturbing the snake.

Experimental protocol

Before beginning the experiments, the surface temperatures of 10 mice were measured in the middle of the body on one side using an IR thermometer. Mice surface temperatures were typically 32–33°C. In view of this, the background thermal conditions were set at 26°C (low-temperature background, LTB), 33°C (low-contrast background, LCB) and 40°C (high-temperature background, HTB). The room temperature was controlled accurately by air conditioning and maintained at 26°C with ±0.5°C variation, while the 33 and 40°C drum background temperatures were maintained by using the apparatus heating system. Two experimental paradigms involving the background contrast settings were used. In paradigm A, the background contrast was 26 versus 33°C and in paradigm B it was 26 versus 40°C. There were three conditions for paradigm A: subject snakes were intact (control), both eyes were covered or both pits were covered. For paradigm B, the snakes' eyes were either both uncovered or both covered – the pits were not covered in either condition.

In paradigm A, 24 snakes were divided randomly into three equal groups of eight, corresponding to the three sensory manipulation conditions. During the first experimental week, snakes of group 1 were free from any sense shielding (control), those of group 2 experienced occlusion of both eyes and those of group 3 experienced occlusion of both pit organs. During the following 2 weeks, these sensory manipulations were randomly assigned to each snake so that each subject experienced all three conditions only once.

After completing experiments in paradigm A, all animals were used in experiments in paradigm B in the subsequent 2 weeks. The 24 snakes were evenly divided into two groups of 12, i.e. control and eyes occluded. We did not include the covered-pit condition in paradigm B experiments because, as described below, no behavioral effect was found for occlusion of both pits with the background temperature contrast in paradigm A (26 versus 33°C).

On the experimental day, the carbon fiber heating film was turned on 10 min before the subject was placed in the drum, in order to stabilize background temperatures at 33 or 40°C. At the beginning of each trial, the snake was a carefully placed into the drum. After 5–10 min, when the snake stopped crawling and tail-shaking, the target mouse was placed at the farthest point from the snake's head. In this way, both predator and prey would have the most time and space to adjust their strategies for hunting and escaping. The test trial ended when the mouse died after the snake attack. The trial continued as long as the mouse remained standing after an attack. If the snake did not attack the mouse within 20 min, the trial was terminated. At the end of each trial, the snake was immediately returned to the home cage with its prey (dead or alive), as any interference after swallowing the mouse might cause the snake to vomit. The base plate of the drum was then replaced with a clean

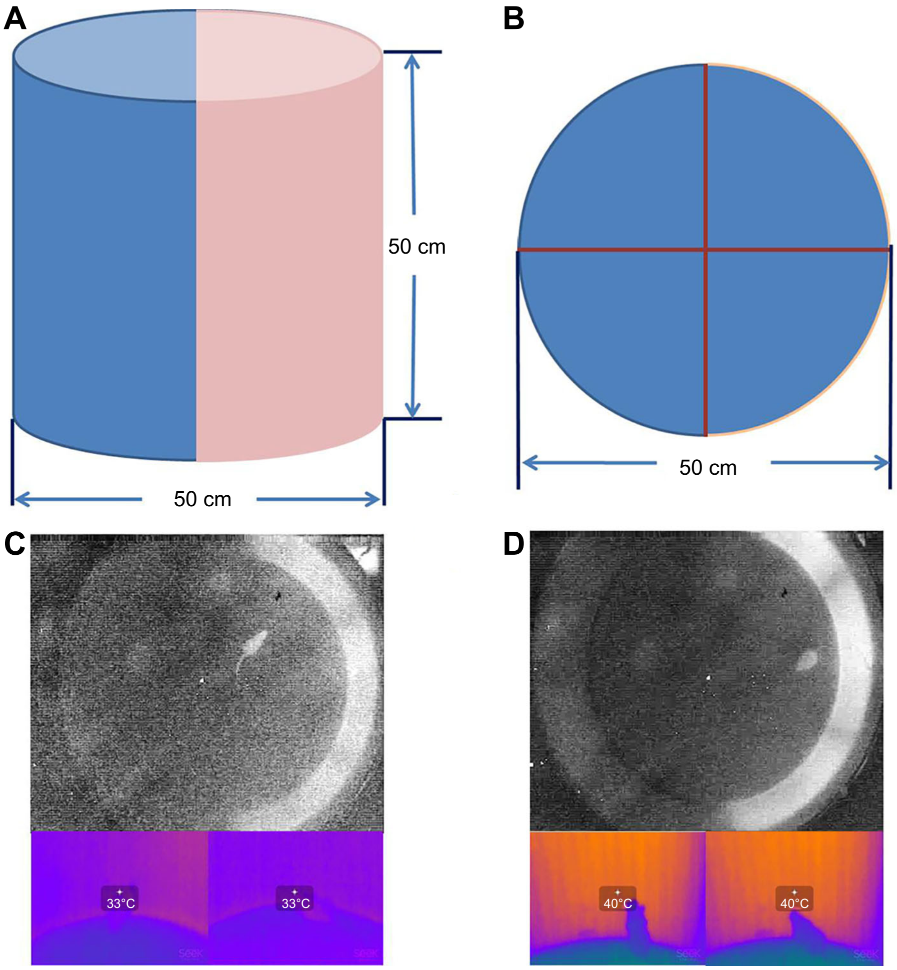

Fig. 1. Schematic and infrared diagrams of the drum-shaped circular testing arena. (A) Lateral schematic diagram of the drum. (B) Plan-view schematic diagram of the bottom of the drum; the circular arena was marked off into four areas in order to score the animals' behaviors. (C) Infrared (IR) plan views of the warm background at 33°C. (D) IR plan views of the warm background at 40°C.

plate and the warmed half-wall (33 or 40°C) was switched to the opposite side, i.e. a 90 or 270 deg horizontal orientation change occurred before the next trial in order to eliminate all possible bias cues.

Behavior recording

All trials were monitored by a video camera and video data (1080p, 24 frames s^{-1}) were downloaded onto a PC (Lenovo, China) for quantifying behavior and data analysis. The following data were measured for each trial in each paradigm with each sensory occlusive mode: (1) the ratio of the time (in s) that the snake spent in the two heated (33 or 40°C) sections versus the time spent in the non-heated (26°C) section of the drum – for cases in which the snake was lying over two sections, the period of time that the head was in a section was counted; (2) the ratio of the time (in s) that the mouse spent in the two heated sections versus the non-heated ones; (3) the number of snakes that did or did not launch strikes in each predation trial; (4) the number of attack strikes, including those in which the prey was hit (i.e. a successful strike) or not hit (unsuccessful); (5) the number of successful (effective) strikes in which the prey was bitten; (6) the latency from trial onset to strike; (7) the orientation of each strike, i.e. the point on the wall of the drum along a line from the head of snake through the middle part of the mouse; (8) the delay between the strike launch and the death of the mouse; (9) the strike distance (mm), which is the distance between the prey and the tip of the snake's rostrum immediately before each strike; (10) the motion state of the snake and mouse before each strike.

Statistical analyses

Prior to statistical analyses, measures of variables (i.e. times spent and/or numbers) were examined for assumptions of normality and homogeneity of variance, using the Kolmogorov–Smirnov and Levene tests, respectively. Some non-quantitative parameters such as the sensory occlusive mode and strike preference (towards the cool or warm wall) were transformed into numbers. Thus, the control condition was coded as 0, the eyes-covered condition as 1, and the pits-covered condition as 2, while for the backgrounds, −1 was assigned to the relatively lower temperature background (26°C) and 1 to the relatively higher temperature backgrounds (33 or 40°C) in both paradigms A and B. Consequently, Pearson and Spearman correlations were used to analyze quantitatively the relationships between some behavioral indices and the conditions associated with foreground/background thermal contrasts (LTB, LCB and HTB). In the present study, $P<0.05$ was considered statistically significant and $P<0.005$ was considered highly significant. The data arrangement and statistical tests were performed using Microsoft Excel (version 14.0 for Windows) and SigmaPlot (version 12.0 for Windows).

RESULTS

General description

All 24 snakes were used in the control, eyes-covered and pits-covered conditions in paradigm A. The same 24 snakes performed predation in the control and eyes-covered conditions in paradigm B. Subjects completed five experimental sessions with each session lasting 1 week over a total of 5 weeks. Snakes successfully hit targets on 78 out of 120 trials. The snakes performed best in the first week, during which there were 18 successful trials, and performed worst in the last week, during which there were 13 successful trials (Fig. 2A). No significant differences in the number of successful strikes between weeks were found (*t*-test, P=0.812). The snakes struck but missed the target in two trials, and did not perform attacks in the remaining 40 trials during the 20 min test periods.

The majority of subjects succeeded in three to five trials (Fig. 2B). The distribution of the number of successful trials across subjects passed the normality test (Shapiro–Wilk, P=0.739). The number of successful trials based on segments (i.e. paradigms versus occlusive conditions) passed the normality test (Shapiro–Wilk, P=0.685). The best performance was found in paradigm A with the control condition (19 successes in 24 trials) while the poorest performance occurred in paradigm B with the eyes-covered condition (13 successes in 24 trials) (Fig. 2C).

For 70 out of 78 successful predations, the snake knocked down the mouse with only one strike. During the other eight successful trials, the snake required more than one hit to knock down the mouse (Fig. 2D). After being effectively struck, the mice struggled for 12–709 s. The latency from snake strike to mouse death across trials failed to pass the normality test (mean 105.97±102.02 s, $P<0.05$).

Each trial began when the animals were placed in the drum and ended when the snake knocked down the mouse. Thus, the duration of predation varied between trials. For this reason, we used the ratio between the time animals spent near the heated wall to the time spent near the opposite wall during each trial to determine position preference. Both the snakes and mice exhibited no obvious preference for waiting within specific floor sections of the drum. In 89 pre-predation video recordings (78 successful+11 unsuccessful trials), the ratio of the time (in s) that snakes remained in the heated sections before striking did not pass the normality test, with a mean of 45.46±36.28 ($P<0.05$). At the same time, the mice avoided the heated sections in six trials and remained in them for 10 trials. The ratios of the time (in s) that the mice spent within a specific section failed to pass the normality test, with a mean of 55.42±29.48 ($P<0.05$).

The strike distance and motion state of each strike were assessed on the basis of the last frame before the strike. The longest successful strike distance was 65 mm; failed strike distances longer than 65 mm were excluded from analysis. In the majority of

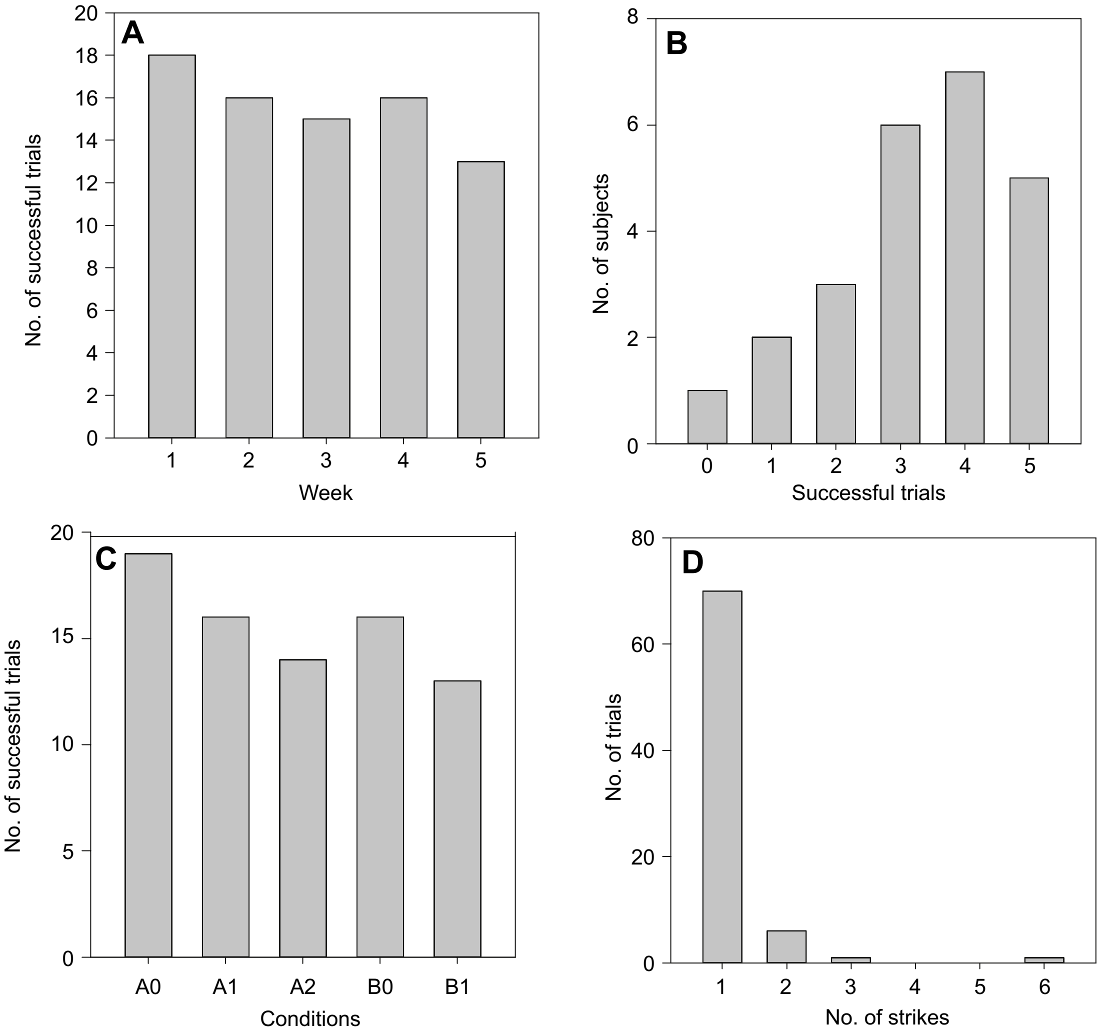

Fig. 2. General results of experimental trials. (A) Number of successful trials during each of 5 experimental weeks. (B) Number of subjects that performed successfully in 0–5 trials. (C) Number of successful trials for each subject condition for each paradigm. A0: paradigm A, control condition; A1: paradigm A, eyes-covered condition; A2: paradigm A, pits-covered condition; B0: paradigm B, control condition; B1: paradigm B, eyes-covered condition. (D) Number of trials during which strikes were performed one or more times.

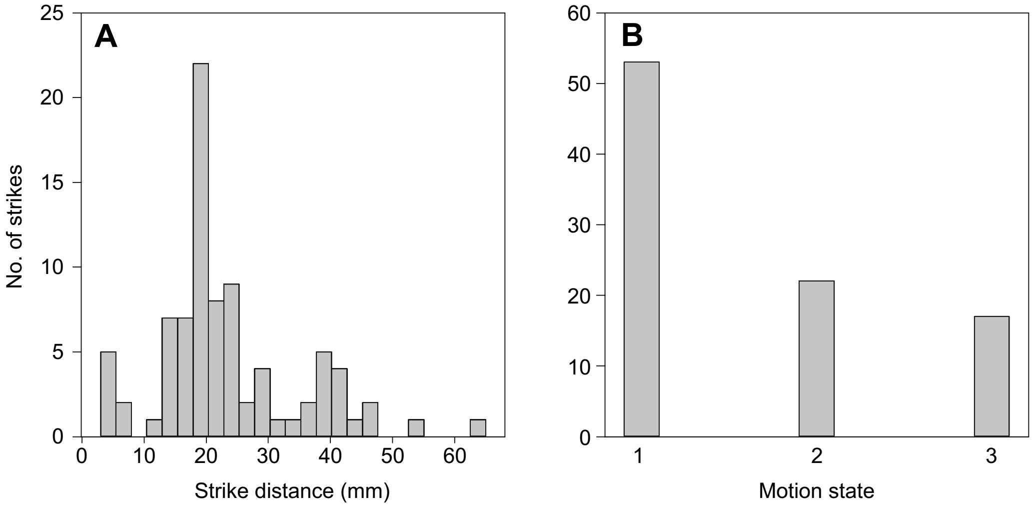

Fig. 3. Distribution of strike distance and the motion state of the animals. (A) Number of strikes launched with for strike distance. (B) Number of strikes performed when the animals exhibited each of three motion states: (1) the snake remained still and waited to strike until the mouse moved into the attack range; (2) the mouse was still and did not move, while the snake actively hunted the mouse; (3) both the snake and the mouse were moving and predation occurred when they met.

predations, strike distance was approximately 20 mm (Fig. 3A), which is approximately equal to the average width of the snakes' head (19.3±1.3 mm). There was no significant correlation between predation condition and strike distance (Spearman and Pearson analysis, $P>0.05$). Three types of motion state before the strikes could be identified: (1) the snake was still and waited to strike until the mouse moved into the attack range; (2) the mouse was still and the snake actively hunted the mouse; (3) both animals were moving and predation occurred when they met. The majority of trials involved the first movement pattern (type 1; Fig. 3B). Nevertheless, there was no significant correlation between predation condition and the animals' motion state (Spearman and Pearson analysis, $P>0.05$).

Behaviors in paradigm A

In paradigm A (26 versus 33°C background), a total of 21 strikes (during 19 trials) were recorded with subjects in the control condition. Strike orientations for nine trials were directed towards the LTB walls while 12 strikes were directed towards the LCB walls, including two unsuccessful strikes. In the eyes-covered condition, snakes struck successfully 14 times with orientations towards the LTB walls and directed four strikes towards the LCB, two of which were unsuccessful. In the pits-covered condition, 10 strikes were directed towards the LTB walls, yielding six successful hits, and nine strikes were directed towards the LCB walls, including one that missed the target (Fig. 4A).

There was a significant correlation between strike orientation and pit condition (occluded versus non-occluded) in the control and eyes-covered conditions (Spearman and Pearson analysis, $P=0.03$). This correlation was greater ($P=0.01$) if unsuccessful strikes were not included. There was no significant correlation between strike orientation and eye condition (occluded versus non-occluded) when comparing the control and pits-covered conditions (Spearman and Pearson analysis, $P=0.55$). This did not change if unsuccessful strikes were not included in the analysis.

For snakes, differences in the ratio of time spent in specific sections did not reach statistically significant levels among the three occlusion modes (Kruskal–Wallis one-way analysis, $P=0.509$). A similar result was obtained for the mice (Kruskal–Wallis one-way analysis, $P=0.369$). For either the snakes or mice, no correlation was obtained between the ratio of time spent in specific sections and snake occlusion conditions (Spearman and Pearson analysis, $P>0.05$). Nevertheless, a highly significant negative correlation for time spent in specific sections existed between mice and snakes when the data from all three occlusion conditions were pooled (Spearman and Pearson analysis, $P<0.001$).

Behaviors in paradigm B

In paradigm B (26 versus 40°C background), snakes in the control mode launched a total of 18 attacks in 16 trials. Nine successful strikes and one unsuccessful strike were directed towards the LTB

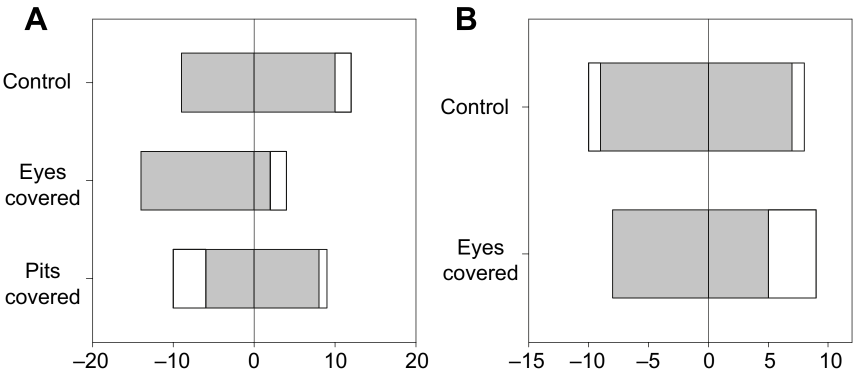

Fig. 4. Number of strikes occurring both toward and away from the low temperature background in the two behavioral paradigms. (A) Paradigm A. Positive values represent strikes toward the low contrast background (LCB, 33°C) and negative values represent strikes toward the low temperature background (LTB, 26°C). (B) Paradigm B. Positive values represent strikes toward the high temperature background (HTB=40°C) and negative values represent strikes toward the LTB (26°C). Gray bars indicate successful hits and white bars indicate unsuccessful hits.

walls, while seven successful strikes and one unsuccessful strike were directed towards the HTB walls. The snakes in the eyes-covered mode struck towards the LTB walls eight times without missing. Five successful and four unsuccessful strikes were directed toward the HTB walls (Fig. 4B).

There was no significant correlation between strike orientation and sensory occlusion condition (i.e. the control and eyes-covered conditions) using Spearman and Pearson analysis (P=0.63). This result did not change when the unsuccessful strikes were eliminated in the Spearman and Pearson analysis (P=0.78).

The ratio of time spent in specific sections was not significantly different for the snakes in the control and eyes-covered conditions (Mann–Whitney rank sum test, P=0.395). In addition, the Spearman and Pearson analysis did not reveal a significant correlation between time spent in specific sections and sensory occlusion conditions for snakes (P>0.05). No difference in section preference for mice could be found between the two snake occlusion conditions (*t*-test, P=0.086) and the ratio of time spent in specific sections for mice was not found to be correlated with snake occlusion condition (Spearman and Pearson analysis, P>0.05). The Spearman analysis showed a negative correlation for the ratio of time spent in specific sections between the snakes and mice (P=0.0325).

DISCUSSION

Sensory manipulations (i.e. occlusion conditions) seemed to have little effect on the motivation for attacking prey, which averaged 19.5 strikes launched by control snakes per experimental session and 18 strikes per session for snakes whose eyes or pits were occluded. All experiments were completed successively in 5 weeks with no obvious differences in behavioral response among weeks, i.e. the subjects displayed a similar motivation to launch attacks and achieved a similar percentage of successful strikes. Our previous study showed successful strikes in 63% of trials (Chen et al., 2012), close to the present 65% success rate. The latency from snake strike to mouse death across trials varied exceedingly, suggesting that the time between being struck and dying might be related to multiple factors, such as health status and metabolic rate of the mice and the amount of venom injected.

The primary prey of pit vipers are endothermic species, such as small mammals and birds. Despite substantial changes in the ambient temperature due to daily and seasonal factors, the homothermal systems of small mammals and birds maintain a body temperature that differs from the thermal background. The current experimental design used stable air temperature conditions, a constant foreground stimulus (the mouse) with a variable thermal background in order to simulate this aspect of natural scenes.

Neither the snakes nor the mice exhibited obvious preferences for situating themselves near either the heated or non-heated drum walls, although snakes and mice tended to stay apart. This is not unexpected, as the mice would be safer when farther from the snake. This ‘random settling’ could be considered as a ‘space baseline’ on which the strike orientation could be measured independent of the initial position of either the snake or mouse. Therefore, the strike orientation towards specific walls in the drum would presumably result from the snakes’ preference to target prey against a suitable thermal background. It has been proposed that pit vipers might select foraging sites where a minimized background temperature would maximize potential thermal contrast with prey (Shine et al., 2002). The pit vipers in our study preferred to stay and wait near the heated background wall (LCB and HTB). That way, it was beneficial for the snakes to launch an attack when prey moved in front of the low temperature background (Fig. 4).

Van Dyke and Grace (2010) measured orientations of the tongue flick, head turn and attack strike and found that a warm target elicited in-phase responsive patterns, a cool target evoked antiphase responsive patterns, while a target with a temperature similar to that of the background caused indiscriminate responses. As IR receptors (e.g. snake TRPA1; Gracheva et al., 2010) on the pit membrane are exclusively sensitive to the heat-responsive pattern, the cool foreground may cast an IR ‘shadow’, blocking IR signals emitted by the warmer background, which would therefore suppress the responses of the heat receptors (Goris and Nomoto, 1967). Therefore, removal of a cool object would be expected to elicit a response similar to the presentation of a warm stimulus, bringing about neuronal spike bursts (de Cock Buning et al., 1981b). Thus, in ‘positive contrast’ situations, pit vipers target the warmer object rather than the cooler background. In ‘negative contrast’ situations, pit vipers target the warmer background rather than the cooler target (Van Dyke and Grace, 2010).

Van Dyke and Grace (2010) kept the background temperature unchanged in their experiments and adjusted the foreground temperatures to be higher (36°C), lower (12°C) or the same (24°C) as the background. In the present study, we used live mice (33°C on average) as foreground stimuli and varied the background temperature to 26, 33 or 40°C. With functioning eyes and pits, the snakes totally missed two strikes in the low-contrast conditions, one in the positive contrast and one in the negative contrast condition, implying that thermal contrasts are important regardless of whether there is positive or negative contrast. In the eyes-covered condition in short-tailed pit vipers, the snakes preferred to launch more strikes under the positive thermal image contrast (77.8%) versus the no thermal contrast (22.2%) (Fig. 4A, middle bar). Such a preference did not exist in the control condition when comparing the positive and negative thermal image contrasts (Fig. 4B, lower bar). Unsuccessful strikes appeared exclusively when attacks were towards backgrounds of either no thermal contrast (50% failure) or negative thermal image contrast (44.4% failure). Similar results were obtained by Van Dyke and Grace (2010) in the eyes-covered condition for two copperheads, insofar as 13 strikes occurred under scenes of positive contrast, and all hit the target, while seven strikes occurred in negative contrast contexts, and all missed the target (Van Dyke and Grace, 2010). The pits-covered condition resulted in more total unsuccessful strikes than the eyes-covered condition did under the same thermal background contexts.

In conclusion, snakes preferred to target prey in front of backgrounds with positive thermal contrasts, but only in the eyes-covered condition (i.e. only with pits uncovered). When the IR system was unavailable (pits occluded), the IR system could not provide useful information (i.e. no information about thermal contrast) or it provided inaccurate information (reverse thermal contrast) and successful strikes decreased. These results are consistent with the view that the visual system in pit vipers does not work independently in targeting prey. Reversing thermal conditions between the foreground and background while maintaining the thermal contrasts had a slight effect on prey targeting in control snakes but substantially decreased attack efficacy when the eyes were occluded. Other measures of predation performance including the strike distance and the motion state of the animals might be related to individual constitutional and other environmental factors.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: Q.C.; Methodology: Q.C., G.F.; Investigation: Q.C., Y.L.; Writing - original draft: Q.C.; Writing - review & editing: S.E.B.; Supervision: Y.T.; Funding acquisition: Q.C.

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