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ORIGINAL PAPER

Behavioural examination of the infrared sensitivity of rattlesnakes (*Crotalus atrox*)

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Abstract Pitvipers (Crotalinae) and boid snakes (Boidae) possess highly sensitive infrared (IR) receptors. The ability of these snakes to image IR radiation allows the assessment of the direction and distance of an IR source (such as warm-blooded prey) in the absence of visual cues. The aim of this study was to determine the behavioural threshold of snakes to an IR stimulus. A moving IR source of constant size and temperature was presented to rattlesnakes (*Crotalus atrox*) at various distances (10–160 cm) from their snout. The snakes' responses were quantified by measuring distinct behavioural changes during stimulus presentation (head jerks, head fixed, freezing, rattling and tongue-flicking). The results revealed that *C. atrox* can detect an artificial IR stimulus resembling a mouse in temperature and size up to a distance of 100 cm, which corresponds to a radiation density of 3.35×10^{-3} mW/cm^2. These behavioural results reveal a 3.2 times higher sensitivity to IR radiation than earlier electrophysiological investigations.

Keywords Snake · Pitviper · IR sensitivity · Detection threshold · Behavioural study

Introduction

Crotaline snakes (e.g. rattlesnakes, bushmasters, bamboo vipers, etc.) as well as boid snakes (boas and pythons) can detect infrared (IR) radiation with their pit organs (e.g. Noble and Schmidt 1937; Bullock and Barrett 1968; de Cock Buning et al. 1981a; Molenaar 1992). These organs contain highly sensitive IR receptors, which respond to minute thermal fluctuations (Bullock and Diecke 1956; de Cock Buning 1983a, b; Molenaar 1992).

The major function of the pit organs is generally taken to be the detection of homoeothermic prey (e.g. Bullock and Diecke 1956; Goris and Nomoto 1967; Bullock and Barrett 1968; Barrett 1970; de Cock Buning et al. 1981b; Kardong and Mackessy 1991; Kardong 1993). This sensory system enables accurate predatory targeting, even in the absence of visual cues (Kardong and Mackessy 1991; Grace et al. 2001). The pit organs are also used for the spatial orientation of basking places (Krochmal and Bakken 2000, 2003; Krochmal et al. 2004), detecting predators (Greene 1992) or selecting a den site (Sexton et al. 1992). To better understand the possible functions of the pit organs, it is necessary to determine the sensitivity, and thus the functional range, of the IR sense.

Several electrophysiological investigations were performed on the IR sensitivity and detection thresholds of pitvipers. By flowing water over the pit membrane of Crotalus while recording from the trigeminal nerve, Bullock and Cowles (1952) and Bullock and Diecke (1956) determined a threshold of 0.003°C. Stimulation of the pit organ with IR-lasers revealed a threshold of 0.1 mW/cm^2 at the membrane (e.g. Goris and Nomoto 1967; Terashima et al. 1968; Moiseenkova et al. 2003). Recordings of the stimulation in the midbrain tectum of *Calloselasma* with a heating element revealed a threshold of 10.76×10^{-3} mW/cm^2 (de Cock Buning et al. 1981b; de Cock Buning 1983a, b). Calculated detection ranges span from 66.6 cm for a

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mouse whose body temperature was 10°C above ambient temperature (de Cock Buning 1983a) to less than 5 cm for a mouse-like stimulus at 37°C (Jones et al. 2001).

Several behavioural studies have addressed IR perception in snakes (e.g. Theodoratus et al. 1997; Grace and Woodward 2001; Grace et al. 2001). Early studies revealed the pit organs to be heat sensitive organs (e.g. Ross 1935; Noble and Schmidt 1937). Other behavioural investigations focused on prey detection (de Cock Buning et al. 1981a; Chiszar et al. 1986; Kardong and Mackessy 1991; Haverly and Kardong 1996; Grace and Woodward 2001; Grace et al. 2001) and the functional usage of the IR sense in the context of thermal regulation (Krochmal and Bakken 2000, 2003; Krochmal et al. 2004).

Young and Aguiar (2002) used behavioural changes during stimulus presentation as evidence for sensory perception in rattlesnakes in order to investigate the auditory system. A similar methodical approach is used in this study. Up to now, no behavioural study has explored the IR detection range of snakes. This study investigates the IR detection threshold (IR irradiance contrast of an object against the background at a critical distance) and the resulting sensitivity of the rattlesnake *Crotalus atrox* to a mouse-like stimulus using a behavioural approach. Behavioural studies have the advantage that the perception and processing of IR cues is reflected as a whole through the behavioural responses of the snakes, whereas electrophysiological studies focus only on certain aspects of the IR perception or processing.

Materials and methods

Animals

Twelve western diamondback rattlesnakes (*C. atrox*) (eight males and four females) were used for this study. Their ages varied from 4 to 12 months with snout-vent lengths of 45–80 cm. The rattlesnakes were captive bred or obtained from commercial dealers. The animals were housed individually in terrariums with a hide box as a shelter, ambient temperature of 28 ± 1°C and a 12-h light/12-h dark cycle. The snakes were provided with water ad libitum and maintained on a diet of one mouse every 10–12 days.

Experimental set-up

Animals were tested in a circular arena with a diameter of 200 cm (Fig. 1). A 100 cm high barrier made out of 1 cm thick white Styrofoam surrounded the arena and shielded the snake from unwanted IR stimuli.

A Peltier element (PKE 128 A 0021, Peltron GmbH, Germany) of 4 × 4 cm^2 was used as an IR stimulus source. Pre-trials had shown that a stationary IR stimulus hardly evoked behavioural responses. So, in order to present the Peltier element in motion, it was mounted at the lower end of a motor driven pendulum, which could be presented to the snakes at any position within the circular arena (see Fig. 1). The temperature of the Peltier element was adjusted to 34.4 ± 0.5°C, constantly monitored with a sensor (PT 100, Peltron GmbH, Germany; height 10 mm, width 2 mm), which was attached onto the surface of the Peltier element and connected to a thermal feedback control unit (PRG H75, Peltron GmbH, Germany) to keep the temperature constant. Previous recordings with a thermoscanner (AGEMA-Thermovision THV 450 D, resolution 0.1°C) revealed that the emitted body temperature of a mouse is between 34 and 35°C ($N = 3$) at the same experimental conditions. The IR radiation was controlled by a shutter (shielded with insulating Styrofoam), which was positioned in front of the Peltier element. When the shutter was closed the temperature in front of the shutter was 23.5 ± 0.5°C. The snakes had a body temperature of 24 ± 1°C (room temperature 23 ± 1°C) measured with an IR-thermometer (minitemp TM, Raytech, USA).

The distance between the snake's head and the IR source was measured to a precision of 0.5 cm. The pendulum with the IR source was attached to a sliding rail of a beam (cf. Fig. 1). The snakes were placed in a lockable hide box on a platform elevated 30 cm from

Fig. 1 Schematic sketch of the experimental setup. *1* IR source (Peltier element), *2* scale (100 cm), *3* perpendicular (not shown). *Arrows* indicate the moving directions of the Peltier element. *Inset* shows blindfolded snake on the platform

the floor in the centre of the arena for distances from 10 to 100 cm. For sessions with distances above 100 cm the platform position was changed towards one side of the barrier utilizing a minimum distance of 70 cm and a maximum distance of up to 160 cm. Overlapping distances (70–100 cm) were tested for reasons of comparability.

Exposure protocol

All snakes were blindfolded with a strip of black duct tape (Fig. 1, inset). Snakes were allowed to adapt to blindfolding for at least 1 day before testing. Only snakes that were not in ecdysis and had their last meal at least 2 days previous to testing were used for the experiments. To minimize habituation, each snake was tested at most every second day, and no session lasted more than 60 min.

The behavioural experiments were performed according to the following protocol: (1) Placement of a snake on the platform in the arena set-up, enclosed in a hide box, followed by (2) a 10 min adaptation phase before (3) the lid of the hide box was lifted. (4) Whenever the snake faced the Peltier element, the pendulum was set into a 0.5 Hz oscillation (oscillation amplitude 30 cm, speed 0.3 m/s) and the shutter was opened to expose the Peltier element for 10 s, before it was shut and the oscillation was stopped again. (5) The behavioural response of the snake was documented. (6) Thereafter, the distance between the Peltier element and the snake's head was arbitrarily varied between 10 and 100 cm and between 70 and 160 cm, respectively. (7) At most one IR stimulus per minute was applied. (8) A session was terminated, when the animal showed no behavioural responses to five consecutive stimuli, one of which had to be at a distance of less than 40 cm (test range 10–100 cm) and one less than 85 cm (test range 70–160 cm), or when the snake escaped from the platform. (9) After each session the hide box was cleaned with liquid soap and water and dried thoroughly to eliminate possible olfactory influences of the antecessor.

Evaluation criteria of behavioural responses

The behaviour of the snakes was scored as a response if a distinct change was observed while presenting the stimulus. The following behaviours were observed and evaluated:

Head jerks: The snake showed rapid lateral head movements towards the Peltier element independently of directed movements of the body during the 10 s of IR stimulus presentation.
Tongue-flicking: The snake showed directed tongue-flicking towards the Peltier element. Tongue-flicking could occur once or several times. In rare cases the tongue followed the movement of the pendulum.
Freezing: The snake paused abruptly for 2–10 s during body movement.
Head fixed: The snake was coiled up, but its head was in motion. It directed its head frontally to the IR source, stopped moving and fixed it, when given an IR stimulus.
Rattling: The snakes rattled at least once during the presentation of an IR stimulus, while their head was directed towards the heat element.

Since the measured responses are all part of the rattlesnakes normal behavioural repertoire, the incidence of these behaviours was determined during three control trials. These trials were performed with (1) oscillating pendulum but inactive heating element, (2) inactive heating element and fixed pendulum or (3) using an active heating element and oscillating pendulum but obscuring the pit organs with Styrofoam balls and tape. As a further control, a number of video records were scored twice, once by the experimenter and again by naive volunteers.

Results

The rattlesnakes *C. atrox* ($N = 12$) responded to the IR stimuli with a variety of behavioural reactions. Four main reactions were observed, which amount to 82% of all positively scored responses. These responses were stimulus directed tongue-flicking (29%), head jerks and tongue-flicking (22%), tongue-flicking and head fixed (16%), and head jerks in combination with tongue-flicking and head fixed (15%). Other combinations of behavioural responses including rattling and freezing did not exceed 3% occurrence in any combination.

During 130 experimental sessions the snakes ($N = 12$) were exposed to 1,705 IR stimuli, offered at distances between 10 and 160 cm. In 1,655 cases the snakes' responses could be scored unequivocally; the remaining 50 trials produced equivocal results and were not included in the data analysis. Of the 1,655 unequivocal trails, 760 trails produced a positive response. At distances of up to 100 cm ($10 \le N \le 12$) 80 sessions with 1,304 stimuli were conducted, and within the distance range of 70–160 cm ($7 \le N \le 12$) 50 sessions with 396 stimuli (see also Table 1). Data from these two separate acquisition sets was pooled for the overlapping distances (70–100 cm). The number of stimulus presentations in the two sets differs, i.e. they are not evenly distributed for each distance interval.

Positive responses (pooled in 10 cm distance classes) ranged from 67% (shortest source distance 10 cm) to 13% (farthest source distance 160 cm) (see Fig. 2). The relationship between source distance and response rate was not constant; the response rate held roughly constant between 50 and 80 cm source distance, and decreased sharply beyond the 100 cm source distance (Fig. 2). At 100 cm the response rate is significantly above ($\chi^2 = 12.202$, $df = 1$, $P = 0.0001$) the control level of 29% (see below), but beyond the 100 cm values the snakes' responses to the experimental stimuli cannot be distinguished from the control response ($\chi^2 = 0.301$, $df = 1$, $P = 0.787$).

Control experiments

As expected, individual snakes responded at different rates during the control trials. Overall, the following ranges of positive responses were observed: trials with oscillating pendulum but inactive heating element (0–29%), inactive pendulum and inactive heating element (0–22%) and with the pit organs blocked (0–13%). The highest positive response rate observed (29%) is taken as the control or baseline level.

Control of response assessment

In addition to the experimenter two further control persons independently assessed the behaviour of the snakes. Five snakes were exposed to 39 IR stimuli in five sessions. One person judged three cases (8%) differently from the experimenter and the second person two cases (5%). In all but one case the discrepancies in assessing the behavioural responses were judged more critically (i.e. "no response") by the experimenter.

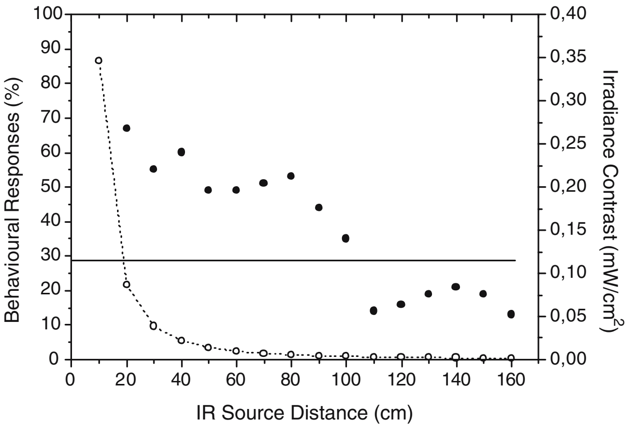

Fig. 2 Percentages of behavioural responses as a function of IR source distance (*black dots*). Class width was 10 cm. *Dotted line*: Irradiance contrast of the IR stimulus calculated in mW/cm^2 and plotted as a function of the distance. *Solid line*: Baseline of spontaneously occurring behaviour (i.e. non-stimulus-bound behaviour) resulting from control trial data

Habituation

The IR stimuli were presented at a distance of 30 cm ($N = 6$, $10 \le n \le 37$), 60 cm ($N = 6$, $7 \le n \le 29$), 90 cm ($N = 6$, $4 \le n \le 18$) and 120 cm ($N = 6$, $5 \le n \le 9$) (Fig. 3). All snakes ($N = 8$) habituated to the IR stimuli. The percentage of positive responses decreased with increasing stimulus number and with increasing source distance. However, the habituation curves of individual snakes differed. For instance, at a

Table 1 Overview of the databases for the analysis and control experiments

Experiment	Number of animals	Number of sessions	Number of IR stimuli settings	Remarks
IR detection range	12	130	1,655	Eighty sessions with 1,304 stimulus presentations (up to 100 cm) Fifty sessions with 396 stimulus presentations (from 70 to 150 cm)
Control experiment for hidden cues	9	9	108	Cold but moving Peltier element
Control experiment to assess spontaneous response-like behaviour	8	8	158	Fictive IR stimulus
Control experiment with blocked pit organs	4	8	201	IR stimulus presentations at close distances (=32 cm)
Habituation	6	24	292	Four constant distances (30, 60, 90, 120 cm)
Control of response assessment	5	5	39	

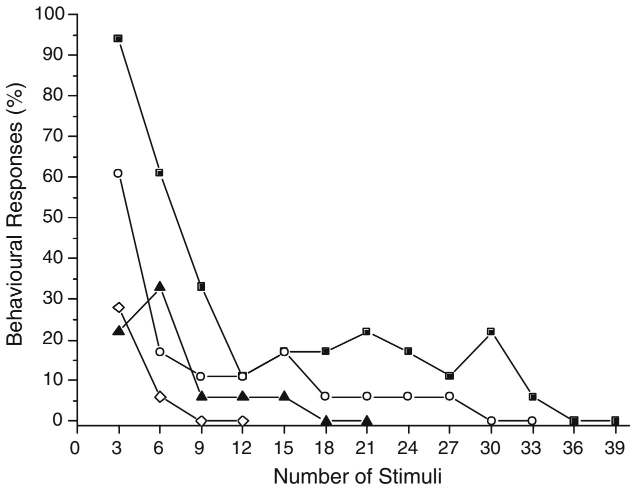

Fig. 3 Behavioural responses plotted as a function of repeated stimulation for four different distances. Note the response decrement to IR stimuli ($N = 6$, in each case three consecutive responses were pooled) at the distances 30 cm (*filled squares*), 60 cm (*open circles*), 90 cm (*filled triangles*) and 120 cm (*open diamonds*)

distance of 30 cm one snake responded to the first six stimuli in 67% of the cases, thereafter no responses occurred. At the distance of 30 cm another individual responded to the IR stimuli with the same percentage even after 30 stimulus presentations.

Discussion

This study was conducted to quantify the distance at which a rattlesnake behaviourally responds to a moving IR source resembling a mouse in temperature and size. The results revealed that rattlesnakes respond up to a distance of 100 cm. The positive behavioural responses were not randomly distributed over different distances, but rather decreased with increasing IR stimulus distance (Fig. 2). At a source distance of 100 cm the incidence of positive responses is still significantly above the baseline value for these behaviours, but beyond 100 cm the responses to the IR stimulus could not be distinguished from baseline (spontaneously occurring) behaviours.

One factor that could influence these results was the use of behavioural, rather than electrophysiological, data to determine the snake's response to the IR stimulus. A distinct behavioural change during the 10 s period of stimulus presentation was valued as a positive response to the IR stimulus. Independent blind scoring of the videos confirmed the accuracy of our evaluation of the responses as positive. Nonetheless, even if a snake senses a stimulus, it might not display a distinct behavioural response. Thus, the willingness for behavioural responses to stimuli was a crucial factor in the present study, because conclusions can only be drawn from positive reactions. Furthermore, a moving stimulus was essential to keep *C. atrox* motivated and responsive. *C. atrox* was used for this study to minimize this problem since it is a very alert and irritable species (e.g. Tennant and Bartlett 2000), which will display distinct behavioural responses to IR stimuli even while in their accustomed housing boxes.

Still, it cannot be ruled out that some IR stimuli were perceived, but did not evoke a behavioural response. Therefore, the actual detection threshold of *C. atrox* may be lower than determined by this study.

A second factor that could influence our experimental results is habituation. All rattlesnakes habituated to IR stimuli, with habituation increasing over the course of a session with increasing number of stimuli (Fig. 3). The snakes might have learned that IR stimuli were neither harmful nor an indication of prey. It should be noted that there were large inter-individual differences. While some snakes habituated rapidly other snakes continued to respond to the IR stimuli. This confirms that response readiness is not only a function of the IR stimulus applied, but also a function of the general response readiness of the snake. In general, habituation increased with increasing source distance. This also indicates that the drop of responsiveness with source distance is more an issue of motivation than of IR perception sensitivity. In terms of the present study it is important to note that habituation would produce false negative, not false positive results, and thus would lead to an underestimation of the snake's IR sensitivity range.

A third factor that could influence the results of this study is the artifice of the IR stimulus, including its constant speed and constant amplitude as well as the square-typed form and the almost homogenous thermal profile of the IR emitter. The area of the temperature regulatory sensor covered about 1% of the upper edge of the IR emitter and, although only 0.2 mm thick, might have thermally insulated this area marginally affecting the homogenous profile. In contrast, a mouse shows a heterogeneous and constantly changing thermal profile based on numerous minute thermal gradients (unpublished observations with IR camera recordings). A biological IR stimulus presented in a natural environment may be more likely to evoke a behavioural response. However, defined physical stimuli and defined experimental conditions were necessary for the determination of behavioural threshold levels. Furthermore, a defined artificial stimulus ensures the exclusion of other hidden sensory cues (e.g. olfactorial cues). The temperature of the stimulus was similar to that of a mouse and it was in motion, fulfilling two requirements in order to evoke a response. The fact that these highly reactive snakes rattled during less than 3% of the trials suggests that the IR stimulus was not so artificial as to startle the rattlers.

The irradiance contrast of the presented IR stimulus was calculated for the distance range 10–160 cm using a modified Stefan–Boltzmann formula (see de Cock Buning 1983b). The irradiance contrast is the temperature contrast between stimulus and background.

$$\text{Irradiance contrast}\,(\mathrm{W/cm^2}) = \frac{\sigma A(T_2^4 - T_1^4)}{\pi D^2},$$

where σ is Stefan–Boltzmann constant [5.6522×10^{-12} $\mathrm{W/(cm^2\,K^4)}$]; A, radiating area ($4 \times 4\ \mathrm{cm^2}$); T_2, temperature (°K) of heat exchanger (34.4°C = 307.55 °K); T_1, temperature (°K) of the shutter (23.5°C = 296.65 °K) and D is the distance (from 10 to 160 cm).

Thus, the temperature difference between the IR source and the shutter (T_2–T_1) as well as the radiating area (A) of the IR source determines the irradiance contrast at the critical distance (D) to the snake. The temperature of the IR stimulus (34.4 ± 0.5°C) and the shutter (23.5 ± 0.5°C) revealed a difference of 10.9 ± 1°C. Taking the size of the IR source (16 $\mathrm{cm^2}$) into account at distances from 10 to 160 cm, the calculated irradiance contrasts range from 0.3463 ± 0.0335 to 0.0014 ± 0.0002 $\mathrm{mW/cm^2}$, respectively (see Fig. 2). Viewing the curve of the irradiance contrast it is conspicuous that the decline of the positive responses is not aligned to it. The sharp drop of responses at a distance of about 100 cm has no relation to the decline of irradiance contrast. As this is a typical characteristic progression for sensory response curves (Bleckmann 1980), the percentage of positive responses is rather related to motivation than sensitivity of the snakes to the stimulus.

Crotalus atrox detected the IR stimuli up to a distance of 100 cm (Fig. 2). In the theoretical model of Jones et al. (2001), the size and surface temperature of a mouse and the absorption of the atmosphere of IR radiation were taken into account to calculate the respective detection distance. According to their model the temperature of the membrane surface increases at the threshold of 0.003°C [depicted by Bullock and Diecke (1956)] at a distance of 5 cm. The detection distance in our study exceeds this value about 20 times. Furthermore, it also exceeds the calculated detection range of 66.6 cm proposed by de Cock Buning (1983a). The responses of tectal neurons of the pitviper *Calloselasma rhodostoma* were examined at different IR source distances. The threshold level of 10.76×10^{-3} $\mathrm{mW/cm^2}$ was calculated with a modified Stefan–Boltzmann formula. Applying the same formula in the current study, the irradiance contrast of the behavioural IR threshold of *C. atrox* is 3.35×10^{-3} $\mathrm{mW/cm^2}$ at a distance of 100 cm. Thus, this study presents the lowest threshold value reported for any IR sensitive snake and any IR sensory system known in animals so far (compare Campbell et al. 2002). For *Calloselasma*, de Cock Buning (1983a) calculated a value of 10.76×10^{-3} $\mathrm{mW/cm^2}$, i.e. a value that is 3.2 times larger. This difference might be due to the different species used in the study but more likely reflects differences in the methodology (behavioural vs. electrophysiological investigation). In addition, the stimulus in the present study was moving and presented for 10 s, whereas in de Cock Bunings study a stationary stimulus was presented for 3.6 s. As can be deduced from the Stefan–Boltzmann formula, neither the time of IR stimulus presentation nor the velocity of movement within the receptive field influences the irradiance contrast of the IR stimulus. In the current study, the motion of the IR stimulus was necessary to evoke a behavioural response. In contrast, a moving stimulus is not necessary to evoke an electrophysiological response recorded from the peripheral receptor, the afferent nerve or the primary sensory area (midbrain tectum) within the central nervous system.

The link between the different methodologies is the calculation of a detection threshold using the modified Stefan–Boltzmann formula, which necessitates a critical distance, the size of a stimulus as well as the temperatures of a stimulus and its background. The method of determining these factors differs, considering whether single neurons and neural pathways in anaesthetized snakes were investigated (electrophysiological) or whether an intact sensory system of an alert snake was tested (behavioural). Behavioural thresholds are usually lower than physiological thresholds (e.g. Bleckmann 1994), which are confirmed by the results of this study. They indicate that the IR detection threshold of rattlesnakes is lower and the detection range for a mouse-like stimulus farther than assumed so far. The design of this experiment suggests that some IR perception did not lead to a positive response, as such this study most likely under-reports the IR sensitivity and detection threshold in rattlesnakes.

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