RATTLESNAKE ORIENTATION TO PREY AS A FUNCTION OF THERMAL BACKGROUND AND EDGES

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Three experiments investigated the effects of thermal background on orientation of western diamondback rattlesnakes (Crotalus atrox) to prey. In Experiments 1 and 2, the snakes responded more strongly to rodent prey in front of cool backgrounds than to identical prey in front of warm backgrounds. Accordingly, we suggest that the pitviper infrared system exhibits contrast effects such that rodent prey at approximately 37 °C are detected more readily if the background is of significantly lower temperature than if it is of higher temperature. Experiment 3 created a thermal background containing an edge between panels at different temperatures (15 °C and 21 °C). Models of prey were placed in front of each panel and at the border between them. Snakes oriented more to the border model than to either of the others, suggesting that the edge was of special significance. In human visual studies, edges between panels varying in brightness give rise to Mach bands which enhance the salience of the edges. Perhaps an analogous phenomenon occurs in the pitviper infrared system.

The ability of pitvipers (family Viperidae, subfamily Crotalinae) to detect thermal (infrared) cues arising from endothermic prey is well documented, especially during the initial (prestrike) stages of predatory episodes (see Molenaaar, 1992, for a review). The facial pits, characteristics of all crotaline snakes, were first shown to be sensitive to thermal stimuli by Noble and Schmidt (1937) and have since been studied with modern electrophysiological techniques (Bullock & Dieke, 1956; Goris & Nomoto, 1967; Terashima, 1987), revealing that pit nerve fibers are capable of discriminating stimuli differing by a few thousandths of a degree Celsius. In a summary of this research area, Cock Buning

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(1983) pointed out that all available neurophysiological information suggests that a rodent 6 °C above ambient temperature probably can be detected by pit nerve endings at a distance of 25-30 cm, with the detection distance changing as a direct function of the thermal differential between target and ambiance. Although there is no reason to question the general features of Cock Buning's calculations or the conclusions he reached from them, it must be recognized that he worked with neural recordings from anesthetized preparations and that no standardized paradigm exists for studying pitviper predatory behavior as a function of thermal stimuli. Therefore, confirming Cock Buning's predictions with unanesthetized snakes will not be a straightforward matter, particularly when the ectothermic nature of snakes is considered. Manipulation of ambient temperature is likely to alter the body temperature and metabolic rate of the snakes, influencing their inclination to attack or ingest prey and, hence, their orientation response in test situations.

The lack of a standardized paradigm caused us to develop analogues to the methods used by Heinemann (1955, 1972) to study brightness contrast in humans. Heinemann used a disk surrounded by a concentric background, the luminance of which could be varied. As the luminance of the background approached that of the disk, the latter was perceived as increasingly dark (i.e., incorrectly perceived as lacking luminance). Instead of varying ambient air temperature as crotalines were studied responding to prey, perhaps prey could be presented in front of disks varying in temperature. Cast iron disks were heated or refrigerated, and freshly euthanized weanling rats were suspended in front of them. Such assemblies were placed directly in front of snakes' cages. If detection of a warm rodent carcass is influenced by the thermal properties of the surrounding background as argued by Cock Buning (1983, see especially his Fig. 2), then stronger responses should be seen when the carcass is in front of a cool disk than when an identical carcass is in front of a warm one. Experiment 1 confirmed this prediction, showing that thermal contrast effects occurred within the infrared sensory system of pitvipers. Experiment 2 used a convergent methodology to generate additional confirmatory evidence. Finally, Experiment 3 provided initial evidence for the existence of Mach-band-like effects created by thermal edges.

Experiment 1

Method
Subjects were eight adult western diamondback rattlesnakes (Crotalus atrox), all adults ranging in snout-vent length from 60-90 cm. All had been in captivity and feeding on weanling rats for at least one year prior to the present study. Snakes were kept singly in glass terraria (61 x 31 x 43 cm) with wire screen tops. Cages contained newsprint floor coverings and a stainless steel vessel filled with water. The laboratory
photoperiod began at 0700 and ended at 1900. Air temperature was kept at 26 °C ± 1 °C by a solid state unit controlling a hot water heating system. Snakes were offered one weanling rat weekly and virtually all prey were always accepted by all snakes. The present trials were run prior to regularly scheduled feeding sessions, and intertrial intervals were one week. Hence, snakes always had seven days of food deprivation before being observed in this experiment.

Stimuli were freshly euthanized weanling rats and iron disks (26.5-cm diameter) with 11-cm handles that fit into a hole drilled into a 35.5-cm length of wood (8.5 x 8.5 cm). When the handle was inserted into the wood, the latter served as a stable platform that held the disk firmly when placed next to a snake's cage. A disk refrigerated overnight was 12.5 °C upon removal from the refrigerator. Upon exposure to laboratory air temperature, the disk gradually warmed as shown in Table 1. A disk heated over a Coleman heater warmed rapidly to 75 °C, and then cooled gradually upon removal from the flame. Nevertheless, as shown in Table 1, the cool disk remained cooler than a euthanized rat and the warm disk remained warmer than the rat, even after 30 min of exposure to lab air temperature. Our trials lasted 10 min and began when stimuli were at the starting temperatures of Table 1.

Table 1

<table>
<thead>
<tr>
<th>Stimulus Temperatures (°C) at Successive 5-Min Intervals after Beginning Exposure to Ambient Laboratory Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stimulus</td>
</tr>
<tr>
<td>Start</td>
</tr>
<tr>
<td>5</td>
</tr>
<tr>
<td>10</td>
</tr>
<tr>
<td>15</td>
</tr>
<tr>
<td>20</td>
</tr>
<tr>
<td>25</td>
</tr>
<tr>
<td>30</td>
</tr>
</tbody>
</table>

The experiment was a 2 x 3 combination of absence vs. presence of a freshly euthanized rat with temperature of the disk (starting temperatures: 12.5 °, 26.0 ° and 75.0 °C). All rattlesnakes were exposed at the rate of one trial per week to each of the six treatment combinations, and a different random order was used for each snake. When a disk of the appropriate temperature was prepared, a euthanized rat was attached to it (or not) by clamping the rodent's tail to the edge of the disk opposite the handle. Thus, when the handle was inserted into the wood block, the rat was suspended downward from the top of the disk such that the rat's body was centered within the disk. Because infrared waves have high transmission through standard window glass (Lerman, 1980), the stimuli could be placed outside of the snakes' cages without significant distortion of thermal cues. Thus, the assembly was
immediately placed directly next to a snake's cage and left there for 10 min during which the observer, sitting behind a plywood blind, recorded the duration of orientations by the snake to the disk. A positive score resulted when a snake oriented directly toward the disk.

**Results**

During the first five minutes of the tests, rattlesnakes generally exhibited defensive behavior (rattling their tails loudly) and ignored the experimental stimuli. However, all snakes relaxed by Minute 5 and orientations toward the stimuli were seen thereafter. Table 2, therefore, presents mean number of seconds spent oriented to stimuli during Min 6-10 of the trials. Because of heterogeneity of variance, data were subjected to a natural log transformation [\(\ln(\#\text{sec}+1)\)] and transformed scores were used in statistical analyses. The critical aspect of the results is that the interaction between a freshly euthanized rat in front of a cool disk received more attention than did any other condition \((F = 7.42, df = 2,14, p < 0.05)\). Disks without rats were not effective in attracting the attention of rattlesnakes. Likewise, disks with rats were ineffective if the disks were warm or at ambient temperature. In fact, the only condition in which orientation scores differed significantly from zero was the cool disk plus rat \((t = 3.03, df = 7, p < 0.05)\).

**Discussion**

Evidence for thermal contrast was provided by the fact that a euthanized rat in front of a cool disk commanded snake attention more than any other condition. Disks without rats elicited little or no orientation. Because visual characteristics were constant across the three conditions in which rats were present, it seems reasonable to infer that thermal cues were responsible for the effect reported here. If the chemosensory system was involved, we would expect the rat in front of a warm disk to be most effective in eliciting rattlesnake attention, as this disk would encourage greater volatilization of molecules. Because rattlesnakes did not orient towards the stimulus assembly in this condition, it is unlikely that chemical cues played a role, lending further support to our assertion that thermal contrast occurred in this experiment.

<table>
<thead>
<tr>
<th>Disk Temperature</th>
<th>Cool</th>
<th>Ambient</th>
<th>Warm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euthanized Rat</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>1.46 ± 1.5</td>
</tr>
<tr>
<td>Absent</td>
<td>(0.0 ± 0.0)</td>
<td>(0.0 ± 0.0)</td>
<td>(0.38 ± 0.33)</td>
</tr>
<tr>
<td>Euthanized Rat</td>
<td>21.6 ± 12.3</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Present</td>
<td>(1.99 ± 0.65)</td>
<td>(0.0 ± 0.0)</td>
<td>(0.0 ± 0.0)</td>
</tr>
</tbody>
</table>

*Note.* Means of natural logs are given in parentheses, ± SE.
No evidence for thermal contrast was observed in the condition involving a rat in front of a disk at ambient temperature, though that disk was on average 8.5 °C cooler than the euthanized rat. Hence, it may be that thermal contrast in our situation requires a disk that is more than 8.5 °C cooler than the prey, and it will be important to determine this threshold in subsequent experiments. It is also possible that adaptation of thermally sensitive receptors occurs in a nonfluctuating ambient temperature long experienced by the snakes, such that the infrared system is less sensitive to contrast effects when the background disk is at the customary ambient level (Hensel & Schäfer, 1981). In any case, the 18.6 °C average difference between rat and cool disk elicited unambiguous orienting responses in the rattlesnakes and thereby provided evidence of thermal contrast.

Experiment 2

This alternative methodology presented pairs of stimulus assemblies to rattlesnake with one assembly on each side of the snakes' cages. Warm and cool disks, each with a freshly euthanized rat, were presented to the snakes in this choice test. The prediction, based on thermal contrast, is that the latter disk-rat assembly should elicit more orientation time than the former.

Method
Snakes were six western diamondbacks, drawn randomly from the colony used in Experiment 1. Maintenance conditions were the same as those described in Experiment 1, as were procedures for preparing stimulus assemblies. A major difference between the experiments was the use of videotape for recording data in Experiment 2. The presence of an experimenter, even behind a blind, elicits defensive behavior from diamondbacks. Our intention was to eliminate this factor by taping each session, so that the experimenter could leave the colony room once the trial initiated. A Panasonic S-VHS videorecorder was mounted on a Brogen tripod (Model 3001), and the recorder was activated as the stimuli were placed on either side of a snake's cage. Upon being assured that the recorder was operating properly, the experimenter left the colony room for 20 min, until the trial concluded. Hence, 20 min of videotape was recorded for each snake and later viewed on a TV monitor. Each tape was scored for the duration of orientation by the snake to each stimulus assembly. Snakes were deprived of food for one week prior to this experiment. Because stimulus assemblies were 180° apart, an angle larger than the infrared receptive field of the snakes, orientation events were easy to score (Terashima, 1987).

Results
The mean number of seconds that snakes were oriented towards the warm disk plus rat was 71.3 ($SE = 41.9$), and the mean for the cool disk
plus rat was 269.3 (SE = 93.7). This difference was evaluated by converting each snake's scores to percentages by diving the sum of the two scores into each of the scores. The mean percent of time snakes were oriented toward the cool disk was 85.3%, and this value was compared to 50% by a single sample t test (t = 6.12, df = 5, p < 0.01). Moreover, the t test remained significant when percentages were converted to arcsines, logits, and probits, which are all useful transformations for reducing skewness sometimes present in percentage data (Table 3).

Table 3

<table>
<thead>
<tr>
<th>Variable</th>
<th>Statistic</th>
<th>Percent</th>
<th>Arcsine</th>
<th>Probit</th>
<th>Logit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>85.3</td>
<td>2.50</td>
<td>1.47</td>
<td></td>
<td>2.89</td>
</tr>
<tr>
<td>SE</td>
<td>5.75</td>
<td>0.22</td>
<td>0.44</td>
<td></td>
<td>1.00</td>
</tr>
<tr>
<td>Ho</td>
<td>50.0</td>
<td>1.57</td>
<td>0.00</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>t(df = 5)</td>
<td>6.12*</td>
<td>4.23*</td>
<td>3.34*</td>
<td></td>
<td>2.89*</td>
</tr>
</tbody>
</table>

* p < 0.05

Discussion

As in Experiment 1, the stimulus assemblies were visually identical and chemically favored the warm disk because of increased volatilization of chemical cues. Yet, the cool-disk-plus-rat generated significantly more orientation in the rattlesnakes, again leading to the conclusion that the rat was more readily detectable against the cool background because of thermal contrast.

Another version of this experiment would use pairs of stimulus assemblies, but each paired comparison would contain a disk at room temperature (plus a rat). Hence, the efficacy of the cool disk would be compared with a room temperature disk, as would the warm disk. Although we have not done this experiment, several pilot trials were conducted, and snakes oriented more toward the cool disk than toward the room-temperature one. When a warm disk was paired with a room temperature disk, there was no difference in orientation times. Hence, although we have not completed this experiment, the preliminary results agree completely with those produced by Experiments 1 and 2, and we are all the more confident in concluding that rattlesnakes' infrared receptors give rise to thermal contrast effects analogous to the brightness contrast effects so well known from human vision research.

Experiment 3

Mach bands represent a special form of brightness contrast occurring at borders of adjacent visual stimuli differing in luminance (reviewed in Fiorentini, 1972). Ernst Mach noticed in such cases "that
there appears to be a brighter band on the bright side of the edge, and a
darker band on the dark side. Hence, the brightness contrast at the edge
is greater in our perception than it is in the physical intensity distribution
itself. The edge has been enhanced” (Haber & Hershenson, 1973). These illusory contrast effects can be taken as an example of the
constructive (or adaptive) nature of perception, and they have inspired
an enormous amount of research so that we now understand the
dependence of the phenomena upon the concentric organization of
excitatory regions and lateral inhibitory surrounds, making up neuron
receptive fields in the retina (Cornsweet, 1970; Ratliff, 1965). Crotaline
infrared receptors project to the tectum, whence receptor cells also
contain excitatory centers and lateral inhibitory surrounds (Hartline,
1974; Hartline, Kass, & Loop, 1978; Haseltine, 1978). In recent years,
the interactions of visual and infrared receptors have been of greatest
interest to investigators (Berson & Hartline, 1988; Goris & Terashima,
1973; Hartline et al., 1978; Terashima & Goris, 1975), giving rise to the
discovery of several classes of bimodal cells in the tectum (Newman &
Hartline, 1981). On balance, all of this interest in modality interaction has
forestalled analysis of interactions between excitatory and inhibitory
afferents within either the infrared or the visual system. That is, no study
has yet tested for the presence of Mach bands in either modality. The
present experiment is an attempt to externalize Mach bands in the
infrared system.

Our reasoning was encouraged by the thermal contrast effects seen
in Experiments 1 and 2. If the border between adjacent stimuli differing
in temperature is enhanced by the organization of the receptive fields
within the infrared system, then a rattlesnake might investigate the
border area more than it investigates either of the adjacent panels of
uniform temperature. It is well known, for example, that humans viewing
pictures spend more time fixating on parts of the picture containing high
information, such as edges, contours and other features exhibiting
brightness contrast (Mackworth & Morandi, 1967). Although many
variables influence information content of a visual scene, brightness
contrast effects are certainly among the more important ones, and they
unquestionably command fixation time. Thus, it may be reasonable, by
analogy, to expect rattlesnakes to attend more to thermal borders than to
uniform thermal planes.

A question of some importance arises immediately, however, because our goal is not simply to study fixation time but to infer an
underlying perceptual process. A border will always be more informative
than a uniform plane because the former contains two pieces of
information (e.g., 2 temperatures ) whereas the latter contains only one.
Hence, a snake may focus more on the border, not because Mach bands
are perceived, but simply because the border has more information than
does either of the adjacent panels. To deal with this problem we argue
that the thermal display formed by two equal-size panels will have a
distribution of information in the ratio of 1:2:1, provided that border area
is approximately equal to the distal areas of the two panels and that each panel is of uniform temperature. Under these conditions, viewing time should be distributed in the ratio of 1:2:1 if viewing time is simply a function of information content. That is, variation in thermal information should produce a bias toward the border such that the snake should spend 50% of its viewing time there and 25% at each of the distal areas. In contrast, if the border has even greater information value because of Mach-band-like contrast effects, then orientation towards it should exceed 50% of the total. Therefore, we suggest that orientation toward the border in excess of 50% would constitute evidence suggestive of infrared perceptual processes akin to Mach bands.

**Method**

Six *Crotalus atrox* from our colony (*N* = 10) were randomly selected as subjects. Maintenance conditions were identical to those described in Experiment 1. The Panasonic videotape system was again used to record data during 20-min trials, as in Experiment 2.

Two glass aquaria (25 x 15 x 21 cm) were used to create thermal stimuli and a border. The aquaria were filled with ice and water to bring one bath to 15 °C and the other to 21 °C. The aquaria were placed next to each other, creating a display that was 50 cm long, which we divided into three sections, each 16.6 cm long. Hence, one section was uniformly 15 °C, one was uniformly 21 °C, and the center contained the border and 8.3 cm of each aquarium. The aquaria and the rattlesnake cage were placed on separate carts and were positioned parallel to one another with 5 cm separating the aquaria and the cage. The videotape system recorded the snake’s movements from the rear of its cage so the scene contained the snake’s head plus the full thermal display.

To generate interest in the aquaria, we needed to add mammal prey. However, warm rodents against these cool backgrounds would undoubtedly create confounding contrast effects, perhaps of sufficient magnitude to overwhelm the edge effect we sought to measure. Accordingly, we used artificial rodents made of tanned rabbit hide and purchased from a local pet store (where the items are sold as cat toys). Three of these (all, of course, at ambient temperature) were mounted on the thermal display, one in the center of each of the three sections. Hence, one of the cat toys was directly in front of the border, and the other two were in the center of each distal section. The toys were suspended by their tails from the tops of the aquaria such that the toys lay directly against the outside surface of the aquarium glass.

After the display and snake cage were in place, the videorecorder was activated and the experimenter withdrew from the colony room. A 20-min segment of videotape was recorded for each snake, and the tapes were later scored by a group of three judges for snake orientation to each of the three sections of the thermal display. Only direct orientations toward rodent models were scored. Interobserver agreement was higher than 90% for all three pairwise comparisons among observers.
Results

Scores for each snake were converted to percentages by dividing orientation score to each segment by total amount of time oriented to all segments. Mean percent of time oriented to the center segment was 69.9% ($SE = 5.52$), and this value was significantly higher than the null hypothesis value of 50% (single sample $t = 3.59, df = 5, p < 0.05$).

Table 4 reveals that orientation to center was significantly greater than the expected value not only for raw percent data, but also for transformed data.

![Table 4](image)

Discussion

Rattlesnakes investigated the border between two thermal planes at a rate greater than we would expect based only on the information content of the display. Hence, we conclude that the border gives rise to perceptual processes that enhance its stimulus value. Inasmuch as Mach bands are our visual analogue, we suggest that Mach-band-like effects arise in the infrared system.

Many experiments remain to be done, however. For example, it is necessary to repeat the present study with different combinations of temperatures in the two aquaria. The border effects reported here should occur across a range of temperature differentials. A useful control would have the two aquaria at the same temperature to make certain that the spatial arrangement of the display does not bias snakes to focus upon the center even when no thermal border is present there. We doubt that this is a problem because it did not occur during pilot observations. Nevertheless, systematic experimental evidence is desirable. Finally, it should be possible to observe border effects with other thermal stimuli, such as lasers or electrically controlled ceramic tiles. Not only would experiments using these stimuli provide evidence convergent with the present data, the more refined technology of the new experiments would pave the way to more precise exploration of the border effects.

General Discussion

In the absence of language, it is extremely difficult to confirm visual
or infrared Mach bands in behavioral experiments, as nonverbal data can provide only indirect evidence subject to alternative interpretation. The only strategy that can lead to unambiguous results is electrophysiological recording from units in the receptive fields. We take the present results as justification for such work.

Although Experiment 3 is suggestive rather than confirmatory of Mach bands within the infrared system of rattlesnakes, Experiments 1 and 2 leave little doubt that thermal contrast effects occur. These, in themselves, represent a type of perceptual enhancement in that warm-bodied rodents are made to "stand out" more boldly in cool ambient air than in warmer air. Because rodent-specializing rattlesnakes are crepuscular or nocturnal (Klauber, 1956), they generally hunt when rodent bodies are well above ambient temperature, such that thermal contrast constitutes an adaptive process increasing the probability of detecting and striking prey. Hence, we take the results of Experiments 1 and 2 to support the predictions of Cock Buning (1983, 1985) as well as his theoretical view of the infrared system as specialized "warm receptors" (Cock Buning, Terashima, & Goris, 1981).

Mach bands would serve to enhance localization and striking of warm targets because sharpened borders between prey and surrounding air creates a clearer target, particularly at night when visual cues are of limited utility. Indeed, it is possible that the thermal contrast effects seen in Experiments 1 and 2 were in part dependent upon enhancement of borders between prey and the surrounding air. Also, Bosch (1983) demonstrated that rodent bodies feature many pronounced isotherms, especially centered around their eyes and ears. These isotherms viewed through an infrared image system most probably create edge effects between the rodent's head and thorax. Pacific northwest rattlesnakes (*Crotalus viridis oreganus*) struck preferentially this boundary region of rodent prey (Kardong, 1986). Because rodents bitten there died more quickly than rodents struck more posteriorly, use of edge contrasts to identify prey and to strike would give crotalines a significant performance advantage (Arnold, 1983) that should be explored in both field and laboratory studies (Greene, 1986).

References


