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Source: *Northwestern Naturalist*, Vol. 74, No. 1 (Spring, 1993), pp. 1-9

Published by: Society for Northwestern Vertebrate Biology

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## STIMULI INFLUENCING THE RELEASE AND AIM OF PREDATORY STRIKES OF THE NORTHERN PACIFIC RATTLESNAKE (*CROTALUS VIRIDIS OREGANUS*)

WILLIAM K. HAYES AND DANETTE M. HAYES

**ABSTRACT**—This study examined the relative importance of visual, chemical and thermal stimuli for releasing predatory strikes of the northern Pacific rattlesnake (*Crotalus viridis oreganus*). In experiment 1, adult snakes deprived of food for 30 days or longer were randomly presented four stimulus conditions (1/day) combining visual, visual-chemical, visual-thermal and visual-chemical-thermal stimuli in moving models resembling mice. Experiment 2 replicated experiment 1 except that snakes were deprived of food 9 days and a fifth condition, live mice, was added. The number of strikes elicited by each condition suggested that visual cues alone were ineffective releasers of the strike, the addition of thermal cues dramatically increased the likelihood of attack, and the presence of chemical cues was not essential for striking. However, differences between the two experiments suggested that the contribution of chemoreception to prestrike behavior increased with prolonged food deprivation. The most effective strike-releasing conditions were struck more quickly and after fewer tongue flicks than less effective conditions, but tongue flick rates (recorded only in experiment 2) did not differ between conditions. Increased length of food deprivation appeared to decrease the latency to strike. Most models were struck in anterior regions, which suggested that directional movement contributed to the strike aim. The proportion of models envenomated during the strike differed between two model conditions, implying that rattlesnakes possess control over the mechanics of venom injection.

The sequential aspects of prey acquisition by rattlesnakes have been well documented in laboratory studies. Rodents, the favored prey (Reinert et al. 1984; Duvall et al. 1990; Rowe and Owings 1990; Wallace and Diller 1990), are killed with an envenomating strike, during which variable quantities of venom are injected into prey (Hayes 1991, 1992a, 1992b, 1993). Adult mice are usually released immediately after being struck to avoid retaliatory injury (Kardong 1986b) and may wander five meters or more before immobilization and death (Hayes and Galusha 1984; Kuhn et al. 1991; Hayes 1992a). Subsequently, the dispatched prey are relocated by strike-induced chemosensory searching, which allows the snake to follow the trail of and relocate the envenomated rodent (Chiszar et al. 1983; Furry et al. 1991).

The proximate factors which release this series of events, specifically those which release the strike, remain unclear. Noble and Schmidt (1937) first demonstrated that the facial pits of crotalines are thermoreceptors, presumably involved in the detection and striking of warm-blooded prey. Subsequent studies (Dullemeijer 1961; Cock Buning et al. 1981; Cock Buning 1983) confirmed the use of thermal (=infrared) as well as visual cues in prey attack. Several investigators (Chiszar et al. 1976; Chiszar and Radcliffe 1977; Chiszar and Scudder 1980) suggested that visual and/or thermal cues mediate orientation and striking of prey, and that chemoreception is essential only for poststrike events. Gillingham and Clark (1981), however, found that rattlesnakes may utilize chemosensory information for relocating prey which has moved out of sight or beyond striking range. Further, Graves and Duvall (1985) demonstrated that avomic rattlesnakes (with vomeronasal organs sutured closed) failed to strike and consume prey while sham surgery

subjects did so, and concluded that prey derived chemical cues contribute significantly to both prestrike and poststrike behavior (see also Duvall et al. 1985, 1990).

Thus, the relative importance of the various stimuli which release rattlesnake predatory strikes remains unclear. The purpose of this study was to test experimentally the hypothesis that visual and thermal cues are much more important than chemical cues in releasing and guiding the aim of the predatory strike of the northern Pacific rattlesnake (*Crotalus viridis oreganus*). In the first experiment, we manipulated the presence or absence of visual, chemical and thermal cues on moving models of mice to see which stimuli were most likely to elicit strikes from snakes deprived of food at least 30 days. We repeated the study in the second experiment with well-fed snakes deprived of food for only nine days.

## MATERIALS AND METHODS

### *Experiment 1*

*Subjects and maintenance.*—Twenty-four adult rattlesnakes of both sexes were maintained in groups of eight or fewer in three large pens (1–1.5 m<sup>2</sup> floor space). Although several were three-year captives, most were collected three months prior to the study, all from Walla Walla Co., Washington. Paper floor coverings, some rocks and water *ad libitum* were provided in each pen. Temperature was 25–35°C during a 14:10 L:D cycle. Prior to the study the snakes consumed live mice on an irregular (1–2 per month) basis. Snakes were normally transferred by snake hook to 38 liter aquaria to be fed individually.

*Stimulus conditions.*—Model mice were prepared by rolling paper toweling into a cylinder 4.6–6.0 cm long × 2.2–2.8 cm diameter. White cheesecloth was then wrapped around the cylinders (*cf.* Hayes and Duvall 1991). Final mass was 5.5–7.5 g. A 70–90 cm white string was tied to one end of the model for presentation to the snakes.

Although there are seven possible combinations of prey stimuli, only four stimulus combinations were tested because it is experimentally difficult to present snakes with moving models of exclusive thermal, chemical or thermal-chemical stimuli. Visual models (V) had no mouse odors and were at room temperature (21–27°C). Visual-chemical models (VC) absorbed odors when placed a minimum of 30 min into a covered 1 liter beaker containing 3–4 live mice. Visual-thermal models (VT) were placed into a 2 liter jar and heated by an electric blow drier (core temperature = 35–41°C; *cf.* Hayes and Duvall 1991). Visual-chemical-thermal models (VCT) were exposed to mouse odors and heat.

*Procedure.*—All 24 snakes were deprived of food for at least one month before the experiment. Each snake was then exposed once to each of the four stimulus conditions at intervals of 1–2 days, in a one-way within-subjects repeated measures design. To minimize the effects of habituation or change in motivation, the order of stimulus conditions presented each snake was randomly assigned. Individual snakes were placed in standard 38 liter glass aquaria, the floors of which were covered with clean brown paper toweling. To minimize extraneous visual disturbance, the aquaria sides were covered with paper towels and wooden lids were placed on top until stimulus presentations were made.

Following a 15 min adjustment to the aquarium, each snake was presented a preassigned condition. Models were suspended by the string and dragged back and forth along the aquarium floor approximately 5–15 cm (*cf.* Hayes 1992a) from the snake's snout. Each presentation lasted 120 sec, by which time the thermal models still retained some of their heat (according to thermometer readings of core temperatures). Snakes were permitted to contact models only by striking. All strikes recorded were of predatory rather than defensive motivation according to the criteria of Hayes and Duvall (1991). Latency to strike (sec) was timed with a stopwatch; if no strike occurred, a latency score of 120 sec was assigned. For snakes which struck a model, a freshly-killed mouse was substituted to determine if the predatory sequence (ingestion) would be completed. Between trials the floor papers were replaced and aquaria were wiped clean with wet paper towels.

The presence of dried yellow venom on the cheesecloth or paper towel core precisely indicated fang penetration of the models. The midpoint between two fang sites (unless only one site appeared) was used to ascertain whether models were struck in the anterior (closest to string attachment) or posterior half. One model struck exactly in the middle was discarded from the analysis.

*Analyses.*—Because each snake was exposed to all conditions and data were thus related, the Cochran Q test was used to evaluate the null hypothesis that strikes were equally distributed across

stimulus conditions. Pairwise comparisons were accomplished by one-tailed sign tests. The latency (sec) prior to striking was subjected to a one-way repeated measures analysis of variance (ANOVA) and *post hoc* contrasts (Student-Newman-Keuls'). The sites of fang penetration were compared with a one-tailed binomial test. Parametric ANOVA's were carried out with PSYCHO-STATS PC (Anderson 1985), while nonparametric tests were performed according to Siegel (1956), with  $\alpha = 0.05$  for all tests.

#### Experiment 2

This experiment was conducted to see if the results of experiment 1 would be similar under slightly different conditions. Specifically, the snakes used had been fed more recently and presumably were less motivated to feed than the subjects of experiment 1.

*Subjects and maintenance.*—The subjects were 14 individuals from the first experiment which struck and consumed live mice 9 days before this experiment began. Maintenance conditions were the same as in experiment 1.

*Stimulus conditions.*—The same models were presented as in experiment 1, with the addition of a fifth condition comprised of live adult white laboratory mice (LIVE). A string was tied to a posterior leg of each live mouse for similar presentation to the snakes.

*Procedure.*—The protocol was the same as in experiment 1, except that (1) only those snakes which had consumed a mouse 9 days prior to start of experimentation were used and (2) no freshly-killed mice were offered subsequent to striking. The five stimulus conditions were presented once per day on five successive days in each of two separate trials ( $N = 14$  and  $10$  snakes, respectively). Tongue flicks were also recorded using a handheld counter. Models were examined to see if the proportion envenomated differed between any conditions.

*Analyses.*—Data were analyzed the same as in experiment 1. Two additional measures, the number of tongue flicks and rate of tongue flicking prior to striking, were analyzed by the same ANOVA design as latency to strike. Since separate ANOVA's indicated the two trials were statistically equivalent, results were pooled for presentation. The probability of envenomation was evaluated by Fisher's exact probability test (Siegel 1956).

## RESULTS

#### Experiment 1

Strikes were not randomly distributed among the four conditions (Fig. 1A; Cochran's  $Q = 19.8$ ,  $df = 3$ ,  $p < 0.001$ ). Few visual models were struck, but the addition of either chemical or thermal cues significantly increased the number of strikes. Pairwise comparisons indicated significant differences between all conditions except between VC and VT and between VT and VCT.

Similarly, the four stimulus conditions differed in their time to elicit a strike (Fig. 1B;  $F(3, 39) = 14.12$ ,  $p < 0.001$ ). Those stimulus conditions struck most often were struck most quickly. Multiple comparisons indicated that all conditions except V *vs.* VC and VC *vs.* VT differed significantly.

Twenty-nine of the 32 (91%) freshly-killed mice offered after strikes were consumed by the snakes, supporting the impression that all strikes were predatory rather than defensive.

#### Experiment 2

The number of strikes elicited by the five stimulus conditions showed a trend similar to experiment 1 (Fig. 2A;  $Q = 40.0$ ,  $df = 4$ ,  $p < 0.001$ ). However, no V models were struck and the addition of chemical cues to V and VT models did not increase the number of strikes. Pairwise comparisons showed that all conditions except V *vs.* VC and VT *vs.* VCT differed significantly.

As in experiment 1, models struck most often were also struck most quickly (Fig. 2B;  $F(3, 48) = 16.86$ ,  $p < 0.001$ , with condition V removed due to lack of variance). Each condition differed from all others except for conditions VT *vs.* VCT.

The models struck most often were also struck after fewer tongue flicks (Fig. 2C;  $F(4,$

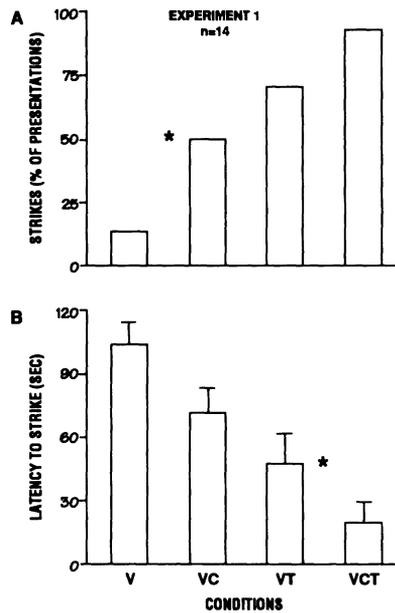


FIGURE 1. Experiment 1. (A) The proportion of stimulus presentations which elicited predatory strikes from northern Pacific rattlesnakes (*Crotalus viridis oregonus*), and (B) mean ( $\pm 1$  SE) latency to strike. The stimulus conditions were models with visual (V), visual-chemical (VC), visual-thermal (VT) and visual-chemical-thermal (VCT) stimuli. \* indicates significant difference between adjacent pairs.

64) = 13.31,  $p < 0.001$ ). Multiple comparisons indicated that the number of tongue flicks prior to striking differed between all conditions except V vs. VC and VT vs. VCT. The rate of tongue flicking prior to striking did not vary significantly among conditions (Fig. 2D). Therefore, the number of tongue flicks prior to striking appears to be a direct function of latency to strike under these experimental conditions.

Compared to experiment 1, the snakes seemed less motivated to feed and preferentially struck those conditions which most resembled actual prey (Fig. 2A). The proportion of model presentations which elicited strikes declined from 57% in experiment 1 to 32% in experiment 2. Also, the snakes of experiment 2 spent more time investigating the conditions prior to striking (compare Fig. 1B and Fig. 2B). Nevertheless, in both experiments the strike-releasing effectiveness of models was in the rank of  $V < VC < VT < VCT$ .

#### *Effects of Successive Presentations*

Because snakes were presented models (in random order) on each of 4–5 successive days, we wished to know whether behavior changed gradually during the period of testing. Thus, additional ANOVA's treated successive presentations (one/day) within each experiment rather than the stimulus conditions as the independent variable. For both experiments, the lack of significance ( $p > 0.10$ ) for the dependent measures (latency to strike and tongue-flicks prior to strike) suggests that behavior was consistent across the duration (4–5 days) of each experiment.

#### *Envenomation Characteristics*

Combining data for both experiments, 37 of 53 models (70%) struck by the snakes showed visible traces of venom. A significant proportion (68%) of two-fang strikes were

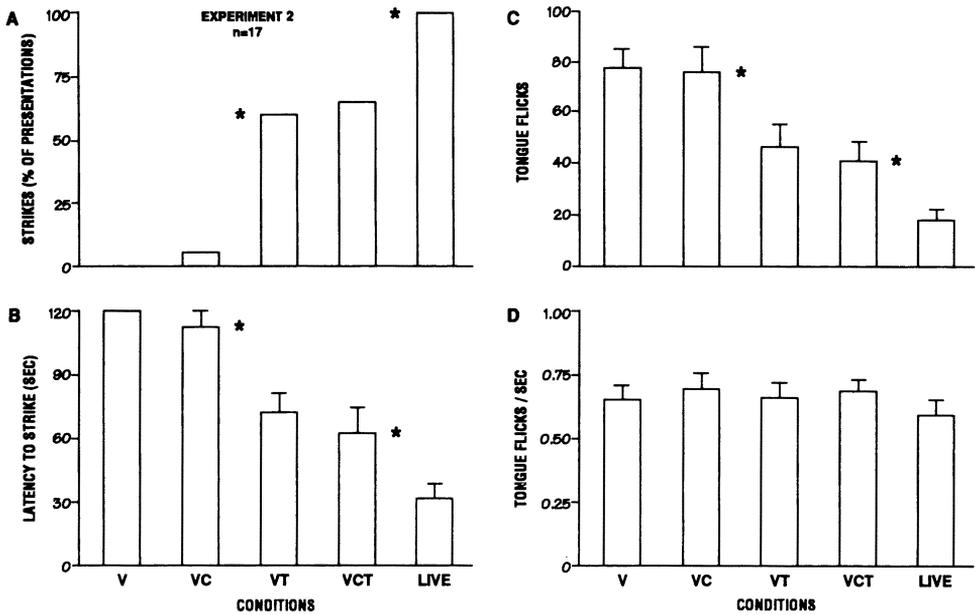


FIGURE 2. Experiment 2. (A) The proportion of stimulus presentations which elicited predatory strikes from northern Pacific rattlesnakes (*Crotalus viridis oregonus*); (B) mean ( $\pm 1$  SE) latency to strike; and (C) mean number of tongue flicks and (D) mean rate of tongue flicking between presentation of stimulus and elicitation of strikes. The stimulus conditions were models with visual (V), visual-chemical (VC), visual-thermal (VT) and visual-chemical-thermal (VCT) stimuli, as well as live mice (LIVE). \* indicates significant difference between adjacent pairs.

delivered to the anterior half of the models (Table 1; models showing venom from only one fang site were not included in the statistical evaluation). In experiment 2, the proportion of VCT models envenomated (7/10) was significantly greater than the proportion of VT models envenomated (1/9) (Fisher's Exact Probability = 0.014).

DISCUSSION

The visual models elicited exceedingly few strikes. Thus, while visual stimuli may assist the snake in locating and tracking prey (e.g., Chiszar et al. 1981b), they are ineffective at releasing strikes in the absence of additional stimuli. Although Noble and Schmidt (1937) reported that two specimens of *C. viridis* consumed mice after having their tongues removed and facial pits cauterized, no mention was made of whether normal strike behavior took place. Many colubrid snakes, in contrast, strike readily at visual stimuli of prey (e.g., Cooper et al. 1990).

Although we were unable to evaluate thermal cues alone, other studies imply their effectiveness at releasing strikes. Dullemeijer (1961) observed that specimens of *C. ruber*,

TABLE 1. Location of fang penetration of models struck by northern Pacific rattlesnakes (*Crotalus viridis oregonus*).

Characteristics	Anterior	Posterior
Two fang sites*	19	9
One fang site	4	4
Combined	23	13

\*  $p = 0.045$  (Binomial probability, one-tailed).

with facial pits covered by masking tape, refused to strike live mice and several times attempted to grasp and swallow mice without first striking. He concluded that thermal cues (in conjunction with movement) help distinguish between live and dead prey. Cock Buning et al. (1981) observed similar behavior (disinterest in live mice and grasp-swallow attempts without striking) in *Agkistrodon blomhoffi brevicaudus* with pits plugged, but blindfolded snakes with unplugged pits continued to strike mice successfully (and, in several instances, at warm spots left behind by mice which had moved). Further, Kardong and Mackessy (1991) observed normal predatory behavior in a congenitally blind *C. v. oreganus*, which even struck mice in the usual head/neck region presumably using thermal cues. Finally, certain viperine (Breidenbach 1990) and colubrid (Kardong and Smith 1991) snakes, which lack infrared-sensitive facial pits, also rely on thermal cues when striking at warm objects (see Dickman et al. 1987 for a possible explanation).

In the present study, the addition of thermal cues to the visual models significantly increased the likelihood of attack. Thus, from our results and those of others (above), we suggest that visual cues alone are relatively ineffective and that thermal cues are more important (but not essential; see Fig. 1A) for release of strikes by rattlesnakes. Visual cues may enhance the strike releasing effectiveness of thermal cues, a process likely mediated by the specialized multimodal neurons which integrate the visual and thermal senses of rattlesnakes (Newman and Hartline 1982; Hartline 1984).

In both experiments, a substantial number of VT models were struck, which suggests that detection of prey-derived chemical cues is not necessary for the release of striking. Other studies also have found that rattlesnakes readily strike at models of mice devoid of mouse odors, both in the laboratory (Chiszar and Scudder 1980; see also Chiszar et al. 1976) and in the field (Hayes and Duvall 1991). Although a functional tongue-vomer-nasal system seems important for normal predatory strikes to occur (Graves and Duvall 1985), it is clear that detection of appropriate visual-thermal stimuli can alone be sufficient for the release of striking.

Differences between the two experiments in the present study suggest that the snakes in experiment 1 were more motivated to feed than in experiment 2. Presumably, either the length of food deprivation prior to testing (30 vs. 9 days, respectively) or the food vs. no food offered subsequent to striking contributed to the change. Because the snakes showed no evidence of satiation (despite meals in close succession in experiment 1) or habituation (striking continued in experiment 2 even without rewards of freshly-killed mice), the length of food deprivation may best explain the decrease in responsiveness. Chiszar et al. (1981a) demonstrated that rattlesnakes exploring an open field arena do not respond to mouse odors with elevated tongue flick rates until deprived of food at least 28 days. Accordingly, they suggested that increased hunger may be the basis for activation of foraging behavior. Thus, a hunger-motivated change in chemosensory responsiveness may explain why the addition of chemical cues significantly increased the likelihood of attack and decreased the latency to strike in the first (Fig. 1; food deprived >30 days) but not in the second (Fig. 2; deprived 9 days) experiment of the present study. We concur with Dullemeijer's (1961) suggestion that increased hunger may heighten the responsiveness of snakes to various stimuli.

It is not clear why the snakes in experiment 1, after consuming a mouse early in the consecutive trials, continued to strike consistently at subsequent presentations. In later trials of experiment 1, these snakes had fed more recently (1-2 days) than the snakes of experiment 2, but continued to exhibit high levels of responsiveness. Perhaps thresholds of feeding responsiveness and perceived hunger do not decline until after several days of digestion.

Rattlesnakes usually strike rodent prey in the head and shoulder region (Kardong 1986b; Kardong and Mackessy 1991; but see Hayes 1992a), which presumably reduces the risk of missing forward-moving prey, provides the quickest means of prey death,

and minimizes the risk of retaliatory injury from rodent teeth and claws (Hayes and Galusha 1984; Kardong 1986b; Hayes 1992a). Kardong (1986b) suggested that rattlesnakes may identify the polarity (anterior *vs.* posterior ends) of rodents by the visual and/or thermal image, or by directional movement of the prey. Because most of the models were struck in the anterior half (Table 1) and the models had no visual-thermal polarity, it appears that prey movement alone can be used to guide the strike to the head/neck region. However, Schmidt et al. (1993) found that rattlesnakes consistently struck anesthetized mice in the head/neck region regardless of whether the mouse was moved forwards or backwards. Hence, when striking live mice the aim is guided primarily by the visual-thermal image rather than by directional movement.

Several explanations can be offered why few VT and most VCT models were envenomated, each of which assumes that a decision was made by the rattlesnake. For example, the snakes may have detected something "wrong" in the stimulus configuration (*e.g.*, no mouse odors) just before launch of the strike or during the strike itself, and a "late" effort to abort may have flawed the mechanics of the strike and disrupted venom delivery (Kardong 1986a). However, in experiment 2 five obvious (perhaps "early") aborted strikes were recorded; of these, the VT and VCT models each elicited two, which does not indicate a greater likelihood of aborted strikes for VT presentations.

Alternatively, the decision not to envenomate may have been in response to incorrect chemical stimulation of the oral tissues during the time that the jaws were in contact with the model (0.07–0.5 sec; Kardong 1986a; Rowe and Owings 1990; Hayes 1992a). This implies that rattlesnakes possess some form of neural control over the venom delivery system. Rattlesnakes detect and respond to oral stimulation during the brief period of contact with prey (Kardong 1986a; Melcer and Chiszar 1989) and control quantities of venom injected into prey of different sizes (Hayes 1992a), so this explanation seems plausible.

In summary, this study supported our hypothesis that visual and thermal cues are more important than chemical cues in releasing and guiding the aim of predatory strikes. However, the relative level of hunger may influence responsiveness to prey-derived stimuli—especially chemical cues. The direction of prey movement, in addition to the visual-thermal representation of prey, may be used to guide the strike aim. Evidence also suggests that rattlesnakes possess control over the mechanics of venom injection.

#### ACKNOWLEDGMENTS

This manuscript benefitted from the critical comments of R. L. Carter, D. Chiszar, S. Corn, D. Duvall, J. G. Galusha, F. E. Hayes, K. V. Kardong and L. R. McCloskey. D. F. Schmidt and D. Wright assisted with collecting the snakes. J. Gibson and R. Norris helped care for the animals.

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