

Effects of novel chemical cues on predatory responses of rodent-specializing rattlesnakes

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We examined predatory responses of prairie (*Crotalus viridis*) and timber (*Crotalus horridus*) rattlesnakes to mouse carcasses misted with diluted perfumes or water. In Experiment 1, snakes showed equivalent latencies to strike, grasp, and ingest perfume- and water-misted carcasses. In Experiment 2, snakes that struck carcasses misted with perfume, water, or no liquid subsequently showed similar increases in tongue-flicking. In no-strike trials, snakes showed very low levels of tongue-flicking regardless of the type of chemical cues on the carcass. We conclude that during and after strikes, rattlesnakes behaved similarly towards both normal and chemically-novel rodent prey, implying that such prey are equally acceptable to the snakes.

Chemical cues play an important role in the predatory behavior of snakes (Burghardt, 1970, 1980; Halpern & Kubie, 1983; Kubie & Halpern, 1979). In particular, rodent-specializing rattlesnakes release their prey immediately after envenomation (Kardong, 1986; Klauber, 1956) and then follow the chemical trail left by the rodent as it wanders away from the site of attack (Duvall, Scudder, & Chiszar, 1980; Golan, Radcliffe, Miller, O'Connell, & Chiszar, 1982; Lee & Chiszar, 1987). Recently Melcer and Chiszar (1988) reported that rattlesnakes acquire specific chemical information from prey during predatory strikes and use it in the subsequent searching process. In those tests, snakes struck mouse carcasses misted with novel chemicals (musk and floral perfumes). An unresolved question is whether these novel chemicals affect or alter the typical predatory behavior of rattlesnakes. That snakes in Melcer and Chiszar's study struck and ingested perfume-misted carcasses suggests that novel chemical cues do not have profound effects on predatory behavior. However, more subtle effects of the perfumes may have escaped our attention. For instance, snakes may perceive the perfumes as mildly aversive and therefore hesitate before striking, trailing, and/or ingesting prey that bear these chemicals. The present experiments assessed these possibilities in rodent-specializing rattlesnakes.

In Experiment 1, we tested the effects of novel perfume on the rattlesnakes' striking and on their subsequent ingestion of prey. A snake's striking at prey induces a large increase in tongue-flicking for up to 2 h following the strike (called strike-induced chemosensory searching, SICS; Chiszar, Radcliffe, O'Connell, & Smith, 1982; Gillingham & Clark, 1981). Experiment 2, therefore, tested how the snakes' striking perfume-misted carcasses affected their subsequent rates of tongue-flicking.

EXPERIMENT 1

The rattlesnakes struck mouse carcasses that were misted with diluted perfume or water. The envenomated carcasses were then left for the snakes to ingest. We recorded the snakes' latency to strike, grasp, and swallow the carcasses. If novel chemical cues disrupt predatory behavior, the snakes should show longer latencies for perfume- than for water-misted carcasses.

Method

Subjects. Six prairie rattlesnakes (*Crotalus viridis*) and 4 timber rattlesnakes (*Crotalus horridus*) about 70 cm long were the subjects. The snakes had been captured as adults and were maintained individually in glass terraria (50 × 27.5 × 30 cm) that contained paper floor coverings and stainless steel vessels filled with water. The room was kept at 26°–28° C during photophase (0700–1900) and at 22°–24° C during the scotophase. All the snakes had been in captivity for several years and had been accepting rodent prey (*Mus musculus* or preweanling *Rattus norvegicus*, of 20–27g) on a biweekly schedule. Previously euthanized rodents were fed to the snakes, and these carcasses were always lowered into the snakes' home cages with forceps in order to elicit predatory strikes. Consequently, the snakes were accustomed to striking prior to ingesting prey. The snakes were 2 weeks hungry prior to testing. Although the snakes had been used in previous experiments that involved the presentation of natural chemical stimuli, no surgical or pharmacological manipulations had been performed on them. Therefore, we considered these snakes to be typical of long-term captive crotalines.

Procedure. All the snakes were studied in their home cages. The mouse carcasses were misted with about 1 cc of water or diluted perfume (Jungle Gardenia, 2 cc perfume in 710 cc tap water). No live mice were used as stimuli; the mice were euthanized by cervical dislocation 2 min prior to the experiment. All the mice were culled from local breeding facilities and all the carcasses were eventually ingested by the snakes. The lid of the home cage was opened and a misted carcass was suspended with forceps, 10 cm above and slightly in front of the snake's head. The carcass was held until the snake struck, and then it was placed on the floor of the home cage about 10 cm from the snake's head.

Each snake was tested twice. On one day the snake struck and ingested a perfume-misted carcass, and on the other test day the snake struck and ingested a water-misted carcass. The time between tests was 2 weeks and the order of the perfume and water tests was counterbalanced across snakes.

The experimenter used a stopwatch to record latency to strike (the time from the presentation of prey until the strike), latency to grasp (the

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time from the strike until the snake picked up the carcass in its jaws) and latency to swallow (the time from the strike until the carcass disappeared in the snake's mouth).

Results and Discussion

All the rattlesnakes struck, grasped, and ingested the perfume- and water-misted carcasses. The two taxa of rattlesnakes did not differ, so their data were pooled for analysis and presentation. The snakes took slightly longer to strike the perfume-misted carcasses ($M = 2.55$ sec; $SE = .32$ sec) than the water-misted carcasses ($M = 1.58$ sec; $SE = .34$ sec) but the difference was not significant [$F(1,9) = 3.43, p > .05$]. The mean latency to grasp perfume-misted carcasses ($M = 271.8$ sec; $SE = 61.5$ sec) was numerically shorter than the mean for water-misted carcasses ($M = 391.0$ sec; $SE = 66.9$ sec), but again the difference was nonsignificant [$F(1,9) = 4.63, p > .05$]. Finally, the difference between the mean latencies to swallow either the perfume-misted ($M = 741.8$ sec; $SE = 73.7$ sec) or the water-misted ($M = 807.8$ sec; $SE = 65.5$ sec) carcasses was not significant ($F < 1.0$). Thus, perfume- and water-misted carcasses appear equally acceptable to rattlesnakes by all of our measures.

EXPERIMENT 2

As mentioned previously, rattlesnakes exhibit SICS following predatory strikes (Chiszar et al., 1982; Chiszar, Stimac, & Boyer, 1983); in Experiment 2, we compared SICS following strikes of perfume-misted prey with SICS following strikes of control prey.

Method

Subjects. Six prairie rattlesnakes (*Crotalus viridis*) were our subjects. The housing and history for these snakes were the same as described for the snakes in Experiment 1.

Procedure. All the tests were conducted in the snakes' home cages, as in Experiment 1. Their rates of tongue-flicking (RTF) were recorded with hand-held counters for 10 min prior to each experimental treatment. Immediately after these baseline observations, the snakes received one of eight treatments and the RTF was again recorded for 20 min.

Each snake was tested in each of the eight treatment conditions. A different random order of the eight conditions was used for each snake. The time between tests was 1 week.

In the four strike conditions, the lid of the home cage was opened and a mouse carcass was suspended with forceps about 10 cm above and slightly in front of the snake's head. The snakes quickly oriented themselves toward the carcass, struck and released it. The stimulus carcass was misted with 1 cc of water (S-Water), Jungle Gardenia perfume (S-J. G.), Halston perfume (S-Halston) or no liquid (S-Normal). The perfume dilutions were the same as in Experiment 1. In the no-strike conditions, the carcass was suspended in the home cage as before, but it was just out of striking range (20 cm) for 3 sec (about the same duration as carcasses remained during strike trials). The stimulus carcass was misted with water (NS-Water), Jungle Gardenia perfume (NS-J. G.), Halston perfume (NS-Halston) or no liquid (NS-Normal). This is a 2×4 factorial design, with two types of prey presentation (strike or no-strike) and four types of carcasses (water, Jungle Gardenia, Halston, or no misting).

The stimulus carcass was removed immediately after it was presented to the snake, without making contact with any part of the snake's home cage.

Results and Discussion

Figure 1 shows the mean RTF for the six snakes during the 10-min baseline and the 20-min posttreatment period of testing. The baseline RTFs were always low, indicating that the snakes were quiescent prior to the presentation of prey.

The snakes showed significantly greater RTFs after strikes than after no-strike presentations [$F(1,5) = 33.59, p < .01$]. These data replicate many previous studies of SICS (Chiszar et al., 1982; Chiszar et al., 1983).

Most importantly, there was no significant main effect of type of carcass (water, no liquid, Jungle Gardenia, Halston) on RTF ($F < 1$). Also, there were no significant interactions between the effects of type of carcass and

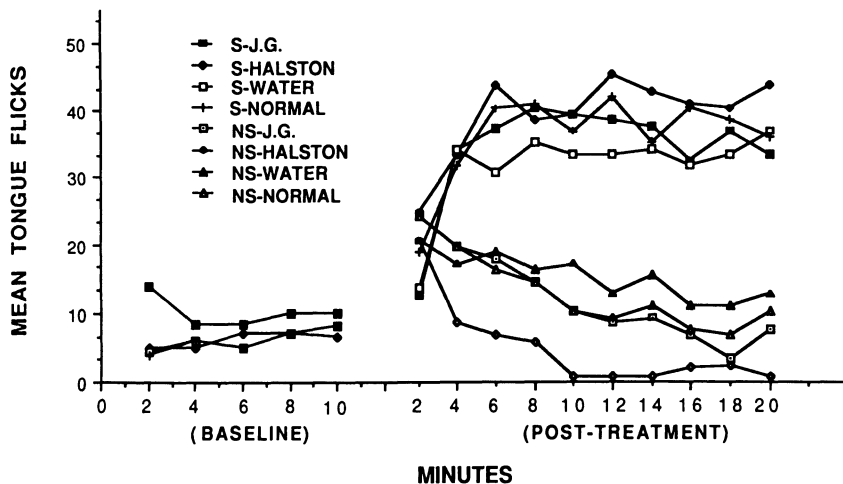


Figure 1. Mean tongue flicks during consecutive 2-min intervals before (baseline) and after (posttreatment) presentation of mouse carcasses. Baselines prior to strike and no-strike trials were averaged for each of the four different types of carcasses (Jungle Gardenia, Halston, water, normal).

strike/no-strike trials or minutes of testing (all $ps > .05$). Hence, the application of novel perfumes to stimulus carcasses did not influence the RTF following predatory strikes or mere exposure to the carcasses.

GENERAL DISCUSSION

Novel chemical cues (diluted perfumes) on mouse carcasses did not alter the predatory behavior of rattlesnakes. Therefore, mice misted with these perfumes are probably not aversive, unpalatable, or otherwise inhibitory to rattlesnakes. Furthermore, the learning and memory phenomena observed by Melcer and Chiszar (1988), who used such mice as stimuli, are probably not artifacts resulting from aversive (and, therefore, salient) prey items. Instead, we suspect that these phenomena are characteristic aspects of rattlesnake predation upon ordinary rodents, and that they function whenever predatory strikes are delivered.

The perfume solutions used in these experiments, although quite diluted, could be detected by rattlesnakes (Melcer & Chiszar, 1988). We acknowledge that application of more concentrated solutions of novel chemicals to prey might very well prove to be aversive and thereby disrupt the typical predatory behavior of rattlesnakes.

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(Manuscript received April 20, 1988.)