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The Role of the Vomeronasal Organ in Rattlesnake *(Crotalus viridis oreganus)* Predatory Behavior

Key Words
Vomeronasal organ
Rattlesnake predatory behavior
Avomic behavior

Abstract
During predatory behavior, rattlesnakes depend primarily upon thermal and visual cues to initially aim a strike. However, it has been hypothesized that prey-related odors sensed by the vomeronasal system act as releasing stimuli of the strike and that such vomodors are primary stimuli during poststrike trailing and swallowing of the envenomated rodent. To test this, northern Pacific rattlesnakes were rendered avomic by bilateral lesions of the vomeronasal nerves, and their vomic and avomic predatory behaviors were compared. Avomic rattlesnakes exhibited fewer strikes and complete elimination of trailing and swallowing behavior. These results support the hypothesis that vomodors sensed via the vomeronasal organ are capable of acting as releasing stimuli of selected rattlesnake predatory behaviors. Sensory input via the vomeronasal organ is important during prestrike/strike behavior, and it is a major route of sensory input during poststrike trailing and ingestion of envenomated prey.

Introduction

The vomeronasal organ (VNO) occurs throughout most tetrapods [Bertmar, 1981; Duvall, 1986]. It is involved in a variety of behaviors [Wysocki et al., 1986; Halpern, 1987, 1988]. Guinea pigs and hamsters that lack a functional VNO show a decrease in sexual response that becomes more pronounced over time [Winans and Powers, 1977; Beauchamp et al., 1982, 1985]. The VNO must be functional in order for sexual odors to retain their attractiveness [Beauchamp et al., 1985]. In male guinea pigs, following VNO deafferentation, there is a marked decrease in sexual behavior [Wysocki et al., 1986].

The role of the VNO in ophidian feeding behavior has been examined by a variety of methods [Burghardt, 1970a, b, 1980, 1990; Burghardt and Pruitt, 1975; Chiszar, 1978; Chiszar and Radcliffe, 1976; Chiszar and Scudder, 1980; Chiszar et al., 1990; Graves and Duvall, 1985a, b; Halpern, 1988; Halpern and Frumin, 1979; Kubie and Halpern, 1978, 1979]. Like the sensory nasal epithelium, the VNO is a chemosensory organ. In garter snakes, the VNO is involved in location and trailing of prey prior to the strike, in courtship, in aggregation behavior [Kubie and Halpern, 1978, 1979; Halpern and Kubie, 1983; Halpern, 1988], and in movement within home ranges [Graves et al., 1993]. The feeding behavior of garter snakes is altered by preventing

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stimulation of the VNO. Garter snakes follow prey trails at chance levels following VN nerve lesions [Kubie and Halpern, 1979]. These animals, with considerable preoperative training, cease attack and ingestion of prey within a matter of a few days following cuts of nerves from the VNO [Kubie and Halpern, 1979].

In rattlesnakes, foraging behavior includes opportunistic elements such as scavenging [Fitch, 1949; Gillingham and Baker, 1981; Hennessy and Owings, 1988] and direct elements such as an envenomating strike [Klauber, 1956; Duvall et al., 1985, 1990] which involve initial detection of selected prey, orientation, strike, recovery, and swallowing of envenomated prey [de Cock Buning, 1983a]. The strike may also be used during defensive behavior [e.g. Klauber, 1956], which includes some different behavioral elements [e.g. Gove, 1979] and different consequences [e.g. Russell, 1980; Kardong, 1986a; Minton, 1987; Hayes, 1991] than predatory strikes [Minton, 1969]. Consequently, the predatory behavior of rattlesnakes is a very complex series of phases that may be released by different sensory stimuli separately or in combinations, part of the multisensory control. Prior research on the use of visual and thermal cues by rattlesnakes suggests that sensory input via eyes and heat-sensitive pits is especially important during prestrike phases of predatory behavior but is less so during poststrike phases [Kardong, 1992]. The relative importance of the vomeronasal organ in pre- and poststrike phases of rattlesnake predatory behavior is less well documented.

In rattlesnakes, closing the oral ducts to the VNO leads to extinction of the strike [Graves and Duvall, 1985b]. However, this response may not be immediate [Kardong, 1992]. Unlike the garter snake studies, which used nerve lesions, these two studies depended upon mechanically blocking ducts to the VNO to produce avomic rattlesnakes, and the two studies scored different variables under quite different conditions to evaluate overall predatory performance. Therefore, the first purpose of our experiments here was to test the effects of VNO deprivation on rattlesnake strikes by using complete bilateral vomeronasal nerve transection (VNX). Predatory behavior of rattlesnakes in control and VNX conditions could then be evaluated using specifically defined variables [Dullemeijer, 1961; Kardong, 1986b, 1992].

Following the release of struck prey, rattlesnakes not only follow the scent trail of the envenomated rodent, they are also able to discriminate this trail from scent trails of other, non-envenomated, rodents of the same species [Robinson and Kardong, 1991; Lavín-Murcio et al., 1993]. Thus, we also used a growing body of research on poststrike trailing behavior [Chiszar et al., 1976, 1977; Chiszar, 1978; Chiszar and Scudder, 1980; Chiszar et al., 1990; Furry et al., 1991; Robinson and Kardong, 1991; Lavín-Murcio et al., 1993] to address specifically the role of the VN system in poststrike prey trailing and prey ingestion.

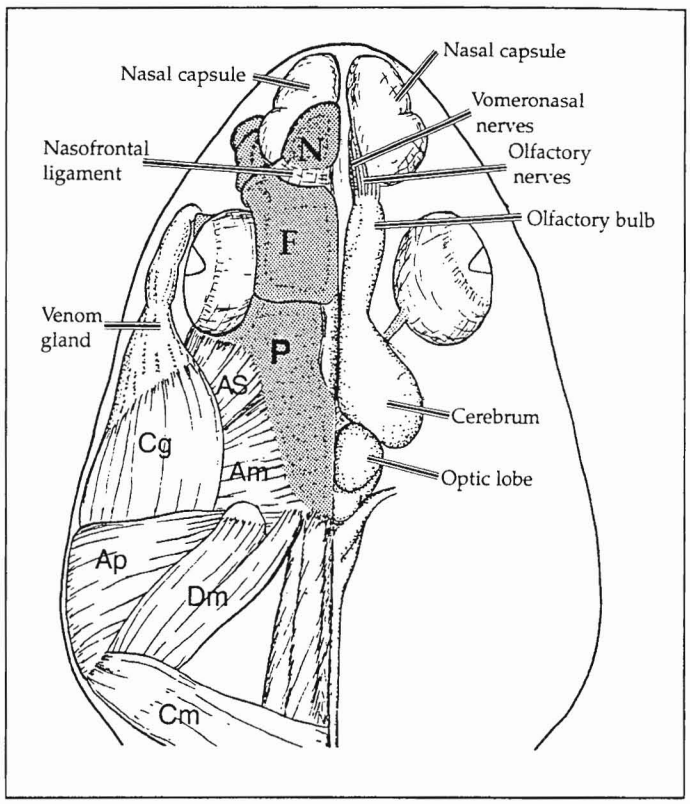

Fig. 1. Dorsal view of rattlesnake head showing the relationship of nerves departing from the nasal capsule and from the vomeronasal organ. Jaw muscles and roofing bones are indicated on the left in stipple; these have been removed on the right to reveal the relative positions of underlying elements of the brain and arriving vomeronasal and olfactory nerves to the olfactory bulb. Note that careful removal of the nasofrontal ligament gives access to these nerves before they enter the braincase. Bones: frontal (F), nasal (N), parietal (P); muscles: adductor mandibulae externus medialis (Am), adductor mandibulae externus profundus (Ap), adductor mandibulae externus superficialis (AS), compressor glandulae (Cg), cervico-mandibularis (Cm), depressor mandibulae (Dm).

Materials and Methods

The results reported here are from eight (8) adult northern Pacific rattlesnakes, *Crotalus viridis oreganus*, 65–75 cm snout/vent length. Four additional rattlesnakes were used in an initial pilot study to develop and evaluate the effectiveness of surgical procedures. All snakes were collected in Grant and Whitman counties of Washington State, were part of a long-term laboratory colony, and were in captivity for at least seven years. Prior to the beginning of these experiments,

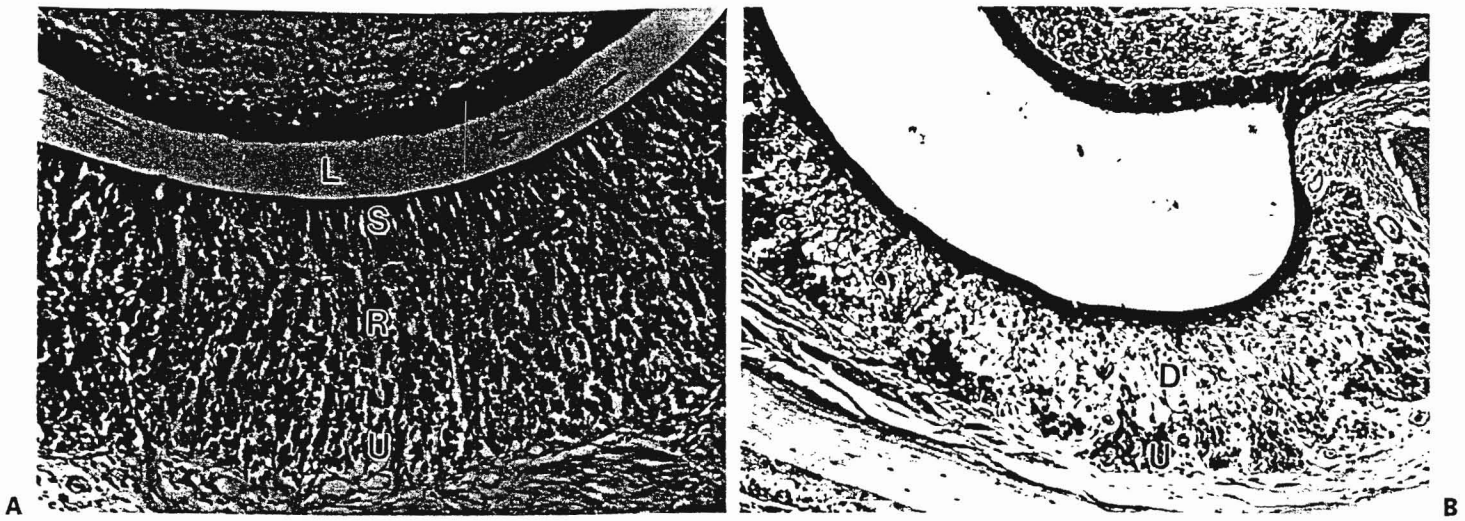

Fig. 2. Vomeronasal epithelium from rattlesnakes showing normal (**A**) and degenerate (**B**) epithelium six weeks postoperatively. In **A**, three layers are recognized, a supportive cell layer (S) facing the lumen of the vomeronasal organ, a basal or undifferentiated layer (U), and between these the receptor or sensory cell layer (R). In **B**, loss of the receptor cells following section of the vomeronasal nerves leaves a large degenerate region (D) within the epithelium.

the snakes were maintained on a diet of laboratory mice offered on an irregular basis and water ad libitum. Occasionally, dead mice were offered, but usually live mice were presented, struck, located, and swallowed within an hour of presentation. The snakes were housed at a constant temperature (27–32 °C) on a 12:12 light:dark cycle. Each snake was housed individually in a terrarium (50×50×90 cm), the floor covered with newspaper. The original research reported here was in compliance with the guidelines for use of animals in research published in *Animal Behaviour* [43:185–188, 1992].

Surgery

In snakes, as in all terrestrial vertebrates, the olfactory and vomeronasal nerves are separate and project to different regions of the telencephalon: the olfactory nerve to the olfactory bulb and the vomeronasal nerve (VNN) to the accessory olfactory bulb [Halpern, 1976]. This makes it possible to selectively deprive snakes of their vomeronasal systems without affecting olfactory input. Initial dissections of preserved *Crotalus viridis oreganus* revealed a unique surgical pathway to expose the VNN in rattlesnakes. Dorsally, between the frontal and nasal bones is a broad ligament that, once removed, allows direct surgical access to the VNN before it enters the braincase. Therefore, unlike in garter snakes [Kubie et al., 1978], it was not necessary to open or remove part of the bony braincase to isolate the VNN.

Snakes were exposed to 1.5 ml Isoflurane on a cotton swab in a closed container for approximately 2 hours, producing initial anesthetization. They were maintained at a low anesthetization plane during surgery by inhalation of 3% Isoflurane mixed with air (one liter/minute). Administration of the isoflurane/air mixture followed de Cock Buning [1983b], whereby a one-way flow was established through the lung, in anteriorly via a tracheal catheter and out posteriorly via an 18 gauge syringe needle inserted into the air sac. Surgery began after a suitable anesthetic plane was reached; this was defined as the point where tail retraction and righting reflexes were extinguished. In addition, heart rate was observed periodically to also monitor the level of anesthesia. Surgery was performed using a Wild dissecting scope [Kubie et al., 1978]. The connective tissue between the nasal and frontal bones was severed, and the exposed blood sinus overlying the nerves was pressed to one side with Gelfoam. The VNN runs underneath the connective tissue to the accessory olfactory bulb from the VNO (fig. 1). Upon bilateral exposure of the VNN, the nerves were lifted up and pulled apart with forceps. The severed nerve ends were allowed to fall back into place. Sham surgeries followed identical procedures, the frontal/nasal connection was cut, Gelfoam was placed to prevent any bleeding, and the nerves were exposed but not lifted and cut. Following both the experimental and sham surgeries the incision was sutured closed and sealed with cyanoacrylate glue (superglue). The isoflurane supply was turned off, and air only passed through the snake's lung until the return of distinctive reflexes (tail retract, righting). The snake was removed from the anesthetizing apparatus, returned to its home cage, and left overnight before beginning feeding trials.

Verification of Lesions

On the fourth to sixth week following surgery, and after completion of experimental trials, five of the eight snakes with vomeronasal nerves cut were placed in a cloth bag, packed in ice for three hours, then removed and killed by decapitation. Each head was immediately peeled free of skin, injected around the snout with Bodian's fixative, then stored in the fixative for 1–3 days. In general, preparation of the heads followed Kubie et al. [1978]. Heads were then trimmed to just the snout and decalcified for 4–6 days in formic acid decalcifying solution (DECAL, Omega Chemical Corp.) changed once daily. When decalcification was complete (nasal bones soft to pin penetration), the snouts were washed overnight with water, dehydrated in progressive ethanol baths to butanol, and embedded in Paraplast. Ten to fifteen-micron sections were cut in transverse plane to the long axis of the body, stained with hematoxylin and eosin, and examined on a compound microscope. Description of basic vomeronasal epithelium and

histological confirmation of sensory mucosa degeneration follows Kubie et al. [1978]. Figure 2 includes photomicrographs of normal (A) and surgically degenerate (B) sensory vomeronasal mucosae. This histological examination confirmed, early in the research, that cutting the vomeronasal nerves under visual inspection was effective in completely severing VNN. Therefore, we felt it redundant and unjustified to kill the last three snakes.

Data Gathering

Data were collected on three behaviors during feeding trials – striking, trailing, and swallowing. Data were gathered prior to surgery to establish baseline behaviors (controls) and then following surgery which produced complete nerve lesions (VNX).

The feeding trials were the same throughout all experiments and followed basic protocols described elsewhere [Robinson and Kardong, 1991; Lavín-Murcio et al., 1993]. A feeding trial took place in a square plastic choice arena (1.25 m side × 0.5 m high) with a large Y-shaped image (60 cm base, 45 cm each arm, 90° between arms) made of black electrical tape on the pressed fiberglass floor of the arena. Before each feeding trial, a fresh sheet of white commercial butcher paper was placed over the floor of the arena; the faint image of the Y beneath the butcher paper could be seen through it to guide the laying of mouse-scent trails. Prior to a feeding trial, a snake was lowered into, and allowed to remain for a minimum of 5 hours within, a wooden holding box with a clear plastic top (30 cm wide × 60 cm × 60 cm) placed at the beginning of the faint Y-shaped image as seen through the paper (fig. 3). After acclimatization, a removable wooden chute was fitted to the outside front of this holding box, replacing a temporary sliding door blocking the entrance. All mice used were white laboratory mice (Swiss Webster), bedded on oak shavings, and fed the same diet of Purina mouse chow. A live mouse was gently lowered down this chute into the holding box with the rattlesnake and kept there until struck or for no more than 15 minutes if unstruck. The mouse was then removed via a line tied earlier to its tail and used to make a scent trail. To do this, the struck mouse, hand-held by the nape of its neck and base of its tail, was pushed smoothly and in one steady pass along a predetermined path along one side of the Y-maze, with its ventral surface kept pressed to the butcher paper. The mouse was slid down one side of the base of the Y-maze, out one arm, and removed from the arena. All mice died within five minutes of being struck and were used later in swallowing tests on the same rattlesnake that made the initial strike (see below). Immediately after this first trail of the struck mouse was laid, a different, live, non-struck mouse of about the same size, but from a different litter was used in the same way to make a second scent trail on the other half of the base of the Y-maze and out the other arm. Care was taken by the experimenter laying scent trails not to touch the floor of the arena. Once the two choice trails were laid down (within 2 minutes of the strike), the temporary door to the wooden holding box was raised and the exprimenter retreated out of view. All subsequent behavior of the snake was observed via a VHS video system through a camera at the edge of the arena.

A snake was considered to be following a scent trail if its head remained within 10 cm of either side of a scent trail. A trial was scored as a 'choice' if the snake followed one scent trail to its end, and 'no choice' if the snake failed to follow (> 10 cm) or failed to move out of the holding box within 15 minutes of lifting the holding box door. Immediately upon conclusion of the feeding trial, the rattlesnake was returned to its home cage. At least 1 week separated feeding trials of each snake. Safety procedures for snakes generally followed those of Gans and Taub [1964].

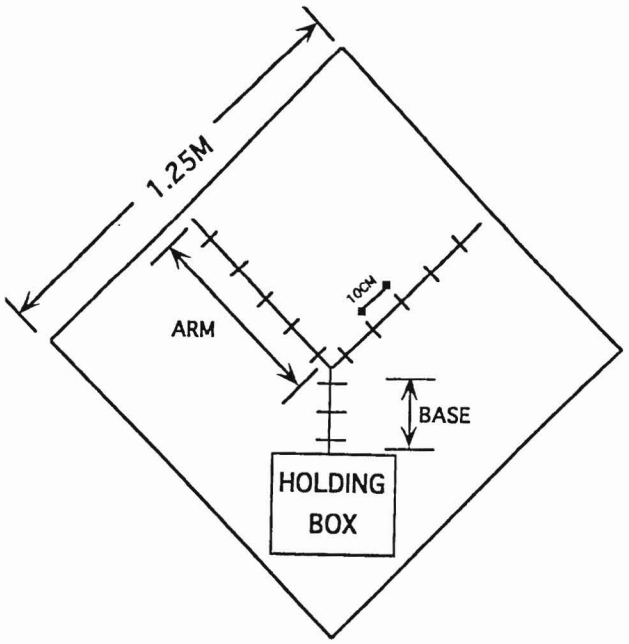

Fig. 3. Diagram of the test arena. The square arena (1.25 m) with 0.5 m high walls defined the area of the Y-maze within. Following presentation of a mouse, the rattlesnake had the opportunity to move out of the holding box following the paired scent trails parallel along the base and diverging out the arms of the Y image seen through white paper covering the floor of the arena.

Striking

During each of the feeding trials, each rattlesnake was tested before surgery (control) and then after VN nerve lesions (VNX) and scored as to whether or not it struck the mouse presented to it while in the holding box in each of these trials. Each of the eight snakes was tested once per week: four to six times in the control condition and up to five times following VN nerve cuts.

Trailing

Using the protocol described above (Striking), each of the eight snakes in the control condition was tested four to six times, once per week, as to its choice of scent trail (trail of struck mouse or unstruck mouse; or no choice) for a total of 40 trailing trials combined. Following VNX, each rattlesnake was again tested once weekly for four weeks. In addition to scoring scent trail following (poststrike behavior), we counted the number of tongue flicks both prestrike and poststrike in control and VNX conditions. Rate of tongue flicking (RTF) was calculated from counts obtained during viedo playback, and expressed as rates per minute [e.g. Chiszar et al., 1990]. Scoring the RTF began when a snake first emerged from the holding box at the base of the Y-maze and continued until the snake reached the end of a choice trail or 15 minutes had elapsed, which ever came first. Snakes were tested for their poststrike trailing behavior only if they struck the mouse presented during that particular feeding trial. In the control condition, all eight snakes struck, and their trailing behavior was scored. In the VNX condition, five of these same eight struck when offered a mouse, and their trailing behavior was scored.

Swallowing

Each of the eight rattlesnakes was presented with a dead (cervical dislocation or struck) mouse four to six times before surgery, on a weekly basis, and then weekly after nerve cut surgery to compare swallowing response in intact and lesioned conditions. Three of the eight were tested on the second and fourth day following VNX surgery, and once each week for the next four weeks, for a total of five weeks. Five of the eight snakes with VNN lesions were presented with dead mice at four weeks after surgery. In both the control and VNX condition, swallowing tests were performed after the rattlesnake had been removed from the arena and returned to its home cage. The dead mouse was left with the rattlesnake in its home cage overnight, and the outcome (swallow or not) was scored the next morning.

Statistical Tests

Paired t tests and ANOVA were performed on the control vs. the VNX condition using SYSTAT statistical package.

Results

The present study continues earlier work on deprivation of VNO input [Graves and Duvall, 1985b; Kardong, 1992]. It provides an alternative method of sensory deprivation, via deafferentation, without direct intervention in the oropharyngeal cavity.

Pilot Studies

During pilot studies on four rattlesnakes, surgeries leaving the VNN partially intact revealed that these snakes continued predatory behavior. Poststrike trailing ability was retained if surgeries left even a few (20–40%) VNN fibers intact.

Sham Operations

The sham surgery did not inhibit or statistically alter rattlesnake behavior from control condition. The sham surgery animals (n = 4) struck, trailed, and swallowed prey at levels comparable to those they exhibited before sham surgery. Sham operated snakes struck 17 of 17 times (100%), followed a choice trail 13 out of 17 trials (76.5%), and swallowed 13 of 13 times (100%).

Control vs. VNX

Significant differences emerged in basic predatory behaviors following cuts in the vomeronasal nerves.

Striking. All eight rattlesnakes prior to surgery (control) struck mice in 40 of 40 (100%) feeding trials. These same eight snakes, following VNN cuts, struck only 16 out of 32 (50%) times (fig. 3). Five of the eight snakes produced the 16 strikes, and all 16 struck mice showed rapid onset of envenomation signs (see Kardong, 1986b, for criteria). Three of the eight snakes in the VNX condition did not strike at all.

Table 1. Trailing ability of snakes in the control condition and in the VNX condition

	Vomic	Avomic
Follow (choice)	31	0
No follow (no choice)	9	32
Total	40 runs (4–6 weeks, 8 snakes)	32 runs (4 weeks, 8 snakes)

Paired t tests of the control versus VNX conditions $t = 13.75$ ($p < 0.0001$, $df = 7$).

Trailing. In the control condition, snakes (n = 8) followed the scent trail of the envenomated mouse in 31 out of 40 poststrike trailing trials (77.5%), the trail of the unstruck mouse once (2.5%), and made no choice eight times (20.0%) (table 1). The same snakes in the VNX condition never exhibited trailing behavior. Out of a total of 32 trials (eight snakes, four weeks), the presented mice were struck on 16 occasions, and the snake was given the opportunity to follow (table 1). The rest of the trials were no-strike situations and the snakes were not released to follow. Therefore, on these 16 occasions, none of the avomic snakes followed a mouse scent trail during the four weeks postoperative.

Five of the eight snakes struck in the VNX condition. Comparison (ANOVA) of the RTF of these five snakes when under control vs. VNX condition showed a significant decline in the RTF [control, $X = 81.9$ (SD, 8.1); VNX, $X = 33.2$ (SD, 15.2); $F1, 4 = 74.9$, $p < 0.0001$]. However, the RTF of these VNX snakes was significantly above their prestrike RTF levels just before the strike [prestrike, $X = 18.2$ (SD, 4.8); VNX, $X = 33.2$ (SD, 15.2); $F1, 4 = 15.6$, $p < 0.001$]. These RTF values for the poststrike VNX conditions were determined after the strike had occurred and 'no choice' trailing behavior ensued.

Swallowing. All snakes in the control condition swallowed mice in 31 of 31 presentations (100%). However, in the VNX condition, none (0%) of these eight rattlesnakes swallowed mice. Three rattlesnakes in the VNX condition were tested on the second and fourth day after surgery and again one week after surgery. Five different rattlesnakes were tested four weeks postoperatively. None (total of n = 8) showed an inclination to swallow the dead mice presented at any tested interval postoperatively.

Histology. Confirmation of complete VNX was further verified by histological examination of the VNO. The normal epithelium contained all three layers of cells: supporting, receptor or sensory, and undifferentiated cell layers [sensu Kubie et al., 1978]. The receptor layer was absent

from the degenerating epithelium of the VNO following section of the VNN (fig. 2).

Discussion

Not all aspects of predatory behavior were affected by deprivation of vomeronasal input. Instead, selective effects of deafferentation emerged in three phases of the predatory behavior.

Striking

The inclination to strike is significantly decreased in the VNX condition, but it is not extinguished entirely. In the control condition, snakes always struck the presented mouse (100%), but with VNN cuts, snakes showed a decrease in the tendency to strike (50%). Rattlesnakes exhibit two basic types of strike behaviors, offensive and defensive [Hayes, 1991; Hayes and Duvall, 1991]. Strikes exhibited by rattlesnakes in VNX condition might have been defensive, offensive, or combinations of both. Although criteria might be used to distinguish these two types of strikes [Hayes, 1991], our experimental setup did not permit scoring of these variables to settle this point.

Trailing

When the VNN was partially intact, rattlesnakes retained predatory behavior and poststrike trailing ability. This is also true for garter snake predatory behavior [Halpern and Kubie, 1984]. When VNO deafferentation was complete, even if the snake struck, it did not exhibit poststrike scent trailing of envenomated prey. Because the olfactory nerve was still intact, this suggests that this alternative route of chemosensory input can not compensate for the loss of sensory input via the VNO during poststrike scent trail following. This supports the view that VNO is the primary chemosensory organ involved in poststrike trailing by rattlesnakes [Chiszar et al., 1990].

Compared to the control condition, VNX snakes that struck mice showed loss of scent trailing. They also exhibited a significant decline in poststrike strike-induced chemosensory searching (SICS), as was demonstrated by the decline in the RTF [Chiszar and Radcliffe, 1976]. Such a decline has been documented in defensive strikes [O'Connell et al., 1982], raising the possibility that in the VNX condition, rattlesnakes that struck did so defensively. However, striking VNX snakes did not exhibit other evidence of defensive behavior. For example, they did not rattle or exhibit distinctive slow, modulated tongue flicks [Gove and Burghardt, 1983; Duvall et al., 1985; Hayes, 1991]. Instead, they head-oriented toward the prey, and often approach the prey before striking, actions associated with predatory behavior [de Cock Buning, 1983a; Hayes, 1991]. Even those VNX rattlesnakes that did not strike exhibited similar evidence of predatory, not defensive, behavior. This suggests that rattlesnakes in the VNX condition retained predatory behavior but, in the absence of VNO stimulation, did not strike at preoperative levels. If these strikes by rattlesnakes in VNX condition were predatory, then the subsequent levels of SICS are apparently also affected by VNO stimulation.

With VNN cuts, rattlesnakes exhibited an average RTF of 33.2. This is significantly below the control condition, but also significantly above the baseline level (18.2 RTF) [Chiszar and Radcliffe, 1976; Kardong, 1986b]. Therefore, SICS occurred in the absence of VNO input but at a substantially reduced level. This implies that SICS are partly independent of VNO stimulation (18.2 vs. 33.2 RTF) and partly dependent upon VNO stimulation (33.2 vs. 81.9 RTF).

Swallowing

Deafferentation removed input from proximate stimuli that are normally received by the VNO and transmitted to the central nervous system. Without VNO input, rattlesnakes cease swallowing prey. Therefore, as in garter snakes, the VNO is important for prey ingestion in rattlesnakes. In garter snakes, prey ingestion declined slowly over several days [Kubie and Halpern, 1979]. In rattlesnakes, however, prey ingestion was abolished by the second day after VNN section and remained abolished for the entire postoperative period (four weeks). Therefore, following deprivation of input from the VNO, rattlesnake prey ingestion declines within several hours [Kardong, 1986b] and is apparently absent by 48 hours (this study) and certainly by more than 48 hours [Graves and Duvall, 1985b].

Overall

Earlier studies of rattlesnake predatory behavior reported declines in strike frequency following VNO deprivation. The degree to which strike behavior declines may be affected by the technique used to produce a VNO deprived condition. When vomeronasal ducts were surgically sutured closed [Graves and Duvall, 1985b], striking ceased entirely, raising the possibility that the mechanical trauma produced by inserting sutures across the oral epithelium itself affected behavior. Alternatively, differences in the degree of strike declines may be related to prior experience of the snakes. For example, if garter snakes are conditioned to anticipate a worm bit reward when searching for prey, there is an opportunity to pair visual, tactile, and perhaps ol-

factory cues with the food reward [Halpern, 1987]. Following vomeronasal nerve lesions, naive garter snakes without such conditioning are more impaired in their prey attack than are conditioned snakes [Halpern, 1987, 1988]. Similar studies have not been done in rattlesnakes, but such effects of conditioning may account for the reported differences [Graves and Duvall, 1985b; Kardong, 1992; this paper] in strike declines in avomic snakes.

Similar learning experiences may affect trailing and swallowing performance. However, the snakes we used had been in captivity for at least seven years. During that time, they had been maintained mostly on live prey that they struck, relocated, and swallowed. Our experimental protocol generally followed this same sequence and was similar to the natural hunting sequence – strike, locate, swallow – exhibited in the wild [Duvall et al., 1985, 1990; Hayes and Duvall, 1991]. This would seem to offer ample opportunity to pair vomeronasally-mediated chemical stimuli with other available sensory systems and give the snakes the experience to trail and swallow envenomated pray in the absence of stimulation of the VNO. This did not happen. Poststrike trailing and swallowing were extinguished completely in these long-term captive snakes when sensory input from the VNO was extinguished. Visual, thermal, tactile, and olfactory cues, as unconditioned cues or as associated, conditioned cues, did not compensate even in part for the absence of VNO input.

In this species of rattlesnake, the vomeronasal system is not required for strike behavior to be elicited, but in its absence, strikes decline substantially. Similarly, the loss of vomeronasal input is accompanied by a complete loss of trailing and swallowing behavior. This supports the view [Graves, 1993] that chemical stimulation of the VNO releases specific behaviors. Therefore, in rattlesnakes, chemical cues mediated through the VNO contribute to elicitation of the strike and are important releasers of predatory trailing and swallowing behaviors.

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