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The Forked Tongue and Edge Detection in Snakes (*Crotalus oreganus*): An Experimental Test

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Many stimulus-detection systems are lateralized to allow for simultaneous comparison of paired stimuli. It has been hypothesized that the deeply forked tongue of snakes and some derived lizards functions as a chemical edge detector where cues gathered by each tine are kept separate to provide two points of lateral odor assessment by the central nervous system via vomeronasal input. While following a chemical trail, one time can be on the trail, the other off, and such differential information prompts the snake to turn back to the trail. The authors tested this hypothesis in rattlesnakes within a predatory context by unilaterally severing the vomeronasal nerves. If edge detection is used by snakes during prey trailing, then unilateral denervation should disrupt trailing ability. The authors found no change in the seven separate trailing parameters measured. Therefore, they found no support for the edge detection hypothesis as it applies to prey trailing behavior. Instead, the deeply forked tongue may represent a chemosensory specialization to increase odor-sampling area, with snakes and derived lizards detecting only the concentration of chemical trails.

Keywords: edge detection, lateralization, vomeronasal, chemoreception, functional morphology

Many animals exhibit lateralization in one or more of their derived sensory systems (e.g., visual, acoustic, chemical), permitting central nervous system processing of separate information from left and right sides (Burne & Rogers, 2002; Lohman & Smeets, 1993). Lateralization enables comparative discrimination between paired stimuli and, conversely, would enhance the information value of a particular stimulus if lateralized detectors can compare input stimuli. The functional significance of lateralization in vertebrates has been most thoroughly examined in the visual and acoustic sensory systems, but comparatively little attention has been given to the role of lateralization in chemical detection systems of vertebrates.

In terrestrial vertebrates, the vomeronasal system (VNS) enables detection of and discrimination between numerous intra- and interspecific chemical signals. The VNS consists of a pair of vomeronasal organs (VNO) lateralized with hypothesized separate processing from each within the telencephalon. In analogy, the VNS is organized much like the antennal system of lepidopterans (moths, butterflies), where both chemical detectors (antennae) and processors (olfactory bulbs) are paired.

We know that many animals are capable of detecting chemical edges where lateral sides of the chemical trail abruptly end (e.g., Peterson & Fitzgerald, 1991; Vickers, 2000), and animals exhibiting such tropotaxis separate their paired chemical detectors maximally to enhance edge detection (see Wyatt, 2005 for a review). The snake's tongue is the chemical detector used to sample environmental odors (Halpern, 1992; Halpern & Kubie, 1983). When protruded from the mouth, the tongue sweeps its spread tines through the air, touches the substrate in front of the animal, and collects a collage of chemical stimuli (Gove, 1979; Ulinski, 1972). The tongue then transfers its chemicals to the vomeronasal system via blind-ended ducts leading to each VNO (Gillingham & Clark, 1981; Young, 1990). The tongue tines may deliver their chemicals to the paired plicae in the floor of the mouth, but destruction of the plicae does not significantly impair transfer of odors to the VNO from the tongue, suggesting that the plicae may not be important in maintaining lateralization of this system (Halpern & Borghjid, 1997). Chemical cues in the lumen of the VNO bind to the sensory epithelial receptor cells of the VNS (Jiang et al., 1990), and the axons of the receptor cells bundle together to form the vomeronasal nerve (VNN). Each VNN projects from its own VNO to its corresponding accessory olfactory bulb (Lohman & Smeets, 1993). This tongue-based system is part of vomerolfaction rather than the more familiar olfaction, which is based on stimulation of the sensory epithelium in the nasal cavity (Cooper & Burghardt, 1990).

Currently, it is believed that the snake's forked tongue functions as an edge detector (Schwenk, 1994). When the tongue tines are

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spread and tap a chemosensory trail, each tine gathers separate chemosensory cues that it then delivers to its own VNO. This would allow lateralized comparison by the central nervous system of differing point stimuli. A snake that deviates from a chemical trail can thus use the differences in point stimuli to make decisions during trailing that directly affect trailing efficiency (Schwenk, 1994).

Rattlesnakes are a good group of snakes for studying chemical trailing behavior because they engage in a stereotyped, specific behavior pattern called strike-induced chemosensory searching (SICS, Chiszar, Radcliffe, & Scudder, 1977). After an envenomating strike, rattlesnakes quickly release rodent prey to separate themselves from the danger of prey retaliation (Furry et al., 1991). The released rodent dies some distance away and must be relocated (Chiszar & Radcliffe, 1976; Fitch & Twining, 1946), which forces rattlesnakes to be excellent chemical trailers. Indeed, the venom-injecting strike is a behavioral releaser of specific, stereotypic trailing behavior (Chiszar & Radcliffe, 1976; Chiszar et al., 1982). Rattlesnakes can successfully distinguish the odor trail of the struck mouse from all other competing substrate odors, including the odor of the same mouse before it was struck (Chiszar, Radcliffe, Feiler, & Duvall, 1983). The poststrike trailing behavior pattern of rattlesnakes is a predictable, quantifiable bioassay with components that will change significantly after disruption of the edge detection system.

The edge detection hypothesis predicts that snakes can both detect and react to differences in chemical cues gathered by the two tines to determine when they stray from a trail. We compared chemosensory trailing performance in rattlesnakes before and after unilateral vomeronasal nerve severing (VNX) compared to a control surgery condition (SHAM). Unilateral VNX should result in no trail scent being sensed at that ipsilateral brain level. Absence of trail scent on the VNX side should result in the "normal" trail response wherein the snake should turn toward the intact side to bring it back on trail. We know from other work that rattlesnakes do not engage in poststrike trailing if both VNNs are severed (Alving & Kardong, 1996), and that other snakes have abolished/altered trailing behavior if both VNO ducts are sealed or if tongue tines are severed (Kahmann, 1932). However, we do not know the effect that unilateral VNN severing will have on either trailing success (relocation of prey) or trailing behavior patterns (e.g., turning behavior, trailing time).

Method

Subjects

We used 20 individually housed Pacific rattlesnakes, *Crotalus oreganus* (adult, long-term captives) collected locally in Whitman Co., WA (USA), under state permits. Length of captivity has been shown to have no significant effect on this rattlesnake's predatory behavior (Alving & Kardong, 1994). Snakes were fed white laboratory mice (Swiss Webster) twice a month and provided water ad libitum. All mice were fed Harlan Teclad 8640 Rodent Diet mouse chow and kept on the same bedding of hard wood shavings. All experimental and husbandry protocols received prior approval by the Institutional Animal Care and Use Committee at Washington State University.

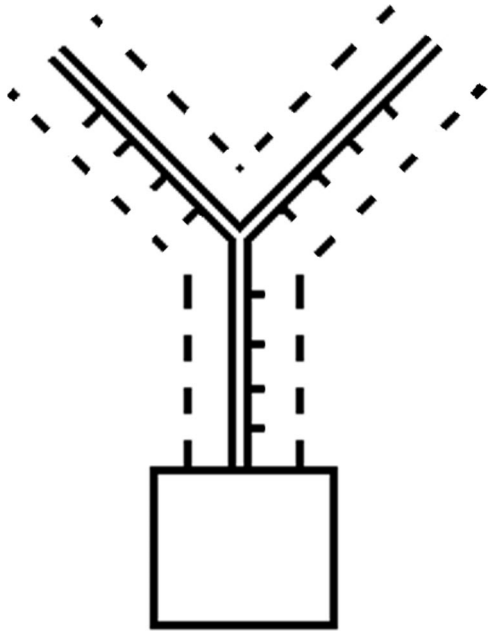

Figure 1. Diagram of the experimental setup. The Y-shaped outline had equal-length arms (50 cm each) with hatch-marks along the base and right arm at 10 cm intervals. The dashed lines represent the perimeter as described in the Methods. The square at the bottom represents the holding box.

Testing Arena Protocol

We conducted all trials in an arena (1.25 m each side) described elsewhere in detail (Lavín-Murcio et al., 1993; Robinson & Kardong, 1991). Temperature in the testing room was held between 25 and 30°C. A Y-shaped outline (see Figure 1) made of black tape was placed on the floor of the arena and covered with a new piece of white butcher paper before each trial. Parallel marks, 10 cm from the trail on either side, allowed us to score the time the snake spent outside and inside this perimeter from the Y-shaped trail. From previous work (e.g., Smith, Kardong, & Lavin-Murcio, 2000), we know that rattlesnakes with intact VNS swing their heads no further than 10 cm to a side while trailing. The Y-outline, 50 cm each arm and the base, could slightly be seen through the white paper and was used to guide the placement of scent trails. The Y-outline is visually homogenous once the snakes reach the junction of the Y, so it would influence neither choice nor trailing behavior in the maze.

Before each trial, we removed a snake from its home cage and placed it in a holding box stationed at the beginning of the Y-outline for 12 hours. Rattlesnakes reliably exhibit trailing behavior only after envenomating prey (Chiszar, Hobika, Smith, & Vidaurri, 1991), so we allowed snakes to strike the mouse they would trail before every trial. The dead mouse was then used to stroke a scent trail along the base of the Y-outline and out one arm, and then the door to the holding box was opened. Based on previous poststrike trailing studies (Kardong & Smith, 2002; Parker & Kardong, 2005), we scored seven performance variables from overhead videos of trailing episodes (see below). Following the baseline trials, we anesthetized snakes and cut the vomeronasal

nerves of one side using sterile surgical procedures (Young & Morain, 2002). Seven to 10 days postsurgery, we ran the same snakes in an identical set of trials and then scored the same performance variables of trailing behavior. The 7 to 10 day interval was chosen because full recovery from surgery occurs in that time, and it precedes any significant nerve regrowth (Alving & Kardong, 1996). Snakes were placed in clean, odor-free cages following surgery to reduce/eliminate exposure to stimuli that may have facilitated neural compensation after sensory deprivation.

Odor Trails and Data Gathering

We introduced a mouse down a front chute to the holding box, allowed the snake to strike it, and then safely removed both the mouse and the chute. The dead mouse was placed ventral side down in a clear plastic sheet with a thin section removed to create a narrow slit (1 × 7 cm) for exposing a standardized width of the mouse scent trail (1 cm). We created the scent trail in one continuous stroke along the substrate from the holding box down the base of the Y and out one arm within a consistent time frame (16 s ± 2 s) and then removed the mouse and sheet from the arena. The room lights were dimmed, the door to the holding box opened, and snake-trailing behavior was videotaped from overhead. Trials were complete when either the snake reached the end of one arm of the Y or 20 minutes had elapsed. Scent-contaminated equipment (chute, plastic sheet, arena walls, holding box) was cleaned (70% ethanol) or replaced with fresh material (butcher paper) before the next trial, and the arm of the Y receiving the mouse odor was determined by coin toss each trial. The snakes were allowed to eat the mice they struck in both experiments to control for hunger effects on trailing behavior.

Scored Variables and Statistics

From playback of the videotapes, we scored seven variables that are significant indicators of rattlesnake poststrike trailing (Chiszar & Radcliffe, 1976; Parker & Kardong, 2005). Rattlesnakes tend to emerge several times from the holding box during any trial (unpublished observations), so some variables were recorded during the first emergence and others during the final emergence. *Total trailing time (sec)*: time from the last emergence of the snake from the holding box until it completed the Y-shaped course. *Time outside perimeter (sec)*: time spent outside the 20 cm perimeter of the trail (10 cm to either side) during the last emergence. *Rate of tongue-flicking* (*RTF*): number of tongue-flicks divided by the time spent trailing (min) during the last emergence. *% Tongue-flicks on trail*: number of tongue-flicks directed at the chemical trail divided by the total number of tongue-flicks during the entire trailing episode. *Crossings*: number of times the snake's head crossed the mouse odor trail. *Turnarounds*: number of times a trailing snake turned farther than 90 degrees to the left or right from the line of the trail as it advanced away from the holding box (Parker & Kardong, 2005). We used paired *t* tests ($\alpha = .05$) to see if there were significant effects of denervation on the mentioned behavioral variables between pre- and postsurgery conditions.

Surgical Procedures

We used a dorsal, surgical window between the frontal and nasal bones to directly expose the VNN (Young & Morain, 2002), a modification of Halpern and Kubie (1980), which permits direct visual identification of each VNN tract before severing. For anesthesia, snakes were initially placed in a sealed container with a cotton ball soaked with 1.5 ml Isoflurane for 30 min. They were then maintained on a low anesthetization plane during sterile surgery by inhalation of 3% Isoflurane mixed with air (1 L/min). Administration of the Isoflurane/air mixture followed de Cock Buning (1983), whereby a one-way flow was established through the lung.

We began surgery after a snake reached the anesthetic plane: the point where tail retraction and righting reflex were extinguished. We periodically monitored heart rate to assess the level of anesthesia. All surgeries were performed using a Wild dissecting scope. Once the surgical window was cut, the exposed blood sinus overlying the nerves was reflected to expose the VNN. Upon unilateral isolation of the VNN and identification of the band by both surgeon and assistant, the nerves were lifted and cut in the VNX snakes. In the SHAM snakes, the VNN band was exposed but left intact. The surgical window was sutured and sealed with tissue glue (cyanoacrylate). Snakes were brought out of anesthesia by flushing the lung with air until the return of distinctive reflexes (e.g., righting reflex). The snake was returned to its home cage and periodically observed over the course of 24 hours and each day thereafter. We then began the second round of behavioral trials 7 to 10 days postsurgery. Upon completion of the experiment, three randomly selected animals were euthanized, and the efficacy of the surgery was confirmed through both dissection ($n = 2$) and histology ($n = 1$). For histology, the snake's head was decalcified then dehydrated through an ethanol series before paraffin embedding. Coronal sections (10 μm) were cut on a microtome, placed on gel-coated slides, and stained with hematoxylin and eosin for light microscopy. For dissection, we used a previous method (Alving & Kardong, 1996), wherein the surgical window in preserved heads was reopened to inspect the surgery. This confirmed that visual identification and severing of the VNN during surgery was completely reliable. Consequently, ethical considerations identified by IACUC made it unjustified to continue to sacrifice animals for purposes of nerve cut verification.

Results

The surgical treatment had no effect on prey relocation success: all rattlesnakes chose the arm containing the poststrike scent trail both before and after unilateral severing of the vomeronasal nerves in both the SHAM ($n = 10$) and VNX ($n = 10$) groups. Rattlesnakes exhibited no statistically significant change in any of the poststrike trailing behavior patterns we measured after either surgical treatment. Because of this, the differences between pre- and postsurgery are reported for the VNX snakes only (see Figure 2). Specifically, there were no significant differences in total trailing time (paired $t_{(9)} = 0.55$, $p > .5$, 95% Confidence Interval [C.I.] for the difference in *M*s = −9.858 to 19.058 seconds), time outside perimeter (paired $t_{(9)} = 0.33$, $p > .5$, 95% C.I. = −16.469 to 24.069 seconds), RTF (paired $t_{(9)} = 1.07$, $p = .3$, 95% C.I. = −19.728 to 7.036 tfs/min), % tongue-flicks on trail (paired $t_{(9)} = 0.12$, $p > .5$, 95% C.I. = −0.0890 to 0.0802), crossings (paired $t_{(9)} = 1.95$, $p = .08$, 95% C.I. = −0.0174 to 5.617), or turnarounds (paired $t_{(9)} = 0.39$, $p > .5$, 95% C.I. = −2.239 to 1.639). Effect sizes (derived from Cohen's *D*) for each set of variables were as

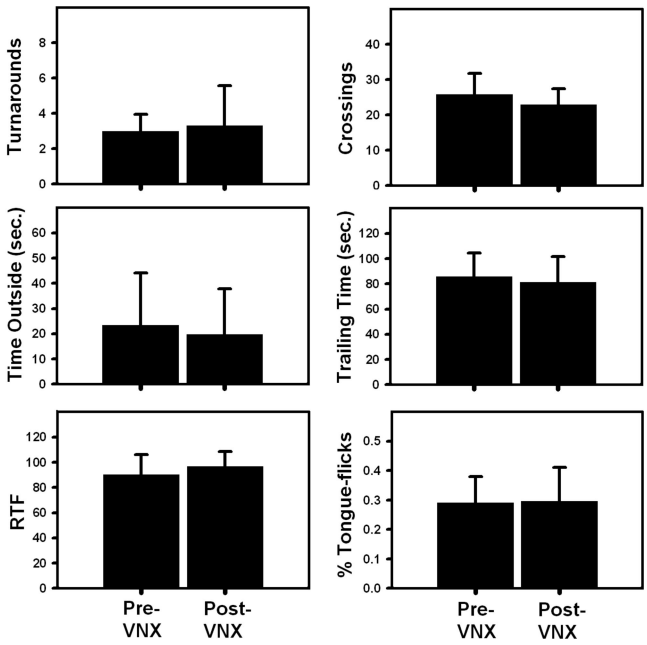

Figure 2. Results. Six behavioral parameters were scored before (Pre-VNX) and after (Post-VNX) unilateral severing of the vomeronasal nerves (VNN) in 10 snakes. The bars represent mean (+*SE*) values. The surgical treatment had no significant effect (paired *t* tests). Turnarounds were 90 degree turns to either side while trailing, crossings were passes of the snake's head over the chemical trail, time outside was time spent outside the 20 cm area surrounding the trail, RTF was the rate of tongue-flicking (tongue-flicks/min), and % tongue-flicks was the percentage of tongue-flicks contacting the trail. CIs (95%) for the difference in means are provided in the text (see Results). SHAM results are not depicted.

follows: total trailing time, 0.234; time outside perimeter, 0.195; RTF, −0.455; % tongue-flicks on trail, −0.043; crossings, 0.528; and turnarounds, −0.173. After VNX, none of the snakes showed circling behavior, and all remained close to the prey trail moving along it as quickly as before denervation.

Discussion

Our results show no evidence that rattlesnakes use their forked tongues as chemosensory edge detectors to keep them on a post-strike scent trail of a mouse. There were no statistical differences in the behavioral variables measured after VNX compared to the intact condition. Therefore, we find no behavioral evidence to support the edge detection hypothesis as it applies to rattlesnakes while poststrike trailing.

If rattlesnakes used edge detection as hypothesized, then several differences should have emerged after denervation. First, rattlesnakes should have exhibited more turnarounds after VNX. Rattlesnakes turn around often in the presence of a weak or ambiguous chemical signal (Parker & Kardong, 2005). Presumably, decreased quality or quantity of a chemical signal will prompt turning behavior in snakes while trailing. If the tongue functions as an edge detector, odors would only have been sensed on the intact side after the snake's tongue came into contact with the chemical trail, resulting in a central nervous system prompt to turn back in the direction of the innervated VNO. This did not occur after unilateral VNX.

A second predicted behavioral response was increased trailing times after VNX. If edge detection is a significant feature of odor trailing and input from one of the tines is eliminated, it should have taken significantly longer for snakes to follow prey trails. This did not happen; trailing times after VNX did not increase. Trailing times may have remained constant if the snakes had increased their rates of tongue-flicking (RTF). This increase in RTF is expected if edge detection is required for differential sampling of chemosensory cues and accurate trailing. No change in RTF emerged after VNX.

Our results may be related to the predatory chemosensory cues we tested rather than testing pheromone (intraspecific) trails (see Ford, 1986; Ford & Low, 1984). Edge detection requires separate collection and processing of chemical cues from left and right tines. However, it has been shown in garter snakes by using radioactive tracer that odorants arrive in both VNOs after the removal of one tine (Halpern & Kubie, 1980). Thus, chemosensory cues can be shared between the VNOs and may not be reliably separated and evaluated. This suggests that the ability to edge-detect may be lost during the mechanical stage of chemical delivery, which occurs before the sensory processing level we manipulated.

Two previous studies of trailing in snakes have explicitly interpreted their experimental results as evidence of edge detection. In one (Ford & Low, 1984), male garter snakes were filmed as they followed female pheromone trails, and males turned back to the odor when one tine exceeded the edge of the trail. Unfortunately, those observations were qualitative, so no statistical treatment was used with those data. In our study, we could only observe when the tongue, not individual tines, hit the trail, but it would be informative to use high-speed video to determine any minute changes in tongue flicking that may occur after unilateral VNX. In a second previous study (Waters, 1993), snakes exposed to prey odor turned in the direction of the intact VNO after unilateral blockage of one duct of the VNO. However, the snakes were exposed to airborne odors, which are more likely detected by the olfactory system (Halpern, Halpern, Erichsen, & Borghjid, 1997). We also know that rattlesnakes with intact VNOs turn in the presence of airborne cues (Parker & Kardong, 2005), and the absence of substrate cues can alone increase turning frequency (Parker & Kardong, 2006). Zuri and Halpern (2003) showed that intact VNOs are necessary for discrimination of airborne stimuli, but recognition of airborne stimuli, which presumably initiates exploration of an airborne chemical plume, is accomplished by olfaction.

Instead of edge detection as an explanation for the deeply forked tongue, we adopt the alternative view suggested by Schwenk (1996) that the paired tines are spread widely apart during tongue-flicking to increase sampling area and increase turbulence of the chemical milieu in the environment. This is consistent with other studies where removal of one tine reduced overall delivery of odorants to the VNOs (Halpern & Kubie, 1980); however, significant behavioral changes during trailing only occur if both tines are removed (Burghardt & Pruitt, 1975; Wilde, 1938). As both tines are removed, the sampling area, and hence concentration of odorants, is markedly reduced, which reduces delivery of chemical cues to the VNS and leads to modified behavioral responses. In the

case of single tine removal or denervation of one VNO (this study), the central nervous system (CNS) may not be capable of detecting this change or its effect is inconsequential, which would explain our observation of no difference in behavioral responses pre- and postsurgery.

Edge detection may play a subtle role in chemosensory trailing that our experimental design could not assess. It may also be possible that snakes, like other animals, compensate after sensory deprivation, and in our case, they may have compensated at the CNS level to heighten perception of and reaction to VNO stimuli. However, given the design and outcome of our study, we found no evidence to support the edge detection hypothesis in this predatory context. The functional significance of the deeply forked snake tongue may simply be to increase chemosensory sampling area. In turn, chemosensory trailing may be based on VNS detection of changes in total odor concentration on and off the trail as sensed by the tongue as a single, not paired, chemosensory sampling tool.

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