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Rate of tongue flicking by rattlesnakes during successive stages of feeding on rodent prey

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Specimens of each of three species of rattlesnakes (*Crotalus enyo enyo, C. durissus culminatus,* and *Crotalus vegrandis*) exhibited no tongue flicking prior to striking live mice during a regular feeding session. All snakes flicked their tongues at high rates (more than 20 flicks/minute) between striking and commencement of swallowing. Also, frequent tongue flicking (10 to 15 flicks/minute) was seen for about 15 min after swallowing. These data indicate that well-acclimated, captive rattlesnakes do not rely upon the Jacobson's organ to detect prey or to guide the predatory attack, but that they do use this sensory system to locate prey after striking. Since an envenomated rodent may wander several meters prior to dying, Jacobson's organ may be very important in finding such prey. It is also of interest that renewed tongue flicking occurs after swallowing. A hypothesis is offered concerning the role of the latter behavior.

Garter snakes and other natricine snakes detect and locate prey mainly by the Jacobson's organ (paired sacs which open into the roof of the mouth and which receive chemical input from the tongue). Indeed, a cotton swab soaked in a solution of surface substances from potential prey will be sampled with the tongue and attacked as if it actually was a prey organism, indicating that olfactory cues are sufficient for the release of both appetitive and consummatory behavior and that visual cues are probably unnecessary (Burghardt, 1969; see Burghardt, 1970 for a review of the literature). In vipers and pit vipers, however, olfactory cues seem less important for initial appetitive behavior (orientation and approach to prey) and for striking than for subsequent trailing and ingestion. Although rattlesnakes can detect rodent prey by odor alone (Cowles & Phelan, 1958), these snakes seem always to strike a live (and moving) mouse when given the choice between live and freshly killed mice, indicating that visual cues are most salient. Moreover, it is our impression that few, if any, tongue flicks are seen before the strike, indicating that no air sampling is required (presumably because visual and/or thermal information is sufficient). The purpose of the present study is to compare the frequencies of tongue flicking during various stages of feeding in order to determine if, in fact, air sampling occurs more often after striking rather than prior to it. Such data should indicate the relative importance of the vomeronasal system during different stages of the feeding episode.

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METHOD

Subjects and Maintenance Conditions

Six rattlesnakes (two *Crotalus enyo enyo:* females, about 4 years old and 40 cm; two *Crotalus durissus culminatus*: males, both about 3 years old and 75 cm; two *Crotalus vegrandis*: one male and one female, both about 3 years old and 50 cm) in the collection of the second author were observed in this study. All snakes had been in captivity for at least 2 years and were maintained in individual glass terraria (50 x 27.5 x 30 cm) kept at 26°-24° C during the light period (0800-2200) and 22°-24° C during the dark period. Each animal was fed one to three adult mice every 2 weeks; the present observations were made during the attack upon and consumption of the first mouse of a regular feeding session for each snake (in its home cage). Care was taken so that the mouse could not be seen by the snake prior to its actual introduction into the cage.

Procedure

During 5 min prior to the introduction of a live adult mouse, the number of tongue flicks emitted by each snake was recorded. This frequency was taken to be the prefeeding baseline. Next, we recorded the number of tongue flicks emitted by each snake between the time the mouse was introduced and the time the snake struck. Third, a count was made of the number of tongue flicks emitted between the strike and the point at which each snake grasped the mouse preparatory to swallowing. Finally, each snake was observed subsequent to swallowing until the prefeeding baseline was recovered, and the number of tongue flicks was recorded after each minute. All recording was done with the aid of hand-held counters which were incremented upon each tongue flick; the observer was seated 1 m from the terrarium front throughout the entire period. (These snakes were accustomed to the presence of humans and no defensive or other unusual behaviors were noted.)

RESULTS

Table 1 contains a summary of tongue-flick frequency for each stage of feeding together with the temporal duration of each stage. Separate frequencies are shown for each individual, and means are shown for species as well as for the entire group of snakes. Almost no tongue flicks occurred during the prefeeding period, indicating that the snakes were relatively inactive or

Table 1
Mean Number of Tongue Flicks Per Minute by Six Rattlesnakes During Each of Four Stages of a Feeding Episode (Prey = Live Adult Mice)

Stage	Prefeeding	Introduction of mouse until the strike	Strike until commencement of swallowing (i.e. trailing)	After swallowing until recovery of prefeeding baseline	
Mean Duration =	5 min (±0)	0.25 min (±.1)	5.8 min (±1.7)	17.5 min (±2.7)	
				First 5 min only	Entire period
C. e. enyo	0.0	0.0	57.0	16.4	17.5
C. e. enyo	0.2	0.0	21.4	8.6	15.1
Mean	0.1	0.0	39.2	12.5	16.3
C. d. culminatus	0.4	0.0	18.5	9.4	16.3
C. d. culminatus	0.2	0.0	26.2	13.2	7.2
Mean	0.3	0.0	22.3	11.3	11.7
C. vegrandis	0.0	0.0	25.8	18.2	8.0
C. vegrandis	0.0	0.0	35.3	14.2	8.7
Mean	0.0	0.0	30.5	16.2	8.3
Mean over all snakes	0.1	0.0	30.7	13.3	12.0

sleeping. Striking occurred almost immediately upon the introduction of prey, implying that the snakes detected the presence of the mouse almost at the instant of its presentation. However, no snake emitted tongue flicks *prior* to striking. On the other hand, every snake emitted many tongue flicks between the time of striking and the time ingestion began. Some of these flicks were emitted while the snake was trailing the prey (the mouse usually moved 10 to 20 cm from the snake before dying), and the rest were emitted while the snake was examining the mouse carcass preparatory to ingestion. (The snakes usually swallowed adult mice head first, and it appeared that snakes were locating the heads of their respective mice in part through the use of Jacobson's organ.)

Tongue flicking ceased when each snake began to swallow and commenced again when the bulk of the prey had passed into the esophagus. At this time each snake initiated an active bout of investigation (i.e., lingual air sampling) during which its terrarium was systematically examined. This episode lasted an average of 17.5 min, after which the animals coiled themselves into resting-sleeping postures that were comparable to those seen during the prefeeding observation.

DISCUSSION

These data strongly suggest that well-acclimated, captive rattlesnakes do not rely upon Jacobson's organ (and perhaps not upon nasal olfaction either) for initial detection and striking of live rodent prey; this conclusion agrees with data on the importance of visual and thermal cues (see Klauber, 1972, for a review). However, since rattlesnakes typically release the prey after striking and since the prey may wander off before dying, the snake is left with the problem of trailing the prey. It is known that European Vipers (*Viper aspis*) accomplish this task mainly by use of Jacobson's organ, nasal olfaction making little additional contribution (Baumann, 1927, 1928). The present data indicate that rattlesnakes also rely upon Jacobson's organ during trailing, since this stage of feeding was characterized by the highest tongue-flick rate (see also Dullemeijer, 1961). Indeed, it is our hypothesis that chemical cues are not required until the rattlesnake strikes prey, and that some aspect(s) of striking (taste cues, proprioception, etc.) activates the tongue-flick system.

It is interesting that tongue flicking continues for some time after swallowing. Perhaps this would allow the snake to detect additional prey that might have remained in the vicinity. If a snake enters a rodent burrow, the probability is high that more than one mouse will be present, and natural selection would probably favor a predator who conducts a thorough investigation of such a place even after eating its first prey. This may be especially true when mice are prey because these animals do not seem to exhibit fear and/or escape responses in the presence of rattlesnakes, even after seeing other mice attacked and devoured by rattlesnakes (Chiszar, 1975). In any case, it would be valuable to determine if postingestive tongue flicking enables rattlesnakes to locate potential prey (i.e., a freshly killed mouse) or other kinds of stimuli which might not otherwise be detected.

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