

## STRIKE-INDUCED CHEMOSENSORY SEARCHING OCCURS IN LIZARDS

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**Abstract**—Strike-induced chemosensory searching (SICS), previously known only in snakes, is experimentally demonstrated in a lizard, *Varanus exanthematicus*. Tongue-flicking rate was significantly greater after striking the prey than following three control conditions. The occurrence of SICS in a varanid lizard suggests that SICS may serve to help relocate dropped or escaped prey not only in snakes, but in other squamates that use the tongue as a chemosensory sampling device during foraging. This in turn suggests the need for further studies of the taxonomic distribution of SICS in squamates and of its relationship to tongue use during foraging and feeding.

**Key Words**—Lacertilia, *Varanus exanthematicus*, Varanidae, prey odor, tongue-flicking, chemosensory searching.

### INTRODUCTION

Strike-induced chemosensory searching (SICS), an elevated tongue-flicking rate observed in snakes following biting, presumably helps these predators to find and follow odor trails of released or escaped prey. It is distinct from trailing itself, being restricted to the increased tongue-flicking rate (Chiszar et al., 1983). The term SICS may thus be interpreted as a poststrike elevation in tongue-flicking rate with no necessary implication that SICS facilitates location of prey by lizards. The elevation in tongue-flicking rate is a specific sequel of striking; rattlesnakes show much higher tongue-flick rates after striking prey than after detecting prey odors (Chiszar and Scudder, 1980). Rattlesnakes also follow scent trails of prey with higher probability after striking and envenomating than after merely seeing (and perhaps smelling by primary olfaction) the prey with-

out striking (Golan et al., 1982). SICS has been studied primarily in venomous snakes that employ a strike-release-trail strategy, which allows them to eat dangerous prey with a greatly reduced chance of being injured (e.g., Chiszar and Scudder, 1980; Chiszar et al., 1982, 1983, 1985, 1986; O'Connell et al., 1982, 1985; Radcliffe et al., 1986).

SICS has also been demonstrated recently in two species of nonvenomous snakes that do not use a strike-release-trail strategy (Cooper et al., 1988). Thus, SICS may have evolved initially to facilitate location of prey known to be nearby, prey that escaped after being bitten. If this hypothesis is correct, SICS might well occur in any squamate that uses the lingual-vomer nasal system extensively during foraging. Occurrence of SICS in a widely foraging lizard such as a monitor (*Varanus*) would be consistent with this hypothesis but would greatly diminish the tenability of the hypothesis that SICS evolved initially in venomous snakes as part of the strike-release-trail strategy.

It was felt that varanids were the lizards most likely to exhibit SICS because varanids have advanced snakelike tongue structure and function, tongue-flick extensively during social situations and during active foraging, and accurately discriminate prey odors from control odors in tongue-flicking tests. Members of the family Varanidae are noted for tongue-flicking during social encounters, especially at their outsets (Auffenberg, 1981; Moehn, 1984; Davis et al., 1986), and during active foraging (Vogel, 1979; Auffenberg, 1981, 1984). The mechanism of transport of chemical cues from the tongue to the vomeronasal organ has not been directly demonstrated in any lizard and the tongue's tips appear not to enter the vomeronasal cavity in monitors (Oelofsen and van den Heever, 1979). However, molecular transfer from tongue to vomeronasal epithelium has been shown in the garter snake (*Thamnophis sirtalis*) (Halpern and Kubie, 1980). Furthermore, there is ample evidence that lizards of several families respond to prey odors and conspecific odors detected by tongue-flicking (e.g., Burghardt, 1973; Duvall, 1979; Simon, 1983; Cooper and Vitt, 1984, 1986; Von Achen and Rakestraw, 1984). In the only laboratory study of varanid responses to prey odors, *V. exanthematicus* fed a consistent diet of mice (*Mus musculus*) in the laboratory show significantly higher tongue-flick attack scores in response to cotton-tipped applicators bearing mouse odors than to those bearing water or cologne (Cooper, 1988).

Varanid tongues appear to be more structurally and functionally specialized as chemosensory sampling devices for the vomeronasal system than those of other lizards. The lingual structure is more similar to that of snakes than that of other lizards in being long and narrow with highly developed tines (McDowell, 1972) and in being devoid of taste buds (Schwenk, 1985). In *V. exanthematicus* the tongue is primarily a chemosensory sampling device that plays no part in food transport during feeding (Smith, 1982). During tongue-flicking, a greater relative area of air is sampled by varanids than by other

lizards. The relative area sampled is comparable to or greater than that of several species of advanced snakes (Gove, 1979).

This study was designed to determine whether SICS occurs in the savannah monitor, *Varanus exanthematicus*. Because this lizard does not normally release living prey after biting, it was necessary to pull the prey from the lizard's mouth. This further required an experimental control for effects on tongue-flicking rate of handling the lizard in addition to the usual controls for disturbance caused by opening the cage, presence of the experimenter, and visual prey cues.

#### METHODS AND MATERIALS

Seven savannah monitors obtained from a commercial dealer were between 284 and 352 mm snout-vent length. Although these lizards appear to feed primarily on invertebrates in the field (Cisse, 1972), they readily consume mice (*Mus musculus*) in the laboratory. The lizards were housed in a laboratory building having translucent walls and a retractable roof that was opened on clear days. They were housed individually in  $49 \times 49 \times 32$  cm glass terraria. Each terrarium contained a sand substrate and water bowl and was covered by a hardware cloth top. Prior to the experiment, the lizards were fed almost exclusively living adult mice.

Each individual was tested in four stimulus conditions, one per day, in random sequence, on May 25-29, 1987, at temperatures from 32.8 to 34.5°C; no tests were conducted on May 27. One condition was a disturbance control (forceps condition) for effects of the presence of the experimenter's hand and opening the cage on tongue-flicking rate. In this condition, the cage top was opened and the experimenter's hand and feeding forceps were placed in the cage for 10 sec and then removed. The ends of the forceps were positioned approximately 10 cm anterior to the monitor's head in this and the other conditions. The second experimental condition consisted of visual presentation of a living adult mouse (mouse condition) for 10 sec without allowing the lizard to closely approach or attack. If the lizard attempted to attack, the mouse was immediately withdrawn. The third stimulus condition served as a control for the effects of pulling bitten prey and lizard apart (pull condition). In this condition, the lizard was pulled away from the mouse just before biting the mouse. When immediate attack seemed probable, as indicated by the lizard's approach and posturing, the experimenter rapidly withdrew the mouse and simultaneously grasped the lizard, pulling it away from the mouse to prevent any oral contact. In the fourth stimulus condition, the mouse was pulled out of the lizard's mouth immediately after having been bitten (strike condition).

Tongue-flicks were counted in all conditions for 2 min after termination of the experimental stimulus. Data were analyzed for homogeneity of variance by

Hartley's test, were square-root transformed, and then were analyzed by a repeated measures design (randomized blocks). Individual comparisons among means were made using Newman-Keuls tests (Winer, 1962). Statistical tests were two-tailed with  $\alpha = 0.05$ .

Although counterbalancing the order of conditions would have been preferable to randomization, too few specimens were available. The sequences actually used showed little deviation from an incompletely counterbalanced design. In the first two and second two trials, the conditions occurred with the following frequencies: forceps condition (3, 3), mouse condition (2, 4), pull condition (3, 3), and strike condition (2, 4). Sequence had no effect on rank tongue-flick rate for individuals. The two lizards in which the strike condition came last had much higher rates in the strike trial than in the others, indicating that the effect does not disappear due to rapid habituation to the general experimental situation.

Testing for the presence of SICS is a difficult experimental problem because handling or similar mechanical disturbance cannot be readily avoided. The experimental design used here seems drastic at first encounter. It is initially somewhat disturbing or offensive because experimenters usually take great pains to avoid disturbing subjects in behavioral studies. Two problems are that (1) the increase in tongue-flicking rate attributed to striking could have merely represented greater disturbance in the strike condition than in the other conditions and (2) there is no adequate control for tactile stimulation to the mouth resulting from pulling the prey out of it. In the study on SICS in nonvenomous snakes, these problems were addressed by determining tongue-flick rates in garter snakes in a control study. In each trial, the experimenter picked up a snake and then forced into its mouth a cotton-tipped applicator bearing either distilled water only or distilled water plus prey odor. Tactile stimuli and mechanical disturbance were identical in the two conditions, yet the snakes emitted much higher tongue-flick rates in the 5 min following the fish odor presentation (Cooper et al., 1988). Thus, it appears that neither mechanical disturbance nor tactile stimulation to the mouth produce spurious indication of SICS and that the experimental design used is appropriate.

Pulling the monitors by hand is an essential control condition for this experiment because separating the lizards from bitten prey required pulling the prey out of their mouths by simultaneously grasping lizard and prey. Pulling is a rather drastic disturbance in both the strike and pull conditions. Grasping a snake in itself may produce an increase in tongue-flicking rate (Scudder and Burghardt, 1983). In a study of SICS in garter snakes (*Thamnophis sirtalis parietalis*) and corn snakes (*Elaphe g. guttata*), pulling the snakes and visually presenting prey induced roughly equal increases in tongue-flick rate (Cooper et al., 1988). Importantly, in both species, a significant further increase occurred when the snakes were allowed to strike prior to being pulled.

## RESULTS

The monitors tongue-flicked in all conditions, often at substantial rates when exposed to prey. There was substantial behavioral variation among individuals in tongue-flicking rates, with one individual having the highest rate in three of the four conditions and another the lowest in two of four. Attack behavior also varied in its dependence on chemical cues. One lizard attacked immediately in all conditions, with no apparent chemosensory investigation. Its data were discarded, reducing the sample size for analysis to six. Tongue-flicking rates in the 2 mins following stimulus removal differed greatly among treatments, with the highest rates being elicited by strikes and the lowest by merely opening the cage and presenting a hand (Figure 1).

Because between-condition variances were not homogeneous (Hartley's  $F_{\max} = 34.17$ ;  $df = 4, 5$ ;  $P < 0.05$ ), data were subjected to square-root transformation. Variances of the transformed data were homogeneous ( $F_{\max} = 9.25$ ;  $df = 4, 5$ ;  $P > 0.05$ ). Using transformed data, the main treatment effect was

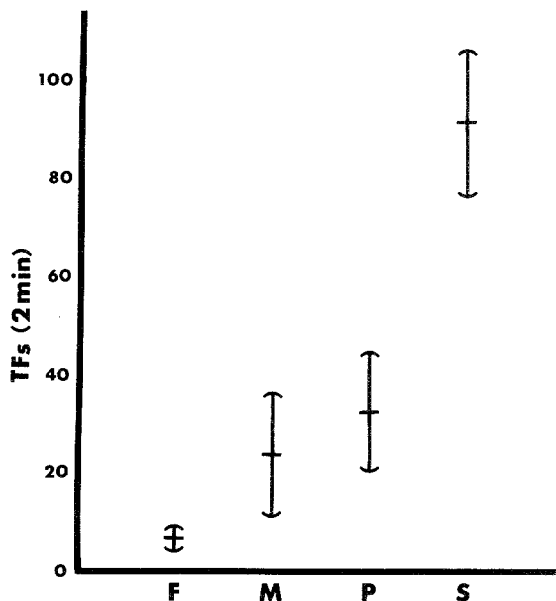


FIG. 1. Tongue-flicks emitted by *Varanus exanthematicus* in the 2 min following removal of the experimental stimuli. F = presentation of empty forceps for 10 sec. M = presentation of forceps and mouse for 10 sec. P = pulling lizard away from prey just prior to strike. S = lizard allowed to strike prey, but prey then removed. Data shown are means (horizontal lines)  $\pm 1$  SE.

highly significant ( $F = 20.54$ ;  $df = 3, 15$ ;  $P < 0.001$ ). Newman-Keuls tests revealed that the mean tongue-flicking rate following striking was significantly greater than that in each of the other conditions at  $P < 0.01$ . Visual presentation of the mouse plus pulling the lizard away from mouse when striking was imminent (pull condition) induced significantly higher tongue-flicking rates than did the disturbance control (forceps condition) without prey ( $P < 0.05$ ), but the substantial difference between rates for visual presentation alone (mouse condition) and for disturbance (forceps condition) did not quite attain significance. Neither did the rates for visual presentation of prey (mouse condition) and visual presentation plus pulling the lizard (pull condition) differ significantly.

#### DISCUSSION

The primary finding is that SICS occurs in a lizard. A poststriking increase in tongue-flicking rate greater than that attributable to disturbance associated with entering the cage, visual and possibly airborne prey odor cues, or handling of the lizard is evident from the individual comparisons between treatment means. SICS has been known until very recently only in venomous snakes, in which it occurs in numerous viperid and elapid species. The first hints that it might also occur in nonvenomous snakes were that garter snakes showed higher tongue-flicking rate to swabs following trials in which they struck than after trials not involving striking (Burghardt, 1969) and bull snakes (*Pituophis melanoleucus*) showed elevated tongue-flicking rates after swallowing (Chiszar et al., 1980). SICS has recently been discovered in at least two nonvenomous colubrid snakes (Cooper et al., 1988), a colubrine constrictor (*Elaphe guttata*), and a natricine nonconstrictor (*Thamnophis sirtalis*). That SICS has evolved de novo in varanid lizards and three ophidian lines seems highly unlikely. Thus, SICS may be primitive in these groups rather than having evolved convergently to support a strike-release-trail strategy in viperids and certain elapids.

If, as appears to be the case, SICS did not evolve initially to support a strike-release-trail strategy, other functions must be sought in varanid lizards and nonvenomous snakes. A lizard or snake, venomous or nonvenomous, biting a prey item may receive oral chemical stimuli sufficient to locate and identify the prey after it has escaped or been dropped. By using the tongue to gather chemical stimuli from its environment for vomeronasal analysis, a squamate could increase its chances of relocating a prey item. It is because the prey is known to be nearby and perhaps injured that the intensive chemical monitoring of SICS is adaptive. In this view, SICS was probably present in snakes prior to adoption of the strike-release-trail strategy, but was immediately useful in locating and following the scent trail of prey released after envenomation (Cooper et al., 1988). Although SICS is probably homologous in lizards, non-

venomous snakes, and venomous snakes, its features may have been evolutionarily molded to enhance its function in the strike-release-trail context. Quantitative comparisons of SICS parameters in venomous and nonvenomous snakes should reveal any such changes. It should be noted, however, that further experiments are needed to establish that the increased tongue-flicking rate actually functions to help locate prey.

Given that SICS is shared by snakes and varanid lizards, its taxonomic distribution among lizard families is of interest. SICS may occur in numerous families, but if its role is primarily location of escaped prey, as hypothesized, it is likely to be fully expressed primarily in groups of active foragers that use the tongue to locate prey. It may well be entirely absent in lizard families such as Iguanidae (e.g., Evans, 1961; Simon et al., 1981, for *Sceloporus jarrovi*) and Agamidae (Cooper, unpublished data), which do not appear to use the tongue to find prey. According to one hypothesis, snakes originated from platanotan stock (McDowell, 1972), i.e., the lizard families Helodermatidae, Varanidae, Lanthnotidae, and three extinct related families. This hypothesis would be supported if SICS among lizards were restricted to this lineage.

Responses of lizards and nonvenomous snakes to the experimental conditions used for varanids are congruent. In both species of nonvenomous colubrids (Cooper et al., 1988) and in *V. exanthematicus*, visual presentation of prey and pulling the predator away from the prey induced higher tongue-flicking rates than did the disturbance control; striking induced a still greater rate. The only difference of significance in the pattern is that the tongue-flicking rate elicited by visual presentation was not quite significantly greater than that following disturbance in the lizard but was so in the snakes. The similarity of response by lizards and snakes in these conditions further hints at possible homology of SICS in varanid lizards and snakes. It should be recognized that proprioceptive cues and oral tactile stimulation produced by striking and thus consistently associated with SICS are absent in the control conditions. Thus, the stimuli eliciting SICS are not necessarily chemical but could be at least in part tactile.

The tongue-flicking rate during the 2 min following striking in *V. exanthematicus* (46/min) was within the range reported for venomous snakes, but below that recorded for two nonvenomous colubrids. Tongue-flicking rates during the same interval range vary from slightly under 20 to over 70/min for various viperids (Chiszar et al., 1980, 1983, 1985; O'Connell et al., 1981, 1982), between 40 and 60/min for several elapids (O'Connell et al., 1985, Radcliffe et al., 1986), and for the nonvenomous colubrids *Elaphe g. guttata* and *Thamnophis s. sirtalis*, ca. 60 and 72.5/min (Cooper et al., 1988). The large rate differences within families and overlaps among families suggest that varanid lizards fall within the normal response range for snakes. However, further interpretation is difficult because numerous features other than inherited taxonomic differences presumably affect these rates, including temperature,

hunger, prey type, prey odor, prior diet, and experimental treatments, among others.

Visual prey cues plus possible airborne prey odors elicited tongue-flick rates considerably higher than did disturbance without such cues, but the difference was not quite statistically distinct (Newman-Keuls observed value = 9.92; value for significance at 0.05 = 11.65). Because the sample size was small and the variability in tongue-flicking rate high, it seems likely that the large difference in tongue-flicking rates represents a true inequality of response. In all three families of snakes studied, brief visual presentation of prey induces elevated tongue-flicking rates (e.g., Chiszar et al., 1985; O'Connell et al., 1985; Radcliffe et al., 1986; Cooper et al., 1988). Activation of tongue-flicking by visual prey stimuli is presumably an investigatory behavior functioning to confirm the visual cues and, if the prey is no longer in sight, to increase the probability of relocating it.

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