Strike-induced chemosensory searching by the anguid lizard *Elgaria coerulea*

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Abstract. Strike-induced chemosensory searching (SICS), including a post-strike elevation in tongue-flick rate (PETF) and searching movements following experimental removal of prey from the predator's mouth, is demonstrated to occur in an anguid lizard, *Elgaria coerulea*. This finding confirms predictions based on the previously established widespread occurrence of SICS in scleroglossan (especially autarchoglossan) lizard families and on a strong association between SICS and active foraging. Reasons why SICS should be favored by natural selection in active foragers are discussed, but the presence of SICS in anguids is attributed to phylogenetic inertia rather than adaptation. SICS was statistically significant only during the first two minutes in *E. coerulea*. Its limited duration in an anguid and much greater duration in heloder-matids, varanids, and snakes suggest that prolonged SICS may have had a single origin in the common ancestor of Varanoidea or, much less likely, of (Varanoidea + Xenosauridae). Uncertainties about origins due to missing data on certain taxa and to unresolved phylogenetic relationships within Scleroglossa are discussed.

Introduction

Strike-induced chemosensory searching (SICS) is search guided by chemical prey cues on substrates for prey that has been released voluntarily or has escaped after having been bitten (Chiszar and Scudder, 1980; Cooper et al., 1989). During the search, including locomotion, chemical stimuli are sampled lingually from substrates. Because lingually sampled chemicals are delivered to the vomeronasal organs and vomerolfaction is required for chemical identification of prey in at least some lizards and snakes (Graves and Halpern, 1989; Cooper and Burghardt, 1990; Cooper and Alberts, 1991; Halpern, 1992), vomerolfaction is presumably the primary chemical sense used during SICS. Locomotion is important to bring the lizard or snake into contact with chemical prey cues and to permiet scent-trailing.

Post-strike elevation in tongue-flicking (PETF) plus increased locomotion constitutes SICS (Chiszar and Scudder, 1980; Cooper et al., 1989; Cooper 1991a). PETF, SICS, or both have been demonstrated to occur in the families Iguanidae (sensu Frost and Etheridge, 1989; Cooper and Alberts, 1993), Eublepharidae (DePerno, 1994), Lacer-

tidae (Cooper, 1991a), Teiidae (Cooper, 1993a), Scincidae (Cooper, 1992a), Gerrhosauridae (Cooper, 1992b), Helodermatidae (Cooper and Arnett, in press), and Varanidae (Cooper, 1989, 1993b). These behaviors were absent in Chamaeleonidae (Cooper, 1994a), Phrynosomatidae (Cooper, 1994a), Polychridae (DePerno and Cooper, 1994), Tropiduridae (DePerno and Cooper, 1993), and Gekkonidae (DePerno, 1994).

Based on this incomplete data set, PETF and/or SICS are correlated with phylogeny and foraging ecology. The two major clades of lizards are Iguania and Scleroglossa (Estes et al., 1988). SICS is absent in all four families of iguanian insectivores studied. In these families PETF is present only in a tropidurid that does not identify prey by lingually sampled chemical cues or exhibit SICS (DePerno and Cooper, 1993). Among iguanians PETF and perhaps SICS have been found only in an iguanid lizard (Cooper and Alberts, 1993). In Scleroglossa SICS or PETF is widespread, occurring in all families listed abve with the exception of Gekkonidae.

Carnivorous lizards typically exhibit one of two virtually disjunct foraging modes, active foraging and ambush foraging (MacArthur and Pianka, 1966; McLaughlin, 1989). Active foragers tongue-flick steadily while searching and can identify prey from chemical cues sampled by the tongue (Cooper, 1994b). Ambush foragers adopt fixed ambush posts where they await the approach of prey; they do not use the tongue for prey chemical discrimination (Cooper, 1994b). All families of active foragers yet studied exhibit PETF and/or SICS and all families of ambush foragers lack these behaviors. Iguanidae, the single iguanian family in which lingually mediated prey chemical discrimination (Cooper and Alberts, 1990) and PETF occur (Cooper and Alberts, 1993), consists of herbivores.

Although the influences of both phylogeny and foraging mode on PETF and SICS appear to be strong, rigorous evaluation of the roles of phylogeny and the possible adaptive relationship between foraging mode and chemosensory behavior in determining the presence or absence of PETF and SICS must await collection of data from members of a few more major lizard families.

Data for Anguidae are important for at least two reasons. The first is to provide missing data on the relationships between SICS, phylogeny and foraging mode. I predicted that PETF and SICS are present in anguids because they are scleroglossans (Estes et al., 1988) believed to be active foragers (e.g., Fitch, 1935, 1989; Karges and Wright, 1987). Second, the duration of SICS in anguids is crucial for understanding the evolution of prolonged SICS. SICS is prolonged in venomous snakes, sometimes lasting upwards of the two hours (Chiszar et al., 1982, 1985). In most lizards it is brief, lasting only a minute or two in representatives of Iguanidae (Cooper and Alberts, 1993), Lacertidae (Cooper, 1991a), Scincidae (Cooper, 1992a), Gerrhosauridae (Cooper, 1992b) and Teiidae (Cooper, 1993a). SICS lasts much longer in helodermatid (45-55 min, Cooper et al., in press) and varanid (about 30 min, Cooper, 1993b) lizards. Because Anguidae and Xenosauridae form a polytomy with Varanoidea (Helodermatidae + Varanidae and probably Serpentes), brief SICS in Anguidae and Xenosauridae would

suggest a single origin of prolonged SICS in the common ancestor of Varanoidea. If SICS is long-lasting in both Anguidae and Xenosauridae, long duration presumably would have arisen in the common ancestor of Anguimorpha. The possibility that prolonged SICS is present in Anguidae or Xenosauridae, but not both, would also pinpoint the advent of prolonged SICS.

In this study the possible occurrence of PETF and SICS and the duration of PETF were investigated experimentally in the anguid lizard *Elgaria coerulea* following removal of prey from the lizards' mouths. Experimental controls were included for effects of the experimental milieu, seeing and perhaps smelling prey, and handling during removal of prey. Relationships between foraging mode and SICS are discussed, as is the origin of prolonged SICS.

Materials and methods

Sixteen adult *E. coerulea* were maintained in the animal care facility at Indiana University-Purdue University Fort Wayne (IPFW) for more than a month prior to the experiment to allow acclimation to laboratory conditions and habituation to human presence. Each individual was housed in a separate 51x26x32 cm glass terrarium having a sand substrate, water bowl, and removable screen top. The lizards were fed domestic crickets to satiation three times per week. Water was available *ad libitum*. Fluorescent and ultraviolet light was supplied on a 14L:10D cycle.

Because temperature strongly affects tongue-flicking rates in lizards (Cooper and Vitt, 1986; Van Damme et al., 1990), it is important to control temperature in experiments on SICS and PETF. To ensure normal feeding motivation, experimental temperatures should be in the range at which foraging occurs normally. The temperature range in addition should be as narrow as environmental control systems allow to avoid both inflation of variance in tongue-flicking rates due to temperature differences and systematic biases between trial days. Ambient temperatures were maintained at 25.5-27.5°C.

Forced removal of bitten prey is necessary for experimental detection of SICS in lizards that rarely release prey voluntarily. This requires that the design include a control for effects of forced removal. An experimental protocol that has proven successful in demonstrating the existence of SICS in several familes of lizards and non-venomous snakes was used (e.g., Cooper, 1989, 1992c; Cooper et al., 1989). The experimental design included an experimental condition in which prey was bitten and removed, a control condition for effects of removing the prey, and two additional control conditions for possible effects on tongue-flicking rate of the general experimental milieu and of combined visual and olfactory exposure to prey.

The existence of PETF and its magnitude and duration were studied by counting tongue-flicks in five consecutive minutes in four experimental conditions. In the primary experimental condition, the strike condition, a large adult domestic cricket tethered between head and prothorax by a thread was lowered into position 10 cm anterior to a

lizard's snout. When the lizard bit the cricket, the experimenter immediately removed the cricket from the lizard's mouth as gently as possible and began counting tongue-flicks immediately after removal. Induction of release required grasping a lizard with one hand and pulling the cricket out of its mouth with the other. Care was taken to avoid pulling crickets apart, but fragile cricket bodies were broken in two in a few trials, leaving a portion in a lizard's mouth. Trials in which crickets were dismembered were discarded and run again later.

The mechanical disturbance condition was similar to the strike condition, but the lizard was not permitted to bite the mouse. As soon as a lizard approached and (sometimes) tongue-flicked a cricket and prepared to bite it, the experimenter withdrew the cricket and grasped the lizard as in forced removal of prey in the strike condition. This handling simulated the mechanical disturbance entailed by removing the cricket from a lizard's mouth. Tongue-flicks were counted starting upon release of the lizard by the experimenter. The mechanical disturbance condition seems to provide a reasonable control for effects of mechanical stimulation caused by handling the lizard, but does not control for intraoral mechanical stimulation and mechanical stimulation due to pulling the cricket. However, in two studies designed to control for these effects, animals were grasped and cotton swabs inserted into their mouths and rubbed on the oral epithelia. Rubbing by swabs impregnated with prey chemicals induced higher tongue-flicking rates than by swabs lacking prey chemicals (Cooper et al., 1989; Cooper, 1992c), indicating a strong effect of oral stimulation by prey chemicals on tongue-flicking in addition to any effects of handling and other mechanical stimulation.

The sight condition controlled for effects of seeing prey and possibly detecting it by airborne chemical cues. In this condition a cricket was held 15-20 cm anterior to the lizard. After ten s the cricket was removed if the lizard dit not approach. If the lizard approached sooner, the cricket was removed at once, barring the lizard from obtaining chemical cues by tongue-flicking the surface of the cricket. In most studies no effect of visual (and perhaps other) cues has been detected (e.g., Cooper, 1989, 1992a,b: Cooper and Alberts, 1993; DePerno and Cooper, 1993). Nevertheless, it is important to include this condition to understand the magnitude of tongue-flicking in some species in which the tongue-flicking rate is elevated in the sight condition with respect the baseline rates (Cooper et al., 1989; Cooper, 1991a; 1993a).

The string condition was the control condition giving baseline tongue-flicking rates in the experimental setting when visual and chemical prey cues were absent. Thread without a cricket was placed in a lizard's cage as in the sight condition. In all other respects the string condition was identical to the sight condition. In the sight and string conditions, counting of tongue-flicks commenced upon removal of the experimental stimuli.

Each lizard was tested in all four experimental conditions in a randomized blocks design. The sequence of conditions was partially counterbalanced such that 16 of the 24 possible sequences were used and each experimental condition was represented four times in each of the four successive trials. The lizards were not fed for two to three days

prior to each trial. This ensured levels of feeding motivation comparable to those at normal laboratory feeding times. Individuals were tested in only one condition per day at 1000-1500 h on 26 November-18 December 1991.

Parametric analysis of variance could not be used because the distributions of tongue-flicks departed greatly from normality due to frequent zero values in the forceps and sight conditions. Instead, nonparametric Friedman two-way analysis of variance (test statistic = χ^2, Siegel, 1956; Hollander and Wolfe, 1973) was used to assess significances of differences in numbers of tongue-flicks among conditions. The Friedman test does not permit testing of the main time effect followed by examination of individual minutes. As an alternative, I tested differences among conditions for the entire five min interval and then conducted separate tests for each minute. Nonparametric individual comparisons between pairs of conditions for use with Friedman two-way analysis of variance (Hollander and Wolfe, 1973) were conducted when main condition effects were significant. Significance tests unless otherwise noted were two-tailed for main effects and one-tailed for directional individual comparisons. The directional hypotheses were that relative numbers of tongue-flicks would be strike condition > mechanical disturbance condition > sight condition > string condition. Alpha was 0.05.

Results

Alligator lizards tongue-flicked at a fairly high rate in the initial minute in the strike condition, but response rates waned rapidly in the following minutes (table 1). All individuals emitted six or more tongue-flicks in the first minute in the strike condition; numbers of individuals tongue-flicking at least once in the remaining minutes were 12,

Table 1. Means, standard errors, and ranges of tongue-flicks for each minute in the four experimental conditions.

Minute	Statistic	Strike	Mechanical disturbance	Sight	String
	$\bar{x}$	22.3	6.5	0.2	0.0
	SE	3.5	1.3	0.1	0.0
1	Range	6-51	0-16	0-1	—
	$\bar{x}$	6.6	1.4	0.0	0.0
	SE	2.0	0.5	0.0	0.0
2	Range	0-23	0-6	—	—
	$\bar{x}$	2.9	0.2	0.0	0.0
	SE	1.0	0.2	0.0	0.0
3	Range	0-11	0-3	—	—
	$\bar{x}$	1.9	0.3	0.0	0.0
	SE	0.6	0.3	0.0	0.0
4	Range	0-8	0-5	—	—
	$\bar{x}$	0.8	0.0	0.0	0.0
	SE	0.5	0.0	0.0	0.0
5	Range	0-7	—	—	—

9, 8, and 3. Response rates were initially much lower in the other conditions, with no individuals tongue-flicking at any time in the sight condition and only three individuals in the sight condition performing single tongue-flicks in the first minute and none thereafter. More tongue-flicking occurred in the mechanical disturbance condition than in the other control conditions, all but two individuals tongue-flicking at least once in the initial minute. The numbers of individuals tongue-flicking in the mechanical disturbance condition dropped rapidly to seven, two, one, and zero individuals in the succeeding minutes.

During the entire five min interval the number of tongue-flicks differed significantly among conditions (χ^2 - 17.0, df = 3, $p < 0.001$). Total numbers of tongue-flicks in five min were: strike condition ($\bar{x}$ = 35.6, SE = 5.2, range 6-71); mechanical disturbance condition ($\bar{x}$ = 8.4, SE = 1.9, range 0-22), sight condition ($\bar{x}$ = 0.2, SE = 0.1, range = 0-1), and string condition ($\bar{x}$ = 0.0, SE = 0.0, range 0). Significantly more tongue-flicks occurred in the strike condition than in the mechanical disturbance condition ($p < 0.025$), sight ($p < 0.001$), and string conditions ($p < 0.001$ each). In addition, the tongue-flick rate was significantly higher in the mechanical disturbance condition than in the other control conditions ($p < 0.03$ each). Tongue-flicking rates in the sight and string conditions did not differ significantly and had very low and similar magnitudes.

Individuals varied greatly in total numbers of tongue-flicks performed in five min in the strike condition and to a lesser extent in the mechanical disturbance condition. Individuals also differed somewhat in rates of tongue-flicking across conditions as revealed by a significant, but loose, Spearman rank correlation between total numbers of tongue-flicks emitted in the strike and mechanical disturbance conditions (r_s = 0.45).

More tongue-flicks were emitted in the strike condition than in any other condition in each of the five minutes, substantially more in all but the last minute, when few individuals tongue-flicked at all (table 1). However, due to large decreases in tongue-flicking rates in the strike and mechanical disturbance conditions by the third minute, the main effect of stimulus conditions was significant only in minutes one (χ^2 = 38.1, df = 3, $p < 0.001$) and two (χ^2 = 9.56, df = 3, $p < 0.02$). In the remaining minutes the condition effect did not closely approach significance (minute 3: χ^2 = 2.68/ minute 4: χ^2 = 2.53: minute 5: χ^2 = 3.63; df = 3, $p > 0.10$ each).

In minute one the number of tongue-flicks emitted in the strike condition was significantly greater than in the mechanical disturbance condition ($p < 0.001$), the sight condition ($p < 0.001$), and the string condition ($p < 0.002$). Significantly more tongue-flicks were performed in the mechanical disturbance condition than in the sight condition ($p < 0.025$) and the string condition ($p < 0.005$). Tongue-flicking rates in the sight and string conditions did not differ significantly ($p > 0.10$). During minute one, 15 of 16 individuals performed more tongue-flicks in the strike condition than in any other condition (sign test, $p < 0.001$ for each comparison).

During the second minute the tongue-flicking rate was significantly greater in the strike condition than in the mechanical disturbance ($p < 0.05$), sight, and string conditions ($p < 0.001$ each). Although substantially more tongue-flicks occurred in the

mechanical disturbance condition than in the other control conditions, the differences were not significant ($p > 0.10$). However, the proportion of individuals tongue-flicking at least once was significantly greater in the mechanical disturbance condition than in either of the control conditions (sign test, $p = 0.0078$). Numbers of tongue-flicks did not differ significantly in the sight and string conditions ($p > 0.10$)).

The only important comparison for movement rates is that between the strike and mechanical disturbance conditions. Locomotion was observed in ten individuals during the experimental trials. All ten moved in the strike condition and four of the same individuals moved in the pull condition. Thus, individuals were significantly more likely to move in the strike condition (sign test, $p < 0.016$). Because nine individuals moved during more minutes in the strike condition than in the mechanical disturbance condition and only one moved during more minutes in the mechanical disturbance condition, locomotion was significantly longer-lasting in the strike condition (sign test, $p = 0.011$). Although distance moved and time spent moving were not measured, it was clear during the experiment that both were greater in the strike condition. No lizards moved in either the sight condition or the string condition. Most movements consisted of slow, deliberate crawling that in some individuals in the strike condition lasted for most of the testing period.

Discussion

SICS is confirmed in the anguid *E. coerulea*. The significantly higher tongue-flicking rate in the strike condition than in any of the control conditions for the entire five-minute interval and specifically in minutes one and two establishes the presence of PETF. In combination with PETF, the reliable occurrence of concurrent locomotory movements demonstrates the existence of SICS. The lizards tongue-flicked for a longer time as well as more frequently in the strike condition. The tongue-flick rate was elevated not only as a consequence of biting prey, but also as a result of being handled. This was shown by the significantly greater rate of tongue-flicking in the mechanical disturbance condition than in the sight and string conditions for the entire five minute interval due to differences in minutes one and two. Viewing prey for ten s did not affect the tongue-flick rate.

The presence of SICS in *E. coerulea* agrees with previous findings that SICS is widespread in Scleroglossa, reinforcing the importance of phylogeny as a predictor of SICS. The results also appear to be consistent with the widespread occurrence of SICS in active foragers. Unfortunately, the data on foraging behavior of anguids are limited to brief qualitative descriptions suggesting that anguids move more slowly than many other active foragers while searching for prey, but do move about in active search (Fitch, 1935, 1989; Karges and Wright, 1987). Detailed study of foraging behavior in anguids is needed to characterize their foraging mode.

Phylogeny strongly affects the presence or absence of PETF and SICS, but it is unclear to what extent SICS may be adaptively adjusted to changes in foraging mode.

In the present case, the ancestors of anguimorphan lizards were very likely active foragers that exhibited both lingually mediated prey chemical discrimination and SICS (Cooper, 1994b,c), as do extant anguids (Cooper, 1990, this paper). Even if current natural selection favors the association between active foraging and SICS, the association between SICS and active foraging in anguids is thus attributable to phylogenetic inertia rather than adaptation. Consequently, even if it becomes firmly established that anguids are active foragers, SICS in anguids adds little to our understanding of a possible adaptive relationship between foraging mode and SICS.

Theoretically, foraging mode should drive PETF and SICS because ambushers cannot search a wide area for chemical prey cues while remaining motionless and rely on immobility to avoid detection by predators (Cooper, 1994b,c). By actively searching for escaped prey, ambushers would have to increase their vulnerability to predators and would miss opportunities to ambush other prey. Furthermore, lingually mediated prey chemical discrimination is adaptively adjusted to foraging mode, being absent in ambush foragers, but used by active foragers to locate and identify prey (Cooper, 1994b). Ambush foragers do not use the tongue to help find prey prior to attack, and may lack the ability to do so. In contrast, active foragers may continue to search for other prey items in the normal fashion during PETF and locomotion. SICS does not radically increase their chances of being detected by predators (Vitt and Price, 1982; Cooper et al., in press).

Despite the continued higher rate of tongue-flicking throughout the five minutes of observation, PETF was demonstrated statistically only during the first two minutes in *E. coerulea*. Elevated frequency of locomotion lasted at least through minute four, with seven individuals moving in the strike condition and only one in the mechanical disturbance condition in each of the last three minutes. Thus, SICS was present for at least two min.

The brief duration of SICS in an anguid species and previous data suggest that after its scleroglossan origin (or origins), SICS was of brief duration. If prolonged SICS is absent in Xenosauridae, prolonged SICS originated in the common ancestor of Varanoidea and may have had a single origin in lizards although data are lacking for amphisbaenians and gymnophthalmids. If prolonged SICS is present in Xenosauridae, either it arose only once in the common ancestor of (Varanoidea + Xenosauridae) or twice, once in the common ancestor of Varanoidea and once in Xenosauridae. Prolonged SICS in Xenosauridae seems unlikely given the lack of extreme lingual forking and elongation (Cooper, in review a,b; Cooper and Arnett, in press), favoring the single varanoid origin of protracted SICS.

In snakes, which may be varanoid derivatives, SICS is sometimes very long-lasting (Chiszar and Scudder, 1980; Chiszar et al., 1982, 1985), but the great duration in venomous ambushers may have evolved due to the reliability with which envenomated prey remain in the vicinity. SICS is widespread in snakes, being known in viperids (e.g., Chiszar and Scudder, 1980), elapids (O'Connell et al., 1985), a few colubrids (Cooper et al., 1989; Cooper, 1992c; Burghardt, 1993)j, and in at least one pythonid (Cooper,

1991b). However, SICS has not been studied in any scolecophidian and its duration is unknown in all but a few highly venomous viperids and elapids. Snakes, having highly variable foraging strategies, may provide excellent opportunities for detecting influences of foraging behavior on existence and duration of SICS.

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