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RESPONSES TO MAJOR CATEGORIES OF FOOD CHEMICALS BY THE LIZARD *Podarcis lilfordi*

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Abstract—Many lizards are capable of identifying food using only chemical cues from food surfaces, but almost nothing is known about the types of compounds that are effective stimuli. We experimentally studied lingual and biting responses by a lacertid lizard, *Podarcis lilfordi,* to single representatives of three major categories of food chemicals, sucrose as a carbohydrate, pure pork fat as a mixture of lipids, and bovine gamma globulin as a protein. In 60-sec trials in which stimuli were presented on cotton swabs, the lizards detected all three stimuli, exhibiting more tongue-flicks, licks, or bites, or a greater tongue-flick attack score (TFAS; overall measure of response strength to prey stimuli) than to deionized water. The initial response to all stimuli was tongue-flicking, but the lizards discriminated among the types of chemical stimuli. After preliminary tongue-flicks, the lizards responded to sucrose solutions by licking at high rates, to pure pork fat by biting, and to protein by a combination of additional tongue-flicks and biting. Biting is a feeding response to prey or solid plant material. Licking is a feeding response to sugars in nectar or ripe fruit. Its frequency increased with sucrose concentration. Our data suggest that lizards can identify several types of chemicals associated with food and direct feeding attempts to sources of such chemicals in the absence of visual cues.

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INTRODUCTION

Food flavors, based on a combination of olfactory and gustatory responses to chemical properties of food, are extremely important to evaluations of food by humans. Many other animals are able to locate and evaluate foods on the basis of perceptual qualities associated with classes of compounds, such as the sweetness of sugars and the bitterness of alkaloids. For many snakes and lizards, for which flavors might be determined jointly by vomerolfaction, olfaction, and gustation, very little is known about the importance of particular categories of food chemicals in stimulating chemosensory investigation and feeding responses.

Lizards that are active foragers (Cooper, 1995, 1997, 2000a) or include substantial quantities of plants in the diet (Cooper, 2000b,c; Cooper et al., 2000a). They are able to identify food using only chemical cues sampled by tongue-flicking, but little is known about the types of chemicals to which they respond or the precise chemical senses that mediate these responses. Only two recent studies document behavioral responses to certain types of food chemicals by lizards (Stanger-Hall, et al., 2001; Cooper and Pérez-Mellado, 2001a), and another study presents evidence that at least one lizard species is capable of rejecting chemically defended plant foods (Schall, 1990).

The major candidates for positive response to foods are proteins, lipids, and carbohydrates. Responses by lizards to proteins in food have not been studied, but specific glycoproteins from earthworms can elicit strong responses by garter snakes (Burghardt et al., 1988; Wang et al., 1988). The omnivorous lacertid lizard *Gallotia caesaris* responds strongly to lipids in pure pork fat and to sucrose, but the responses to these chemicals differ qualitatively (Cooper and Pérez-Mellado, 2001a). When responding to fat, the lizards tongue-flick at increased rates and frequently bite the stimulus source.

In contrast, lizards responding to concentrated sucrose solutions exhibit no elevation in tongue-flick rate or likelihood of biting (Cooper and Pérez-Mellado, 2001a). Instead, they lick the stimulus source at high rates after preliminary tongue-flicks, the rate of licking increasing with sucrose concentration. In studies of food chemical discrimination, the omnivorous lacertid *Podarcis lilfordi* licked in response to stimuli from nectar-producing flowers and licked nectar in the field (Cooper and Pérez-Mellado, 2001b), also suggesting a specific response to sugar. The only other evidence regarding responses to carbohydrates by lizards is that some individuals of the polychrotid lizard *Anolis carolinensis* preferred to eat crickets dusted with a dextrose/aspartame powder, and one licked the residue of this powder in a food bowl after eating a cricket (Stanger-Hall et al., 2001).

Evidence that lizards can use chemical cues to avoid chemically defended foods is limited to responses to the alkaloid quinine. *Cnemidophorus murinus*, an omnivore, avoids eating plants in its natural habitat that contain high concentrations of alkaloids (Schall and Ressell, 1991) and rejects experimental food that has been treated with a low concentration of quinine (Schall, 1990). Some individuals of *A. carolinensis,* an insectivore, exhibited aversive responses to crickets treated with quinine solution and showed aversive responses to crickets treated with quinine powder (Stanger-Hall et al., 2001). The signs of aversion included spitting the crickets out prior to swallowing and regurgitation. The lizards significantly avoided eating crickets treated with quinine powder.

We studied lingual and biting responses by *P. lifordi* to single representatives each of protein, lipid, and carbohydrate stimuli presented on cotton swabs. *Podarcis lilfordi* eats a wide range of invertebrate prey, occasional vertebrate food, and diverse plant species (Salvador, 1986; Pérez-Mellado and Corti, 1993). Plant parts and products consumed that are likely to contain high concentrations of sugars are fruits and nectar (Pérez-Mellado and Corti, 1993). *Podarcis lilfordi* is an excellent subject for studies of responses to types of food chemicals due to its broad diet, its abundance, and existing knowledge about its responses to food chemicals (Cooper and Pérez-Mellado, 2001b, 2001c). These lizards can discriminate between odorless and odorous control substances and surface chemicals from prey and plant foods by lingually sampling them (Cooper and Pérez-Mellado, 2001b).

We predicted that animal protein and the complex lipid mixture in pure pork fat would elicit strong responses indicated by tongue-flicking and biting and that the sucrose found in plant foods eaten by these lizards (Pérez-Mellado and Corti, 1993) would elicit licking. We also examined the effects of sucrose concentration on rates of tongue-flicking and licking and observed responses to sucrose by the lacertid species, *Lacerta perspicillata*, which is insectivorous (Barbadillo et al., 1999). The goals of the study were to assess the importance of protein to food chemical discrimination by lizards, to extend previous findings for lipids and a carbohydrate to another species, and to determine whether the licking response to sucrose was limited to species that eat plants.

METHODS AND MATERIALS

Subjects and Maintenance. Adult *P. lilfordi* were collected on the islet of Aire, offshore from Menorca, Balearic Islands, Spain, and adult *L. perspicillata* were collected in a quarry near Ciutadella on Menorca. Both were transported to a laboratory on Menorca. They were housed individually in transparent plastic terraria (40.5 × 25.0 × 26.5 cm). The side walls of terraria were covered with white paper to reduce disturbance to the lizards by movements of the experimenters and by other lizards. Each terrarium contained a floor of indoor–outdoor carpet and a water bowl. The natural regional light cycle was maintained by light through a window, and additional light and heat were provided by incandescent heat lamps, one suspended above the ends of each cage to permit thermoregulation. Ambient temperatures during testing were 30.9–32.2°C. Body temperatures were not measured during this experiment, but some lizards measured in these conditions at other times voluntarily attained temperatures of over 35°C, slightly warmer than the body temperature of most individuals during spring (Salvador, 1998). The lizards were fed mealworms and continuously provided water in the laboratory but were not fed for 24 hr prior to testing. All tests were conducted while lizards were active from 09:00 to 14:00 hr.

Experimental Procedures. All observations were made for responses during 60-sec trials to chemicals presented on the cotton tips of wooden applicators (15 cm). To begin a trial, an experimenter slowly moved the cotton swab to a position 1.0–1.5 cm anterior to a lizard's snout. A trial began when the lizard directed the first tongue-flick to the swab and continued for 60 sec unless the lizard bit the swab, at which time the trial was terminated. In each trial, the experimenter recorded the number of tongue-flicks, occurrence of and latency in seconds to a bite, and number of licks.

These variables and the tongue-flick attack score (TFAS) were analyzed. The tongue-flick attack score (Burghardt, 1967, 1970a; Cooper and Burghardt, 1990) is a composite variable that combines tongue-flicking and biting data to give a single index of response strength. For experiments having repeated-measures designs, TFAS(R), it is equal to the number of tongue-flicks if the lizard does not bite the swab. If a lizard bites, TFAS(R) has two components, one being based on latency to bite and the other on tongue-flicks. The term (60 minus latency to bite in seconds) is added to a term expressing a maximum number of tongue-flicks (Cooper and Burghardt, 1990). The latency term gives heavier weight to bites at shorter latency because bites at short latency indicate rapid identification of food. The other term is the maximum number of tongue-flicks by that individual in any one of its trials (Cooper and Burghardt, 1990). The tongue-flick term assures that bites are more heavily weighted than any number of tongue-flicks because bites reflect predation attempts.

In an experiment designed to detect responses to major categories of organic compounds found in prey, the stimuli tested were sucrose as a carbohydrate, pure pork fat as a complex mixture of lipids (mainly triglycerides), and bovine gamma globulin (Sigma G7516) as a protein. The fat and protein stimuli are not those from normally consumed foods. They were selected for this first study because they are readily available and inexpensive, and in preliminary trials they were found to elicit responses observed to whole foods. Sucrose is appropriate as a major contributor to the sweetness of ripe fruits and nectar although free frutose may also contribute. Deionized water was used as an odorless control stimulus.

To prepare stimuli, swabs were either dipped into deionized water or a saturated sucrose solution (6.27 M), inserted into pure pork fat, or immersed in water and then brought into contact with crystalline protein.

Twenty individuals of *P. lilfordi* were tested in a repeated-measures (randomized blocks) design. Each individual was tested in all four conditions in which the sequence of stimuli tested was varied among individuals in a partially counterbalanced order to preclude any sequential bias that might have occurred if the same sequence of stimuli were used for each individual. The minimum intertrial interval was 0.5 hr.

The effects of sucrose concentration on number of tongue-flicks, tongue-flick attack score, and number of licks were examined in an experiment having an independent-groups design in which 21 individuals of *P. lilfordi* were tested at each concentration. The concentrations of sucrose in deionized water solution were 6.27 M (saturated), 1.57 M, 0.39 M, 0.10 M, 0.02 M, 0.01 M, and 0.00 M (pure deionized water). The two highest concentrations are unlikely to be encountered in nature but are included to examine the full range of responses. Due to the independent-groups design, the tongue-flick attack score must be calculated slightly differently. TFAS is the same as TFAS(R) with the exception that the tongue-flick term for individuals that bite is the maximum number of tongue-flicks performed by any individual in the experiment. Responses by six adult *L. perspcillata* to a saturated sucrose solution were observed. We studied effects of variation in concentration only for sucrose, in part because we lacked time for additional studies during a brief visit to Menorca. In addtion, responses to protein were not as clear-cut as the licking response to sucrose, and the pork fat is a mixture of substances.

Statistical Anaylsis. Some data from both experiments were analyzed nonparametrically due to intractable heterogeneity of variance and/or nonnormality. For the experiment on responses to representatives of major categories of organic compounds, data for the continuous variables were analyzed using Friedman two-way analysis of variance. Where main effects were significant, differences among pairs of conditions were tested for significance using nonparametric multiple comparisons procedures described by Zar (1996). Data on the number of individuals that bit were analyzed using a Cochran Q test. Paired comparisons of the numbers of individuals that bit were made using sign (binomial) tests. Raw probabilities are reported for these tests, but significance tests were conducted by a sequential Bonferroni procedure to adjust for the number of tests (Wright, 1992).

Tongue-flicks in the experiment on sucrose concentration were analyzed by parametric analysis of variance for a single-factor experiment having an independent-groups design after variances were found to be homogeneous using Hartley's $F_{\max}$ tests (Winer, 1962). Paired comparisons for this variable were made using Newman-Keuls procedures. Data on number of licks from the experiment on effect of sugar concentrations were analyzed using Kruskal-Wallis analysis of variance for continuous variables, followed by Dunn's tests for signficance of difference between pairs of sucrose concentrations when the main effect was found to be significant. An additional analysis of differences in the proportions of individulas that licked at least once between pairs of 1/4, 1/16, and 1/64 saturated solutions was conducted using Fisher exact probability tests (Zar, 1996) with Bonferroni adjustments as above. Except where indicated otherwise and justified by directional prediction, all significance tests were two-tailed, with $\alpha = 0.05$.

RESULTS

Responses to Chemical Types. All individuals of *P. lilfordi* tongue-flicked in every trial, with the greatest mean number of tongue-flicks in response to protein, but none of the stimuli elicited large numbers of tongue-flicks (Table 1). The number of tongue-flicks varied among stimuli ($\chi^2 = 8.36$, $df = 3$, $P < 0.040$). The only significant difference between pairs of conditions was that there were fewer tongue-flicks in the sucrose condition than in the deionized water condition ($P < 0.05$). There were marginally fewer tongue-flicks in the sugar condition than in the protein condition ($P = 0.063$).

The latency to bite varied among conditions, the mean being much shorter in the fat condition than in all others (Table 1). The main stimulus effect was significant ($\chi^2 = 13.61$, $df = 3$, $P < 0.004$). Latency to bite was shorter in response to fat than to deionized water ($P < 0.05$) and sucrose ($P < 0.01$). There was a nonsignificant trend for latency to bite less in response to fat than protein ($0.05 < P < 0.10$). No other differences among pairs of stimuli were significant, but latency to bite was substantially less in response to protein than to sucrose ($0.05 < P < 0.10$). Results

TABLE 1. NUMBERS OF TONGUE-FLICKS AND INDIVIDUALS THAT BIT[a]

Variable	Sucrose	Pork fat	Gamma globulin	Deionized water
Tongue-flicks				
Mean	3.1	3.9	10.2	7.0
SE	0.5	0.6	3.3	1.5
Number that bit	11	20	14	11
Latency to bite (sec)				
Mean	42.8	5.1	24.7	34.8
SE	20.7	4.5	27.0	28.7
TFAS(R)				
Mean	24.5	68.7	48.8	33.3
SE	5.1	3.3	5.0	6.4

[a] Twenty adult *Podarcis lilfordi* were used in 60-sec trials with cotton swabs bearing a saturated sucrose solution, pure pork fat, bovine gamma globulin, or deionized water.

for the number of individuals that bit swabs (Table 1) had the same pattern of significance as did latency to bite. The stimulus effect was significant ($Q = 17.25$, $df = 3$, $P < 0.001$). More individuals bit in the fat condition than in the sucrose ($P = 0.008$) and deionized water conditions ($P = 0.003$). The difference between the fat and protein conditions closely approached, but did not attain, significance after Bonferroni adjustment ($P < 0.042$ vs. adjusted $\alpha = 0.0123$). Differences among the other pairs of stimuli were not significant.

Variation among conditions in TFAS(R) was substantial (Table 1). The main effect was highly significant ($\chi^2 = 16.49$, $df = 3$, $P < 0.001$). TFAS(R) was greater in the fat condition than in the sucrose ($P < 0.05$) and deionized water ($P < 0.01$) conditions. It was also greater in the protein condition than in the sucrose ($P < 0.01$) and deionized water ($P < 0.05$, one-tailed) conditions. The remaining differences between pairs of stimuli were not significant.

Numbers of licks (Table 1) varied dramatically among conditions. Licks began only after at least one tongue-flick. Lizards licked swabs bearing sucrose rapidly, with a mean of over twice per second, but none licked swabs bearing protein. Four of 20 individuals licked swabs bearing fat. Only one individual licked a swab in the water condition, but it licked 75 times. Numbers of licks differed among conditions ($\chi^2 = 55.43$, $df = 3$, $P < 0.001$). There were more licks in the sugar condition than in the fat, protein, and deionized water conditions ($P < 0.001$ each). No other differences between pairs of stimuli were significant.

All *L. perpicillata* initially tongue-flicked swabs bearing sucrose and then licked the swabs. Numbers of licks were 36.00 ± 14.74 (SE), with range 1–103.

Sucrose Concentration and P. lilfordi. Tongue-flicks varied among sucrose concentrations ($F = 2.46$; $df = 6, 140$; $P < 0.028$; Table 2). The number of tongue-flicks in response to saturated sucrose was less than in the other conditions

TABLE 2. TONGUE-FLICKS AND TONGUE-FLICK ATTACK SCORES (TFAS)[a]

	Concentration (M)						
Variable	6.27	1.57	0.39	0.10	0.02	0.01	0.00
Tongue-flicks							
Mean	4.3	10.4	11.0	10.5	8.8	10.3	7.6
SE	0.6	2.2	2.0	1.6	1.0	1.5	0.9
TFAS							
Mean	43.9	37.2	53.7	34.2	17.4	23.6	24.2
SE	7.4	8.1	9.1	8.2	5.8	6.9	7.7
Licks							
Mean	118.4	21.0	21.3	2.4	0.0	0.0	0.0
SE	7.4	4.7	0.8	2.4	0.0	0.0	0.0

[a] Adult *Podarcis lilfordi* were used in 60-sec trials with cotton swabs bearing aqueous sucrose solutions of varying concentration. $N = 21$ for each concentration.

($P < 0.05$ each), but no other differences between pairs of concentrations were significant. TFAS differed among conditions ($F = 2.77$; $df = 6, 140$; $P < 0.015$; Table 2). The only difference in TFAS between pairs of concentrations was the greater TFAS in the 0.39 M versus 0.02 M solution ($P < 0.05$). Nevertheless, there was a trend for TFAS to be greater at the higher sucrose concentrations; the three highest TFAS scores occurred at the three highest concentrations.

The number of licks increased with the concentration of sucrose (Table 2; $\chi^2 = 100.09$, $df = 6$, $P < 0.001$). By far the greatest numbers of licks were performed in response to the 6.27 M sucrose solution, more than in all other conditions ($P < 0.05$ each). The only other difference among conditions was that the 1.57 M solution elicited more licks than each of the three solutions having the lowest concentrations ($P < 0.05$ each), none of which elicited any licking.

There were substantial differences in responses between the 1.57 M and the 0.39 and 0.10 M solutions that were not revealed in the ordinal analysis. In response to the 1.57 M solution, 14 of 21 individuals licked at least once, whereas only four and one did so in response to 0.39 M and 0.10 M solutions. A greater proportion of individuals licked in the 1.57 M group than in the 0.39 M (Fisher $P = 0.004$) and 0.10 M (Fisher $P = 0.001$) groups. A greater proportion of individuals licked in the 0.10 M group than in the combined groups at the three lower concentrations (binomial test with equal probability of licking in each group, $P = 0.008$).

DISCUSSION

Chemical Types. Podarcis lilfordi can detect and discriminate among major types of organic compounds from foods using only chemical senses. Sucrose as a representative carbohydrate, pure pork fat as a mixture of lipids, and bovine gamma globulin as a protein all elicited elevated responses by *P. lilfordi* that differed significantly among chemical types. Pork fat and sucrose elicited the strongest feeding responses; the most marked response to protein was elevated TFAS(R). It may be concluded that the lizards are capable of identifying a variety of chemicals associated with food and responding to them by investigative and feeding behaviors.

Podarcis lilfordi discriminated pork fat from sucrose and water, and exhibited a different feeding behavior in response to lipids from sucrose. Because any natural source of concentrated lipids is likely to indicate the presence of prey or plant food, feeding attempts upon detection may be adaptive even in the absence of visual cues. Lizards discriminated between bovine gamma globulin and sucrose, but there was no clear statistical evidence for discrimination between protein and pork fat. Although 70% of lizards bit in protein trials, this response was not significant because many individuals bit in all conditions. This unusual behavior for lizards may be a response to visual properties of the swabs and motion (Cooper and Pérez-Mellado, 2001b).

That protein and lipids elicit strong responses is adaptive because both are closely linked to nutritious foods. In garter snakes, specific proteins from natural prey elicit the strongest responses (Burghardt et al., 1988; Wang et al., 1988). Furthermore, some snakes tongue-flick and bite more in response to chemical cues from preferred prey than from species that are less preferred or not eaten (Burghardt, 1970b, Arnold, 1981; Cooper et al., 1990, 2000b). Response strength by lizards presumably varies among proteins within and between source species and may do so among individual lipids and lipid mixtures, emphasizing the need for future tests using chemicals from species eaten by the lizards.

After a few tongue-flicks to sucrose, lizards switched to licking, a feeding response. This change in behavior from investigation to consumption indicates rapid identification. Licking is a specific response to sucrose and likely to other sweet carbohydrates. Licking upon detecting sugar may be adaptive for omnivorous and herbivorous lizard species that frequently consume nectar or ripe fruits. The licking response was first observed for *P. lilfordi* responding to surface chemicals from nectar-producing flowers and in the omnivorous *G. caesaris* responding to a sucrose solution (Cooper and Pérez-Mellado, 2001a,b). However, that the insectivorous *L. perspicillata* licks swabs bearing sucrose hints that this behavior may be widespread in lacertids and perhaps other lizards, rather than limited primarily to omnivores and herbivores.

Licking may be an efficient means of consuming nectar and is frequently observed when *P. lilfordi* feeds on flowers in the field (Pérez-Mellado, personal observations). Occasional licks in response to pork fat suggest that licking might be a feeding response to soft or fluid substances that can be ingested without biting. In this study, excess fat could be ingested by licking. No licks occurred when excess fat was removed by wiping on a paper towel (Cooper and Pérez-Mellado, unpublished data).

Sucrose Concentration. Efforts to consume sucrose by licking appear to increase with concentration. Licking in nature would be likely to occur in response to sugars concentrated in nectar and ripe fruits. The shift from tongue-flicking to licking indicates identification of sucrose as food, which occurs more rapidly at the higher concentrations (Cooper and Pérez-Mellado, 2001a). In this, *P. lilfordi* differs from *G. caesaris*, which exhibits no variation in tongue-flick rates over a wide range of sucrose concentrations (Cooper and Pérez-Mellado, 2001a).

In a related experiment, *Gallotia caesaris* licked at a rate similar to that by *P. lilfordi* when responding to saturated sucrose but at much higher rates to 0.39 M and 0.10 M solutions (Cooper and Pérez-Mellado, 2001a). These differences might indicate that *G. caesaris* is more sensitive to sucrose or that sugar is a more important component of the diet than for *P. lilfordi*, possibly due to scarcity. Another possibility is that the two species do not differ intrinsically, and the apparent difference is an artifact of differences in experimental design. In the present study each individual was tested only once, but each *G. caesaris* was tested at six different concentrations (Cooper and Pérez-Mellado, 2001a).

Chemical Senses. The senses that mediate food chemical discriminations by lizards are poorly known, but the major candidates are vomerolfaction, olfaction, and gustation. In garter snakes of the genus *Thamnophis* (Halpern and Frumin, 1979) and in the iguanid lizard *Dipsosaurus dorsalis* (Cooper and Alberts, 1991), vomerolfaction is required to discriminate between chemical cues from food and control chemicals. In contrast, *P. lilfordi* can locate hidden fruit using only airborne chemical cues (Cooper and Pérez-Mellado, 2001c), suggesting that olfaction also has a role in identificaiton of food by some lizards. Typically, the vomerolfactory system responds to large, nonvolatile molecules sampled by tongue-flicking (Halpern, 1992). However, vomerolfactory response to airborne volatiles cannot be excluded without experimentation.

The other chemical sense likely to participate in evaluation of food is gustation, but its function has been controversial in lizards (Schwenk, 1985). However, most lizards have taste buds on the tongue and oral mucosa (Schwenk, 1985), and substances that are sweet and bitter to humans elicit responses by *A. carolinensis* having blocked vomerolfaction (Stanger-Hall et al., 2001). Although *Anolis* lizards appear to have less well developed olfactory systems than most lizards, olfaction was not excluded in the experiment.

Some lingual behaviors provide presumptive evidence about sensory roles. When responding to sucrose, *G. caesaris* tongue-flick initially, contacting the anteroventral tip of the tongue with the swab, thereby indicating vomerolfactory sampling (Cooper and Pérez-Mellado, 2001a). They rapidly switch to licking, where the dorsal surface of the tongue that contains taste buds is brought into contact with the swab. Because licking did not occur in trials with prey surface chemicals or fat, but only in response to sucrose, it may be a specific response to carbohydrates, especially to those having a sweet taste.

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