Gustatory Responses of a Tropical Frugivorous Bat

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Gustatory Responses of a Tropical Frugivorous Bat[1]

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Abstract. The electrical activity of the chorda tympani nerve in response to chemical stimulation of the tongue of the tropical frugivorous bat *Artibeus jamaicensis* was compared to that of several rodents and carnivores. The slope of the NaCl response-concentration curve is much steeper than curves for the other animals and the maximum response is reached at a lower concentration (approximately 0.25M NaCl). NaCl is a more adequate stimulus than NH_4Cl, LiCl is approximately equal to NaCl, and KCl response is low. These results are similar to those previously found for the rodents but quite different from those for the carnivores. Response is lower to sucrose stimulation than to quinine or HCl, and response to all three is slightly higher, when compared to the NaCl response, than for most o fthe rodents and carnivores. Responses to monovalent chloride salts and the other taste qualities are quite different from those of the little brown bat, *Myotis lucifugus*.

The NaCl response is not maintained at a steady-state level as in the rat but shows a constant decline after the initial response. A high water response, almost equal to the initial taste response, is obtained after stimulation with 0.01NHCl. Two types of water response are shown.

Differences in gustatory responses of various small mammals to chemical stimulation of the tongue, as measured by the activity of the chorda tympani nerve, have been shown by a number of studies (Beidler, 1953; Beidler, Fishman and Hardiman, 1955; Fishman, 1957, 1959; Pfaffmann, 1953, 1955; Tamar, 1956; and others). Animals belonging to various phylogenetic orders have been included in these studies. The forms ranged from the extremely polyphagous opossum to the relatively stenophagous guinea pig. However, none of these represent groups of closely related forms having entirely different stenophagous diets.

The order Chiroptera is the only order of small mammals in which closely related species have evolved such widely varied, yet narrowly limited, feeding habits. Though there is not much variability in feeding habits exhibited within a genus, diets vary widely among genera in some families. The Chiroptera includes species which exist entirely on the blood of other mammals, species which eat only fruit, others which eat only insects, some which use only fish, and others which exist on a diet of nectar. Here, then, is a group which seems ideal for a study of closely related forms whose feeding habits vary enough to offer the possibility of determining what relationship, if any, there may be between feeding adaptations and taste sensitivity. Thus, this investigation was undertaken and the following is a report of the information obtained from one species of frugivorous bat, *Artibeus jamaicensis*.

METHOD

About 60 *Artibeus jamaicensis* were collected near the village of Paso de Ovejas in the state of Veracruz in southern Mexico. The bats were acclimatized for a few days before being shipped by air to the United States. In our laboratory the bats were maintained in especially constructed cages similar to those described by Wimsatt and Guerriere (1961), approximately 20 bats to the cage. The animal room was maintained at approximately 23°C with fluctuations limited to only a degree or two. No attempt was made to regulate humidity. The bats were transferred to clean cages once every two weeks. They were fed on slices of ripe banana (about 20 grams per bat per day) with occasional chunks of apple and fresh or canned peaches. Every other day a drop of commercial vitamin solution was placed on each banana slice.

The bats can be maintained in this manner in an apparently healthy state for long periods. Jamaicensis seems to be a hardy species and we suffered only minor losses over a 3-year period except, of course, for those sacrificed to the taste experiments.

Animals were anesthetized with interperitoneal injections of sodium nembutal. The chorda tympani nerve of one side was exposed, freed from surrounding tissues and cut at a point near the middle ear. The peripheral end of the free nerve was placed on cotton wick electrodes. The anterior two-thirds of the tongue, which contains the fungiform papillae innervated by afferent axons of the chorda tympani, was placed in a small, glass flow-chamber through which a uniform flow of test solution could be passed, bathing a constant area of the tongue. Test solutions were flowed over the tongue for 15 to 20 seconds at a rate of 3 to 5 ml per second.

Continuous distilled water rinses were used between successive stimulations. Stimulations were separated by at least a 2-minute water rinse. In most instances this was ample time to remove the effect of the stimulant entirely, allowing the nerve activity to return to resting, or base, level.

The impulses were amplified and displayed on an oscilloscope and recorded on a Sanborn recorder after being electronically summated in the manner previously described by Beidler (1953). The magnitude of the response to stimulation of the tongue with chemical stimuli was measured as the total height of the summated electrical activity. Responses were reproducible within 3-5% for any given animal under the usual conditions of the experiment. Control stimuli were adequately dispersed between test stimuli to insure that no change had occurred during the run. When control responses could no longer be maintained within a 5% reproducibility, the experiment was abandoned.

Most experiments lasted for several hours, indicating that little or no irreversible damage was caused by the relatively frequent stimulation of the tongue. Every hour or two during an experiment the nerve was removed from the electrodes and inundated with Ringer's solution for about 15-20 minutes to prevent desiccation. More frequent washing was unnecessary since the nerve and electrodes were kept deep within the chamber of tissues left by the dissection. This apparently retarded undue desiccation effectively.

RESULTS AND DISCUSSION

Chloride Salts and Taste Qualities.

A summary of some of the data obtained from *Artibeus jamaicensis* is presented graphically in Figure 1 along with similar data from the white rat as a basis for comparison.
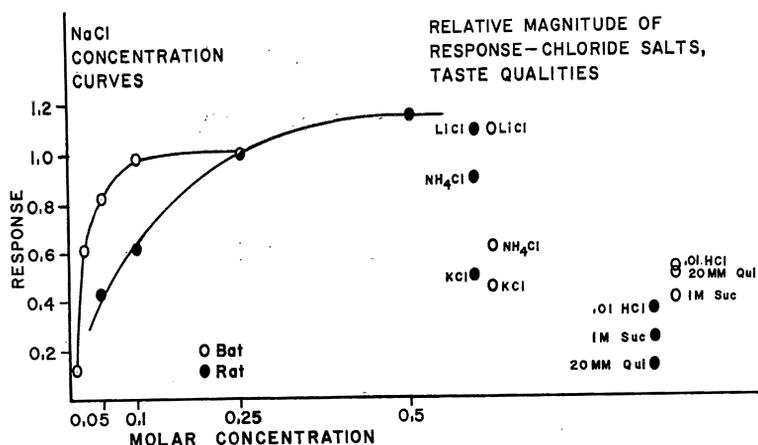

Figure 1. Relative magnitude of response with chloride salts and taste qualities.

Detailed information on the rat and other species has been presented by Beidler, (1953), Pfaffmann (1953, 1955), Beidler, Fishman and Hardiman (1955) and others. As with the rodents, NaCl represents the most adequate stimulant of the chloride salts for *A. jamaicensis*. NaCl, therefore, was used as the control stimulant throughout this study. However, sensitivity to NaCl above threshold concentration seems to be greater in *A. jamaicensis* than in the rodents as the NaCl response concentration curve has a much steeper slope in *A. jamaicensis* and the maximum response is reached at lower concentration. Whereas maximum response to NaCl is obtained in the rat at about 0.5M concentration, maximum response in *A. jamaicensis* is reached at approximately 0.25M. Though threshold studies have not been made for *A. jamaicensis*, the shape and slope of the response-concentration curve can be used as a general indication of NaCl sensitivity.

A comparison of responses of a number of animal species to equal concentrations of a series of chloride salts indicates the following:

1.   LiCl and NaCl always elicit the same relative magnitude of response.

2.   NaCl is a more adequate stimulant for the rodents than NH_4Cl whereas NH_4Cl is a more adequate stimulant for the carnivores than NaCl.

3.   KCl always elicits a much lower response than the control substance (NaCl for rodents, NH_4Cl for the carnivores).

4.   LiCl and NaCl both elicit lower responses than KCL in carnivores.

Thus, the order of response in the rodents (rat, hamster, guinea pig, 13-lined ground squirrel and Arizona gray squirrel—Fishman, unpublished data) is:
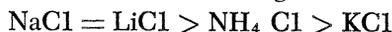
$$NaCl = LiCl > NH_4 Cl > KCl$$
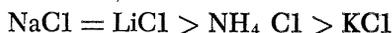
The order in the carnivores (Dog, Cat, Raccoon) is:

$$NH_4 Cl > KCl > NaCl = LiCl$$
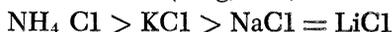
The white faced, ringtail monkey (Fishman, 1959) resembles the carnivores with regard to these salts.

A. jamaicensis exhibits the following order of response:

$$NaCl = LiCl > NH_4 Cl > KCl$$

and therefore falls into the same general category as the rodents with regard to their response to these salts. However, there is a closer resemblance to the hamster, guinea pig and squirrels than to the rat in relative magnitude of response to NH_4Cl. In the rat NH_4Cl elicits about 0.9% the magnitude of response to NaCl whereas with the other rodents and *A. jamaicensis* the response to NH_4Cl is 0.6% or less of the NaCl response.

In previous studies, 0.01N HCl, 20mM quinine hydrochloride, 0.5M or 1.0M sucrose, and NaCl have been used to represent the four taste qualities acid, bitter, sweet and salt. Comparative data for the phylogenetic groups can not be summarized in a few general statements except that the response to the control salt (NaCl for the rodents, NH_4Cl for the carnivores) is always considerably greater than the response to any of the other three substances. However, the relative response to these substances varies greatly with the species of animal. For example, the rat and hamster show a greater response to 0.01 HCl than to either sucrose or quinine, whereas the guinea pig responds better to sucrose than to the other two. The 13-lined ground squirrel (*Spermophilus tridecemlineatus*), the eastern fox squirrel (*Sciurus niger*) and the Arizona gray squirrel (*Sciurus arizonensis*) all exhibit a very high magnitude of response to sucrose, whereas the southern flying squirrel (*Glaucomys volans*) shows a very poor sweet response, much like the other rodents so far examined (Fishman, unpublished data).

Similarly, the dog, cat and racoon exhibit varied responses to the taste qualities. The dog and raccoon show a better sweet response than bitter or acid, while the cat responds better to acid than to sweet or bitter. The white faced, ringtail monkey exhibits a uniquely high acid response and a sweet response second only to that of the squirrels.

A. jamaicensis exhibits a response to acid, sweet and bitter somewhat higher than that of the rat and also in a different order. HCl is highest in both, but sucrose is lowest in the bat while quinine is lowest in the rat. However, the relative effevtiveness of the three substances in the concentrations used is so nearly the same in each of the animals that the exact order may not be significant. This bat species, it would seem, has a somewhat better general sensitivity to HCl, sucrose and quinine than the other animals tested except for the monkey, rabbit, and possibly the hamster. The best evidence is that *A. jamaicensis* is exclusively frugivorous and thus represents a different type diet from any of the other animals for which data are available, with the possible exception of the ringtail money, which is also frugivorous but is occasionally omnivorous.

The little brown insectivorous bat, *myotis lucifugus* (Tamar, 1956), and *A. jamaicensis* exhibit significantly different taste responses. The position of NaCl and NH_4Cl in the salt series is reserved for the two bats, and, though the responses to the taste qualities are more difficult to compare because the concentrations of sucrose, quinine and acid used by Tamar were different from those used in this laboratory, indications are clear that

sucrose is a much more efficient stimulant for *lucifugus* than for *jamaicensis* and quinine response is much lower in *lucifugus* than in *jamaicensis*. *The difference in sucrose response, and* perhaps even the quinine response, is not too surprising since many closely related species may show similar differences in their response to sweet and better, e.g. the squirrels. The differences in salt response, however, are much more interesting. Since the two bats differ greatly in feeding habits this may be evidence of more than a casual relationship between adaptations and taste sensitivity. Of course these two bats are of different families, live in quite different climates, range over widely different parts of North America and are quite different in a number of other respects, both behaviorly and anatomically. Perhaps more conclusive indications of a relationship between feeding adaptations and taste sensitivity will be obtained when similar studies are concluded on bat species more closely related. A study is currently in progress in this laboratory on three additional tropical species: One other species of the genus *Artibeus* (*A. literatus*) and *Corollia perspiculatum,* both frugivorous, and a sanguivorous bat, *Desmodus.* Also, it is hoped that a tropical insectivorous species from the family Molossidae can be obtained for study in the near future.
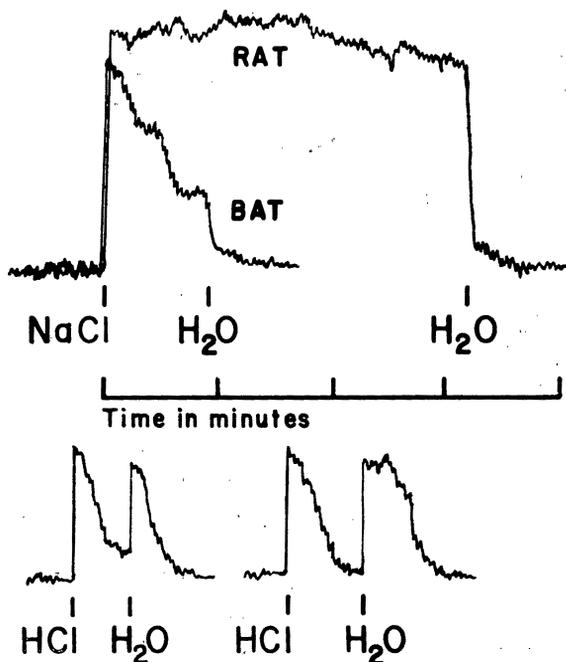

Figure 2. Above characteristics of sodium chloride response.
Figure 3. Below characteristics of water response.

Temporal Pattern of Response.

With the rat, monovalent salts in concentrations of 0.25M or 0.5M can be applied to the tongue continuously over a relatively long period of time without an appreciable decrement in the steady-state response. This is also true of the other animals studied and is illustrated in Figure 2 by the activity of a rat chorda tympani nerve to stimulation of the tongue with 0.5M NaCl. *A. jamaicensis* shows no such maintenance of activity to monovalent salt stimulation. This is also illustrated in Figure 2. The bat response has been enlarged in the figure to correspond in magnitude to the rat response and superimposed on the rat response for better comparison. The bat response is to 0.25M NaCl.

A. jamaicensis response to monovalent salts is similar to rat response to divalent salts such as $CaCl_2$, $MgCl_2$ and $BaCl_2$, all of which show a rapid decrement of activity to a low steady-state level or to zero activity.

Water Response.

Some animals exhibit a burst of nerve activity when certain chemical stimulants are washed off the tongue with water. This is especially true of the rabbit. Some other species exhibit a water response only after stimulation with very high concentrations of certain substances. *A jamaicensis* is typical of most animals in that it shows no water response whatever after normal stimulation with monovalent salts, 1.0M sucrose and 20mM quinine. However, there is a striking and consistently reproducible water response after stimulation with 0.01MHCl. The water response is usually almost as great in magnitude as the initial response to the acid and frequently lasts longer than the acid response. This is illustrated in Figure 3 which shows the two types of water response noted in *A. jamaicensis.*

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472   IOWA ACADEMY OF SCIENCE   [Vol. 70

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Measurement of Standard Metabolism, Water Loss and Body Temperature of the Little Brown Bat[1]

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Abstract. A complete description is given of a respirometer, suitable for unrestrained five to ten gram bats, from which the following variables were simultaneously directly measured: air and body temperatures, relative humidity, oxygen consumption, carbon dioxide production, water loss, and electrocardiograms. Temperature was measured with specially mounted bead thermistors and a wheatstone bridge. Relative humidity was measured with an adsorptive electronic sensor which was excited by a transistorized oscillator, and had the voltage output rectified and fed to an oscillograph. Electrocardigrams were taken with custom-made "safety" pins chronically indwelling through the dorsolateral thoracic epidermis. Electrical connection was made with common clothing snap fasteners. Various controlled humidities were produced by bubbling air through saturated salt solutions. Water vapor was converted to acetylene and collected along with respiratory gases over mercury for subsequent analysis with a gas chromatograph.

As part of an environmental physiological investigation of responses of bats to various combinations of temperature and humidity a monitoring system was developed. The apparatus was capable of directly and simultaneously measuring oxygen consumption, carbon dioxide production (therefore respiratory quotient and heat production), electrocardiograms (and heart rate), evaporative water loss, and body temperature from unrestrained animals. This paper describes by components the entire system as it has evolved.