

Comparative Gustatory Responses in Four Species of Gerbilline Rodents

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Summary. Integrated taste responses to chemical stimulation of the tongue were recorded from the intact chorda tympani nerve in four species of gerbils (*Meriones libycus*, *M. shawi*, *M. unguiculatus* and *Psammomys obesus*).

1. Sucrose was one of the most effective stimulants.
2. In comparison with sucrose, NaCl was less effective in gerbils than in other rodents. The smallest NaCl responses were found in those gerbil species whose native habitat and food subject them to the greatest osmotic stress.
3. The non-linearity of the NaCl concentration-response data suggested there may be more than one type of NaCl receptor site.
4. Two groups of cations were recognized as stimulants in *Meriones* species: (Na^+ , Li^+) and (K^+ , Rb^+ , Cs^+).
5. The stimulating effectiveness of methyl α - and β -D-glucopyranoside was compared with several naturally occurring sugars. From this analysis, it was concluded that the stimulating potency of glucopyranoside is increased by an alpha linked substituent, as in sucrose.
6. The only reliable neural responses to water rinse occurred with the divalent cations in the two species not found in extreme desert. It is improbable that gustatory water responses play a role in the water balance of desert rodents.
7. Sunflower seeds contain 4.28% sucrose which is the dominant sapid substance. Lipid soluble chemicals did not stimulate the taste receptors.
8. Some aspects of the evolution of gustatory systems are discussed.

Introduction

Four species of gerbils from Northern Africa and Central Asia were examined in an attempt to relate their taste physiology to habitat and feeding behavior. *Meriones libycus* is an inhabitant of extreme deserts. *Meriones shawi* occurs in arid and semi-arid regions; it has never been reported in extreme desert. The natural habitats of *Meriones unguiculatus*, the Mongolian gerbil, include stream banks and oases of the desert (Bannikov, 1954). *Psammomys obesus*, the sandrat, is found in arid regions on alkaline soils, especially where chenopod shrubs occur. Of the *Meriones* species, *libycus* is subjected to the most severe conditions of aridity and *unguiculatus* to the least (Lay, 1972).

Rodents in arid regions commonly feed both on seeds and leaves of several plants and also show seasonal shifts in the mixture of food plants (Bannikov, 1954; Bradley and Mauer, 1971; Cameron and Rainey, 1972). *Psammomys obesus*, which feeds heavily on succulent halophytes of the family *Chenopodiaceae* that grow on alkaline soils (Petter, 1961) and *Dipodomys microps*, the chisel-toothed kangaroo rat, which feeds predominantly on the saltbush, *Atriplex confertifolia*

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(Kenagy, 1972), are exceptions to the usual granivorous feeding pattern in arid regions. Even in these cases of restricted plant diet, both geographical and seasonal variation in soil aridity and salinity cause shifts in the ionic and water content of plants (Aharonson *et al.*, 1969; Kenagy, 1973). From these considerations, it is reasonable to conclude that the taste system of desert rodent herbivores evolved in the context of variable plant solute and water content.

There is considerable species variation in the gustatory responses of mammals to chemical stimulation of the tongue (reviewed by Oakley and Benjamin, 1966; Fishman, 1971). In some instances this variation follows an orderly pattern. For example, carnivores have a higher sensitivity to NH_4Cl than NaCl , whereas herbivores generally respond better to NaCl (Beidler *et al.*, 1955). This is also true within related species; the fruit-eating bat (*Artibeus jamaicensis*, Fishman, 1963) has a larger response to NaCl than NH_4Cl , whereas the reverse is true in the insectivorous bat (*Myotis lucifugus*, Tamar, 1961). NH_4^+ responsiveness may be related either to amino groups of proteins and peptides (preference) or to spoilage of meat (aversion). NaCl responsiveness may relate to the need for supplemental Na^+ in the diet of herbivores (Bott *et al.*, 1967).

We investigated the possibility that the ability of various species of gerbils to subsist upon seeds or succulent but salty plants might be reflected in adaptive variation in their gustatory system. Since it has been amply demonstrated (reviewed by Schmidt-Nielsen, 1964) that rodents subjected to the stress of desert living have distinctive behavioral and physiological adaptations to cope with problems of heat and aridity, conceivably there are also adaptations in the gustatory system which optimize ingestion of useful food items. In the context of adaptation to desert conditions we were particularly interested in evaluating the taste responses to NaCl and to water rinse.

Materials and Methods

A. Electrophysiology

The Mongolian gerbil, *Meriones unguiculatus*, was obtained from a closed colony maintained by J. J. Hasenau of Northville, Michigan. *Meriones shawi*, *Meriones libycus*, and *Psammomys obesus*, whose parents were collected from the desert of Morocco and Egypt, were obtained from Dr. Douglas Lay, Department of Anatomy, University of North Carolina. All animals used in these experiments were less than one year old. In order to record from the chorda tympani nerve, gerbils were anesthetized with an initial intramuscular or intraperitoneal injection of sodium pentobarbital (35 mg/kg). One-half of this dose was given at 30 min intervals until the animal was completely anesthetized. A tracheal cannula was inserted and the animal secured to a headholder which immobilized the skull.

In *M. libycus*, *M. shawi*, and *M. unguiculatus* the chorda tympani nerve is readily accessible within the middle ear. The surgical approach was made through the external auditory meatus. Using a binocular microscope, a small patch of skin (Fig. 1A) and the large ceruminous wax gland (Fig. 1B) were removed. When the accessory tympanum (Fig. 1C) was removed, it revealed the chorda tympani nerve spanning the gap between the processus brevis manubrii of the incus and the posterior lamina of the tympanic bone (Fig. 1D). It was unnecessary to cut or desheath the nerve for electrophysiological recordings. In *M. shawi*, which lacks an accessory membrane, the nerve was exposed by removing the thin bones that replace this membrane. The usual mandibular approach (Beidler, 1953) was used with *P. obesus*, because the nerve could not be easily approached through the middle ear.

Electrical activity was recorded by touching the intact nerve with a nichrome electrode (100 μm dia) which was led to a differential amplifier (Grass P-511). Neural activity was

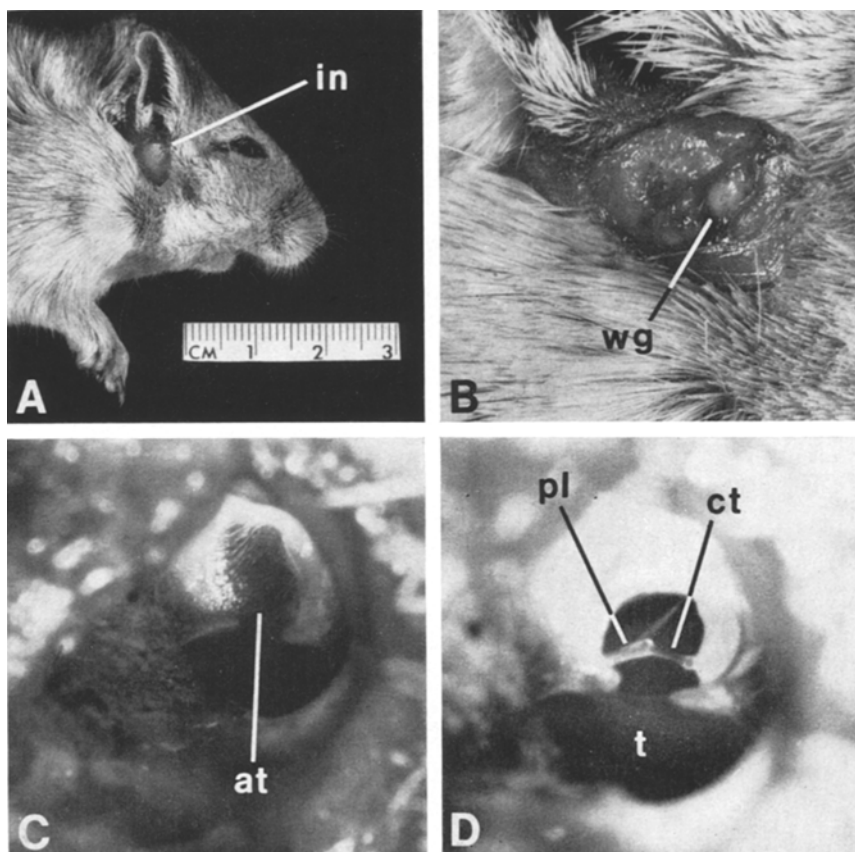


Fig. 1A—D. Exposing the chorda tympani nerve in *M. unguiculatus*. (A) Lateral view of gerbil's head showing the level at which the incision (*in*) was made to approach the middle ear. (B) Wax gland (*wg*) underlying the superficial muscles near the external auditory meatus. (C) A view into the auditory meatus showing the accessory tympanum (*at*). (D) Upon removal of accessory tympanum, the chorda tympani nerve (*ct*) can be seen hanging without support and coursing along the surface of the posterior lamina (*pl*) of the tympanic bone. The tympanum (*t*) can be seen. The nerve has a diameter of about 0.1 mm

displayed on an oscilloscope and could be monitored by means of a loudspeaker. Since the integrated discharge of the whole chorda tympani nerve represents a summation of activity from many receptor cells (e.g. Kimura and Beidler, 1961), this method was used to characterize the gustatory system. A response in this study was defined as the difference between spontaneous activity and the greatest integrated potential elicited by a given solution applied to the tongue. The integrator (Grass Model #73PA) time constant was set at 0.5 sec, full wave rectification. The indifferent electrode was placed on a nearby piece of moist tissue within the bulla.

B. Stimulation

In order to guarantee effective stimulation, the tongue was gently extended with a small hook, which was inserted into the ventral epithelium of the tongue contralateral to the responsive side of the tongue. Over the extended tongue distilled water was continually flowed at a rate of 0.13–0.17 ml/sec. Test solutions (2–4 ml) were alternated with the distilled water

rinse without interruption of fluid flow. A control standard solution (0.5 M sucrose or 0.2 M NaCl) was presented between test solutions, typically after every 3 test chemicals. When control or test responses varied more than $\pm 10\%$, all interjacent responses were rejected. The following molar chemical concentrations were used: NaCl, (0.0001, 0.0003, 0.001, 0.003, . . . , 1.0); sucrose, (0.001, 0.003, 0.01, 0.03, . . . , 1.0); 0.01 HCl; 0.02 quinine-HCl; 0.2 molar concentrations of LiCl, KCl, CsCl, RbCl, NH_4Cl , CaCl_2 , MgCl_2 , and SrCl_2 ; 0.5 molar concentrations of sucrose, D-glucose, D-fructose, D-mannose, D-galactose, methyl α -D-glucopyranoside, methyl β -D-glucopyranoside. The sapid components of sunflower seeds were artificially reconstituted as a mixture of the following chemicals (final concentrations, w/v): 0.25% glucose, 4.28% sucrose, 0.14% *myo*-inositol, 0.4% raffinose, 2.0% chlorogenic acid, and 0.2% caffeic acid. All chemical solutions were made with distilled water. A decoction containing the sweet inhibitor gymnemic acid was extracted from *Gymnema sylvestre* leaves. The aqueous extract was effective in blocking the taste of sucrose in humans. All solutions were presented at room temperature (24–28°C).

C. Preparation of Sunflower Seed Extracts for Taste Stimulation

Homogenized sunflower seed (*Helianthus annuus*), was centrifuged (1 g raw husked seed to 5 ml water) and the supernatant saved as a taste stimulant. The diffusate and retentate of dialyzed homogenized sunflower seed were also used as taste stimulants. Water and lipid soluble components were separated from chopped raw seed in the following manner: chopped seed was gently refluxed in each of three volumes of chloroform:methanol, 2:1, for one hour. After filtration, the insoluble residue was refluxed again in the same solvent for another hour and filtered. This residue was washed with two volumes of solvent and filtered. The solvent washes were pooled and partitioned into water and lipid phases for taste stimulation. The remaining dry, defatted residue was washed with several volumes of water. The centrifuged residue and supernatant were tested as taste stimulants.

All extracts and residues were prepared for testing by adjusting the volume with water or rotary evaporation to make the final concentration equivalent to one gram of seed in 5 ml.

D. Sugar Analysis of Seed Extract

1. *Trimethyl Silylation*. Samples of a few mg of unknown sugars were dissolved in pyridine and then trimethylsilylated according to the method of Sweeley *et al.* (1963). Pyridine was removed by evaporation and the 0-trimethylsilyl ether derivatives were dissolved in 0.2 ml chloroform. An aliquot (2 μ l) was analyzed by gas-liquid chromatography. A 0.25×72 inch SE-32 glass column was used at 165°C for monosaccharides and 290°C for oligosaccharides. Helium was the carrier gas.

2. *Alditol Acetates*. A known amount of sunflower extract was reduced with NaBH_4 and acetylated according to the method of Sawardeker *et al.* (1965). The reaction mixture was evaporated to dryness and the acetylated derivatives were taken up in chloroform. L-Fucitol was used as an internal standard. A 0.2 μ l sample was analyzed by gas-liquid chromatography using a 0.25×48 inch 3% ECNSS-M glass column at 190°C with helium carrier.

3. *Paper Chromatography*. Sugars were analyzed by descending paper chromatography with Whatman No. 1 paper. Solvent systems used were n-butanol:acetic acid:water (BAW₁) (5:1:4), n-butanol:pyridine:water (BPW) (6:4:3), ethyl acetate:pyridine:water (EAPW) (10:4:3), phenol:water (PW) (4:1) and n-propanol:ethyl acetate:water (PEAW) (3:1:1). For better separation of the sugar components, many of the chromatograms were run two or three times. Spots were detected using either silver nitrate (Trevelkyn *et al.*, 1950), *p*-anisidine-HCl (Hough *et al.*, 1950) or Dimedon spray as described by Adachi (1964).

Descending preparative paper chromatography on Whatman 3MM paper with the EAPW solvent system was used on the seed extract. This system was run twice and the sugars were located with *p*-anisidine-HCl spray on thin strips cut from the edge of each developed chromatogram. The individual sugars were recovered by eluting the filter paper bands with water and methanol.

4. *Glucose Determination*. Quantitative determination of glucose was done enzymatically on the seed extracts using glucose oxidase (Glucostat-Worthington).

Results

A small tonic increase in neural activity was observed with application of Ringer's (Locke's without glucose) solution to the saliva-saturated tongue. Subsequently, during rinsing of the tongue with distilled water, the activity was reduced to a level slightly less than had been observed in the saliva-saturated tongue.

When any effective chemical was flowed onto the tongue, there was an initial rapid rise of activity (Fig. 2A) whose magnitude was dependent upon concentration (e.g., Fig. 3).

A. Responses to the Four Taste Qualities

The four traditional taste qualities are represented by sucrose, NaCl, HCl, and quinine. Relative to the other fundamental chemicals, sucrose evoked the greatest response in the four species of gerbils examined (Table 1). In comparison, the albino rat's response to sucrose (Beidler *et al.*, 1955) is the lowest of all rodents studied to date. It can also be seen from Table 1 that *M. unguiculatus*, *M. libycus*, *M. shawi* and *P. obesus*, which are associated with habitats scarce in fresh water, have relatively smaller NaCl and larger sucrose responses.

Table 1. Relative summated gustatory responses in several rodents to the four classical tasted qualities. All responses are calculated as a fraction of the response to 0.5 M sucrose, which is assigned a value of 1.0. 95% confidence intervals are indicated for *Meriones* species

Animal	(N)	Taste stimulus			
		0.5 M sucrose	0.2 M NaCl	0.01 M HCl	0.02 M quinine HCl
<i>Meriones unguiculatus</i>	(5)	1.0	0.84 ± 0.14	0.43 ± 0.18	0.57 ± 0.12
<i>Meriones libycus</i>	(5)	1.0	0.67 ± 0.05	0.38 ± 0.06	0.52 ± 0.12
<i>Meriones shawi</i>	(4)	1.0	0.59 ± 0.10	0.27 ± 0.12	0.44 ± 0.11
<i>Psammomys obesus</i>	(1)	1.0	0.47	0.31	0.25
<i>Rattus norvegicus</i> ^a		1.0	4.80 (0.1 M)	2.89	0.96
<i>Mesocricetus auratus</i> ^a		1.0	1.33 (0.1 M)	1.13	0.44
<i>Cavia cobaya</i> ^a		1.0	1.61 (0.1 M)	0.71	0.39

^a Data recalculated from Beidler *et al.* (1955).

B. Response to Inorganic Salts

Na⁺ and Li⁺ are equally effective as stimulants (Table 2). For all *Meriones* species K⁺, Cs⁺, Rb⁺ produce equivalent responses (Fig. 2C and D); they are also the least effective salt stimuli. The divalent chloride salts are the most effective salt stimulants for the three gerbil species associated with the most arid habitats, generally lacking fresh water (Fig. 2B and C).

C. Water Responses

In some instances, rinsing the taste solution from the tongue with water causes an increased neural discharge. This so-called "water response" is contingent

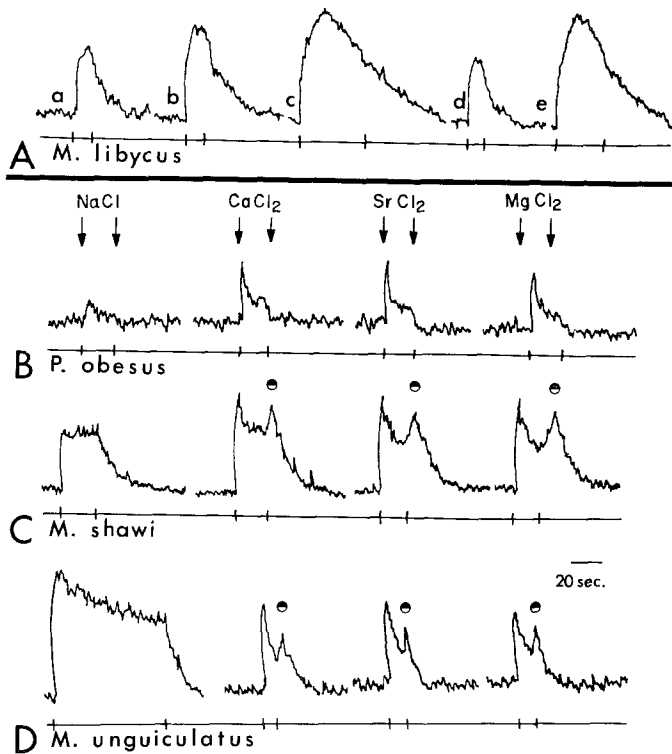


Fig. 2A—D. Summated taste responses from the chorda tympani nerve in four species of gerbils. A, (a) 0.2 M NaCl; (b) 0.2 M CaCl_2 ; (c) 0.5 M sucrose; (d) 0.2 M NH_4Cl ; (e) 0.5 M sucrose. In the rows B, C, and D, the stimuli are 0.2 M solutions of NaCl, CaCl_2 , SrCl_2 and MgCl_2 . Vertical marks indicate the onset of stimulus and water rinse. Responses to water rinse indicated by a half-filled circle

Table 2. Relative magnitude of gustatory response of seven species of rodents to 0.2 M concentrations of inorganic chloride salts. Responses are relative to 0.2 M NaCl. Italicized entries are consistently associated with water rinse response. 95% confidence intervals for *Meriones* species, ranged from ± 0.04 – ± 0.18

Animal	(N)	Salt								
		NaCl	LiCl	KCl	CsCl	RbCl	NH_4Cl	CaCl_2	MgCl_2	SrCl_2
<i>M. unguiculatus</i>	(5)	1.0	0.98	0.34	0.34	0.35	0.65	<i>0.76</i>	<i>0.67</i>	<i>0.63</i>
<i>M. shawi</i>	(4)	1.0	1.0	0.59	0.56	0.56	0.68	<i>1.33</i>	<i>1.23</i>	<i>1.21</i>
<i>M. libycus</i>	(5)	1.0	0.95	0.57	0.58	0.54	0.87	<i>1.33</i>	<i>1.35</i>	1.50
<i>P. obesus</i>	(1)	1.0	0.93	0.62	0.66	0.50	1.72	2.42	2.23	2.23
<i>R. norvegicus</i> ^a		1.0	1.1	0.25	0.21	0.29	0.85	0.55	0.42	0.50
<i>M. auratus</i> ^b		1.0	1.1	0.38	—	—	0.62	0.60	0.38	0.38
<i>C. cobaya</i> ^b		1.0	1.0	0.36	—	—	0.66	0.71	0.52	0.55

^a From Beidler (1953).

^b From Beidler *et al.* (1955).

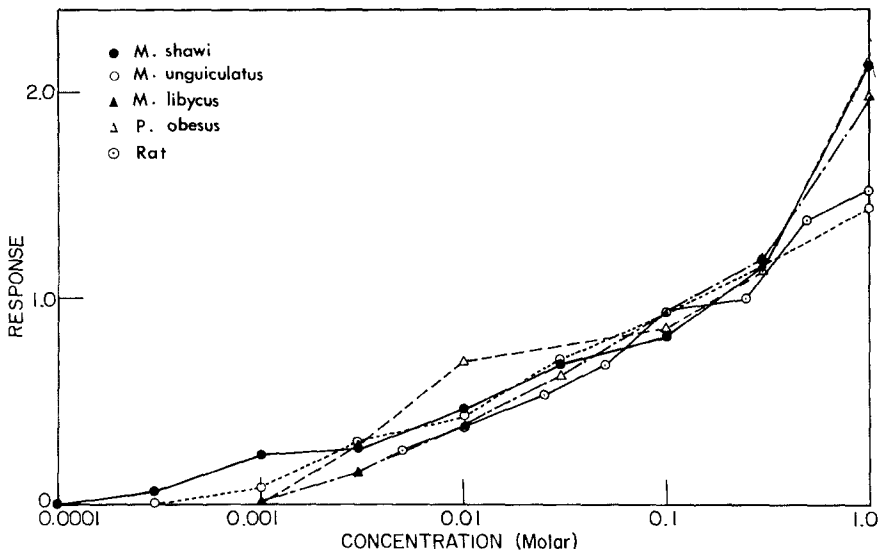


Fig. 3. Response of four species of gerbils and domestic Norway (hooded) rat to increasing concentrations of NaCl. Response is calculated as proportion of response to 0.2M NaCl. *M. libycus* ▲—; *M. unguiculatus* ○...; *M. shawi* ●—; *P. obesus* △---; hooded rat ○— (rat data from Beidler, 1953)

upon the type of chemical being rinsed away. In the case of gerbils, reliable water responses were observed only after removal of divalent chloride salts and only in *M. shawi* and *M. unguiculatus* (Fig. 2C and D).

Occasionally, other water responses were observed. In one of four *M. shawi*, 0.2 molar solutions of NH_4Cl , KCl, CsCl and RbCl gave water responses. In one of seven *M. libycus*, small water responses were observed after some, but not all, presentations of 0.5 M sucrose, 0.2 M NH_4Cl , 0.2 M CaCl_2 and 0.2 M NaCl.

D. NaCl Concentration Function

Increasing the concentration of NaCl in the stimulating solution caused an increasing neural discharge (Fig. 3). From 0.002 M–0.2 M, the slope of the concentration function was similar for all species. Electrophysiological NaCl thresholds for the rat (Pfaffmann *et al.*, 1967) appear to be similar to the gerbils'. Even though, in reference to sucrose, the chorda tympani nerve of the rat responds more vigorously to NaCl than that of the gerbils (Table 1), the similarity of the concentration-response curves (Fig. 3) suggests that the receptor mechanisms for NaCl are similar in rat and gerbils.

According to Beidler's analysis (1954, 1961), stimulation of the taste cells by NaCl in the rat involves reversible binding of one Na ion per NaCl site. This idea led to the development of the "fundamental taste equation":

$$C/R = C/R_m + 1/KR_m,$$

where C = concentration of stimulus; R = response; R_m = maximum response; K = association constant.

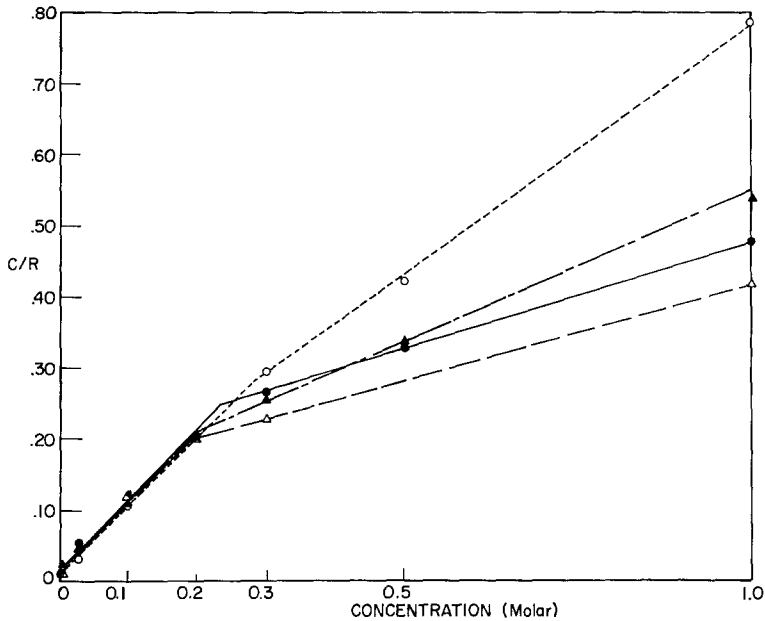


Fig. 4. Plot of gerbil's NaCl response according to Beidler (1954). C concentration; R response. Data and symbols from Fig. 3

Assuming that this is an accurate reflection of the molecular events occurring at the gustatory cell surface, a plot of C/R vs C would lead to a straight line. A plot of data from the four species of gerbils shows that the data do not follow a straight line (Fig. 4).

E. Response to Sugars

Concentration-response functions indicate that gerbils are highly sensitive to sucrose (Fig. 5). These curves are linear in a Beidler plot. Sucrose was clearly the most effective sugar tested (Table 3). Methyl α -D-glucopyranoside was the more effective methyl glycoside. D-Fructose is the most stimulatory reducing sugar in most rodents with D-galactose being the least effective. The extract of the plant *Gymnema sylvestris* failed to block or depress the neural response to 0.05 M sucrose in any of the four species of gerbils.

F. Response to Sunflower Seed Extracts

Crude aqueous extract of sunflower seeds evoked a strong neural discharge in the chorda tympani when applied to the gerbil's tongue (Fig. 6a). Molecules of less than 10000 m.w. were responsible for the major portion of the response of water soluble stimulants (Fig. 6b). The dialysis retentate evoked a small response (Fig. 6c), which is not unexpected, since it is known that some higher molecular weight compounds, such as polypeptides, possess gustatory properties (Cagan, 1973). The gustatory stimulants were in the water soluble extracts (Fig. 6e and g)

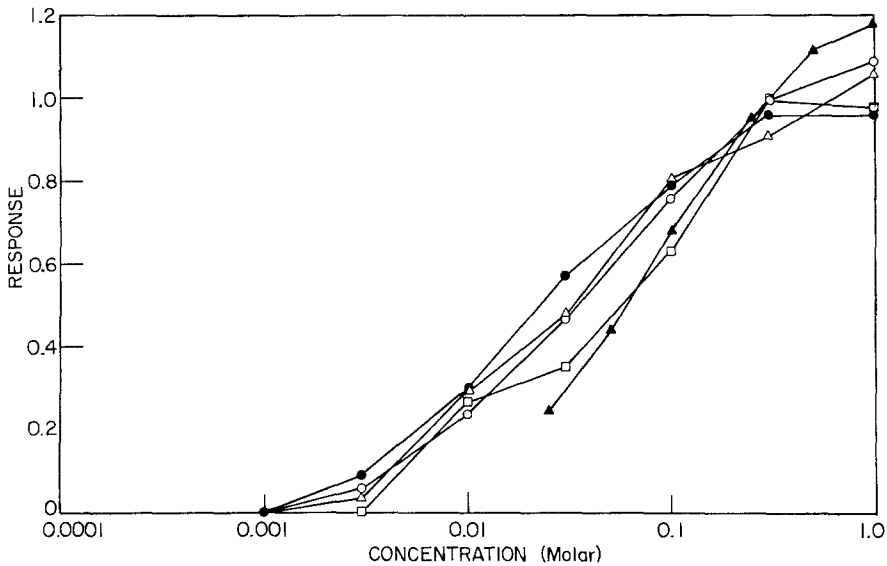


Fig. 5. Response of four species of gerbils and rat to increasing concentrations of sucrose. *M. libycus*—●—; *M. unguiculatus*—○—; *M. shawi*—△—; *P. obesus*—□—; rat—▲— (rat data from Hardiman, 1964). Response calculated as proportion of response to 0.2 M sucrose

Table 3. Relative magnitude of gustatory response in 6 species of rodents to equimolar sugars (0.5 M). All responses are relative to sucrose. 95% confidence intervals are indicated

Compound	Animal (N)					
	<i>M. libycus</i> (7)	<i>M. unguiculatus</i> (6)	<i>M. shawi</i> (3)	<i>P. obesus</i> (1)	Rat ^a	Hamster ^a
Sucrose	1	1	1	1	1	1
D-Glucose	0.58 ± 0.14	0.53 ± 0.06	0.67 ± 0.06	0.52	0.59	0.41
D-Fructose	0.68 ± 0.08	0.58 ± 0.11	0.69 ± 0.06	0.55	0.80	0.55
D-Mannose	0.61 ± 0.13	0.64 ± 0.07	0.66 ± 0.20	0.53	—	—
D-Galactose	0.52 ± 0.15	0.47 ± 0.15	0.55 ± 0.05	0.53	0.44	0.44
Methyl α-D-glucopyranoside	0.81 ± 0.10	0.77 ± 0.07	0.89 ± 0.12	0.86	—	—
Methyl β-D-glucopyranoside	0.53 ± 0.10	0.52 ± 0.04	0.64 ± 0.06	0.55	—	—

^a Hardiman (1964).

and not in the lipid extract (Fig. 6f) or in the residue after lipid and water extraction (Fig. 6h).

The high concentration of sucrose as a free sugar in the sunflower seed (Table 4) accounted for about two-thirds of the neural discharge elicited by the water extract of the seed (Fig. 6j and l). The addition to sucrose of glucose, *myo*-inositol,

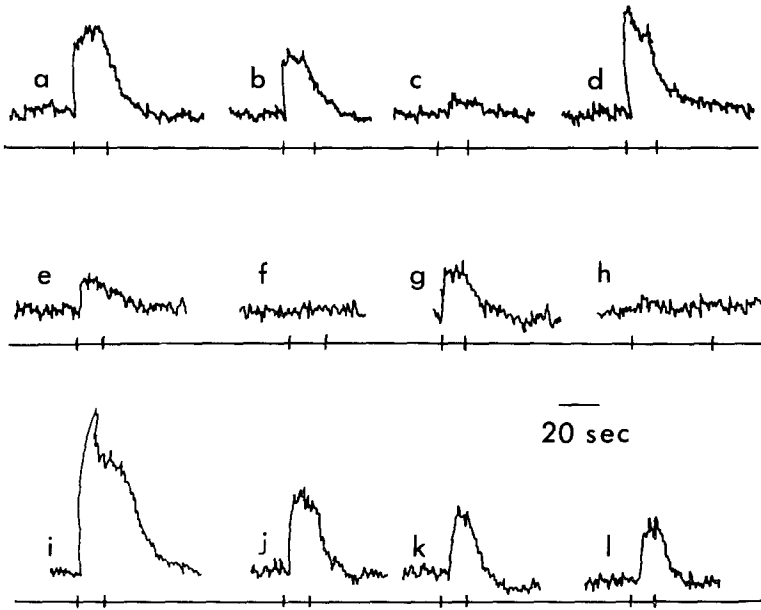


Fig. 6. Summator records from the chorda tympani nerve of *M. unguiculatus* in response to sunflower seed (*Helianthus annuus*) extracts flowed over the tongue. (a) Aqueous extract of homogenized seeds; (b) dialysis diffusate; (c) dialysis retentate; (d) 0.2 M NaCl; (e) water layer of lipid extraction; (f) lipid extract; (g) water extract of defatted meal; (h) residue after water and lipid extraction; (i) 0.5 M sucrose; (j) diffusate of aqueous extract of homogenized seeds; (k) artificial mixture of sapid constituents of diffusate of aqueous extract (see Methods); and (l) 4.28% sucrose (w/v)

Table 4. Sugars found in aqueous taste extract of husked, homogenized sunflower seed

Sugar	Concentration (w/w) (% defatted meal)	Solvent system
Ribose	0.06	EAPW, PW, PEAW
Fructose	0.55	EAPW, PW, BPW
Glucose	0.25	PPW, EAPW, PW
Galactose	0.10	PPW, EAPW, PW
Sucrose	4.28	EAPW, PEAW, BAW ₂
<i>myo</i> -inositol	0.14	BAW ₂ , EAPW, glc
Raffinose	0.49	BAW ₂ , EAPW, glc
Arabinose	trace	glc ^a

^a glc = gas liquid chromatography.

raffinose, and the phenolic compounds, chlorogenic acid and caffeic acid (Levin, 1971; Mikolajczak *et al.*, 1970), in appropriate concentrations (see Methods; Table 4), increased the amplitude of the summated discharge slightly (Fig. 6k). The concentration of fructose in the seeds (Table 4) was sufficient to account for some of the remaining 15% of the neural discharge to water extract.

Discussion

In the gerbil the Beidler plot for NaCl (Fig. 4) cannot be described by a single straight line. Data for the rat shows a similar but less pronounced break in the curve (Pfaffmann *et al.*, 1967). If the integrated neural discharge is a valid measure of binding to the receptor, then a more complex receptor model for NaCl, such as two independent sites (Beidler, 1961), is required. Two independent receptor systems with different affinities for NaCl could also account for the fact that in humans low concentrations of NaCl are sweet and higher concentrations salty (Renqvist, 1919).

Sucrose was the most effective gustatory stimulant of all the sugars tested. Evidence that α -glucose is sweeter than β -glucose in humans (Cameron, 1943) suggested to us that sucrose might be highly sweet because it is a glucopyranoside with an alpha linked substituent. The ability of methyl α -D-glucopyranoside to stimulate the gerbil's receptor better than methyl β -D-glucopyranoside or the equilibrium mixture of D-glucose supports this hypothesis. (Glycosides are useful in investigating the chemical basis of sweetness, because unlike reducing sugars they do not isomerize in aqueous solution, but adopt well-defined conformations and configurations). This is similar to responses of fly taste receptors (Evans, 1963; Jakinovich *et al.*, 1971; Hanamori *et al.*, 1972), which point to the presence of a glucopyranoside receptor where the C-1 substituent must be axial to maximally stimulate the sugar receptor.

Rinsing various chemicals from the human tongue with water leads to taste sensations whose character (sweet, salt, bitter, sour) and intensity depend systematically upon the nature and concentration of the chemical rinsed away (McBurney and Bartoshuk, 1972). Positive neural discharges to water rinse are easily recorded from the chorda tympani nerve of a variety of mammals (reviewed in Oakley and Benjamin, 1966). It is tempting but unwarranted to assume that it is this positive discharge which is responsible for the taste of water rinse; the function of the neural water response is not understood. This caution is underscored by the failure to observe discharges to water rinse in recordings from the human chorda tympani nerve (Diamant and Zotterman, 1959; Diamant *et al.*, 1965). As one approach to the function of the neural water response, we wished to determine whether it is related to the need to evaluate the dilution of wet ingestible materials under conditions of water shortage. In gerbils, however, water responses were rare and were less reliable than other responses to chemical stimulation. No reliable water responses occurred in the gerbil from the most arid desert conditions (*M. libycus*) or in the gerbil with the most highly developed urine concentrating mechanisms (*P. obesus*). It seems evident that water responses have not evolved as an adaptation pertaining to water balance in desert rodents.

The large sugar response of desert rodents may represent an adaptation to satisfy physiological requirements. Most species of gerbils are almost exclusively herbivorous or granivorous (Lay, 1972). Our electrophysiological results with the sunflower seed extracts support the hypothesis that sucrose is important in encouraging ingestion of seeds. Schmidt-Nielsen (1964) has pointed out that the kangaroo rat's survival can depend upon choosing high carbohydrate seeds; high protein seeds produce a negative water balance. The Mongolian gerbil, *M. ungui-*

culatus, typically inhabits all types of semi-desert (Bannikov, 1954) and depending upon the season it will eat green parts of plants or seeds. Among the gerbils studied it is subjected to the least amount of water stress. Its response to sucrose was the poorest of all the species studied. *M. shawi*, as an inhabitant of the dry Mediterranean littoral zone of North Africa, had a vigorous nerve response to sucrose. Drinking water is rarely available to this species. *M. libycus*, which inhabits the extreme desert of North Africa and Arabia, responded best to sugar when compared to NaCl. From these results it would appear that the sucrose response of the *Meriones* species increases with the severity of water shortage. This trend suggests a linkage of water balance mechanisms with sugar taste. Further data will be required to assess the large sucrose response of the sand rat *P. obesus* whose diet is primarily succulent halophytes.

It is our view that a better understanding of the diet will help clarify the results of comparative taste physiology. For example, the red fox (*Vulpes fulva*) and the domestic cat are both carnivores, yet the fox's sucrose response is vastly superior to the cat's (Fishman, 1971). The red fox, however, eats a substantial amount of grass and wild fruit (Korschgen, 1959). Certainly, additional research efforts are desirable in mammals to isolate, identify, and characterize electrophysiologically the gustatory stimulants in diets, particularly of selective feeders.

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