

An Analysis of Hamster Afferent Taste Nerve Response Functions

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ABSTRACT Sensitivities to moderately intense stimuli representing four taste qualities to man were determined for 79 hamster chorda tympani fibers. Some fibers were very sensitive to sucrose, sodium chloride, or hydrochloric acid, but none were very sensitive to quinine. These sensitivities were not randomly distributed among fibers: the sucrose sensitivity was separated from and negatively correlated with the other sensitivities which were associated and positively correlated with each other. Moreover, there were a limited number of sensitivity patterns: (*a*) fibers responding best to sucrose responded second-best to salt, less to acid, not to quinine; (*b*) fibers responding best to salt either responded second-best to sucrose and not to acid or quinine; or second-best to acid, less to quinine, and not to sucrose; and (*c*) fibers responding best to acid responded second-best to salt, more to quinine, and less to sucrose than other fibers. Therefore, if four stimuli of different taste qualities are ordered from acceptable to unacceptable, neural response functions of most hamster chorda tympani taste fibers peak at one point.

Sensitivities to nine other moderately intense stimuli which vary in quality to man were also determined for 46–49 of the fibers. Sensitivities to sweet stimuli were always associated with each other and separated from sensitivities to non-sweet stimuli. Sensitivities to nonsweet stimuli were all associated with each other; however, the strongest correlations were between sensitivities to stimuli of like quality, e.g., the three acids or the two sodium salts.

INTRODUCTION

Many single mammalian taste nerve fibers respond to substances which are in different chemical classes and of very different taste quality to man. Because of this, they are described as being “broadly tuned.” However, most single fibers will respond more vigorously to stimuli of one quality than to others. Threshold intensities for any one substance vary from fiber to fiber; in fact, compounds which are highly effective for some taste fibers may not stimulate other fibers at all. Response levels from threshold to maximal response of a particular fiber differ for different substances and the response levels to a particular substance vary among different fibers. Thus, although

they are broadly tuned, different taste fibers certainly do have very different sensitivities (Pfaffmann, 1955; Cohen, Hagiwara, and Zotterman, 1955; Fishman, 1957; Ogawa, Sato, and Yamashita, 1968).

Some fibers are more broadly tuned than others. That is, fibers vary in extent of tuning both in the number of quality classes to which they respond and in the degree to which response levels to different qualities differ. Each individual taste fiber has a unique set of sensitivities which is not exactly matched by any other fiber. Some fibers respond to one quality, some to two, some to three, and some to four taste qualities. In fact, sensitivities to solutions which man would classify as salty, sour, bitter, and sweet appear to be associated in a random manner in fibers of the taste nerves of the rat (Frank and Pfaffmann, 1968; Ogawa, Sato, and Yamashita, 1968).

Yet, two substances which are of the same taste quality or taste alike to man¹ will either both stimulate or both not stimulate a given fiber. The more alike the taste of two substances, the greater the similarity of the pattern of response they evoke across the population of fibers. This is reflected in higher correlations across fibers for responses to substances with similar tastes. Two substances of different taste qualities evoke different response patterns and across-fiber correlations are low, even though certain fibers may respond to both substances (Erickson, 1963; Marshall, 1968; Ganchrow and Erickson, 1970).

Nerve fibers in the chorda tympani nerve innervate taste receptors in the fungiform papillae on the front of the tongue. Fibers in the glossopharyngeal nerve innervate receptors in the circumvallate and foliate papillae on the back of the tongue. There are major differences in the sensitivities of the fibers in these two nerves. There are also differences in the sensitivities of either nerve in different species (Appelberg, 1958; Beidler, Fishman, and Hardiman, 1955; Yamada, 1967; Pfaffmann, 1955; Pfaffmann, Fisher, and Frank, 1967). For example, (a) the cat chorda tympani contains many more fibers sensitive to bitter substances and fewer fibers sensitive to sweet substances than the rabbit chorda tympani; and (b) the rat glossopharyngeal contains more fibers highly sensitive to bitter substances and fewer sensitive to salty substances than the rat chorda tympani (Pfaffmann, 1955; Bartoshuk, 1965; Frank, 1968; Nagaki, Yamashita, and Sato, 1964). Therefore, the choice of nerve and species to be studied will determine which and how many taste qualities will be well represented.

Much of the information about mammalian taste nerve fiber sensitivities has been gathered from the rat chorda tympani nerve and an across-fiber pattern model for taste quality discrimination has been developed with this information (Erickson, Doetsch, and Marshall, 1965; Erickson, 1967).

¹ The similarities of taste of different compounds are known for man (Schiffman and Erickson, 1971; Pfaffmann, 1959) and appear to be comparable in other mammals (Morrison, 1967).

Although it is acutely sensitive to salts and acids, its sensitivities to sweet and bitter solutions are minimal. Very few fibers can be isolated from this nerve which will respond to stimuli of these latter two qualities, even if test stimuli are very strong; and when fibers do respond to sweet or bitter substances, the response is usually small in comparison to responses to salty or sour substances. Therefore, generalizations about taste quality discrimination from those data should be limited to the salty and sour tastes.

Much less is known of the distribution of sensitivities to the bitter and sweet tastes and their discrimination by mammalian peripheral nerve fibers. The hamster chorda tympani nerve has a strong sensitivity to sweet, as well as sensitivities to salty, sour, and bitter comparable to those of the rat chorda tympani. Its study has shown that sensitivities to sucrose and saccharin are isolated from those for the other taste qualities in single fibers (Fishman, 1957; Ogawa, Sato, and Yamashita, 1968 and 1969; Frank, 1972). In the present work, the distribution of sensitivities to a number of stimuli of moderate intensity, categorized as sweet, salty, sour, or bitter by man, among hamster chorda tympani fibers are examined in detail. The result is the emergence of a considerable regularity in the organization of taste sensitivities among single fibers when the qualities are hedonically ordered, that is, when they are ordered: sweet, salty, sour, bitter or from behavioral acceptance to rejection.

METHODS

79 single taste nerve fibers were functionally isolated from 13 hamster chorda tympani nerves. Each hamster was deeply anesthetized with sodium pentobarbital, the trachea cannulated, and the left chorda tympani dissected free from the point where it joins the lingual nerve to its exit from the bulla, where it was cut. The sheath which surrounds the nerve was removed and small bundles of fibers separated from the nerve trunk. Each nerve bundle was lifted onto a Nichrome wire recording electrode. Action potentials were differentially amplified with respect to an indifferent electrode positioned in the wound near the nerve. The animal was grounded through a head clamp. Solutions (50 ml in 15 s) representing the four taste qualities, at room temperature (23°–26°C), were flowed from a funnel above over the anterior part of the tongue which was enclosed in a chamber. If the responses of a single active fiber could be reliably identified, judging by the size and shape of the impulses with oscilloscope and audio monitor displays, stimulation was continued according to a prearranged schedule.

Responses were recorded on analog tape for future "off-line" processing. Photographs were taken of the oscilloscope displays and the number of action potentials in the first 5 s of the response to each solution counted. The response to a first presentation of any stimulus was always used unless the noise level was too high but improved in a later presentation. This 5-s response, a fairly long measure, was chosen since (a) the time-course of the response varies across fibers and stimuli; (b) the inter-spike interval is highly variable; and (c) the exact time a solution contacted the papillae

innervated by the fiber on the electrode was not known and the point at which a response started was estimated from the photographs. The 5 s response measure was used throughout the data analysis. Fig. 1 is a series of photographs of one fiber's responses to 10 stimuli. At least 1 min elapsed between successive stimulations and the tongue was rinsed with water for at least 15 s before and after each stimulus was presented. A spontaneous response rate, the mean rate in the four 2-s periods just before stimulation with the basic taste stimuli, was also determined for each fiber.

Choice of stimuli, substances and concentrations, followed recording the whole

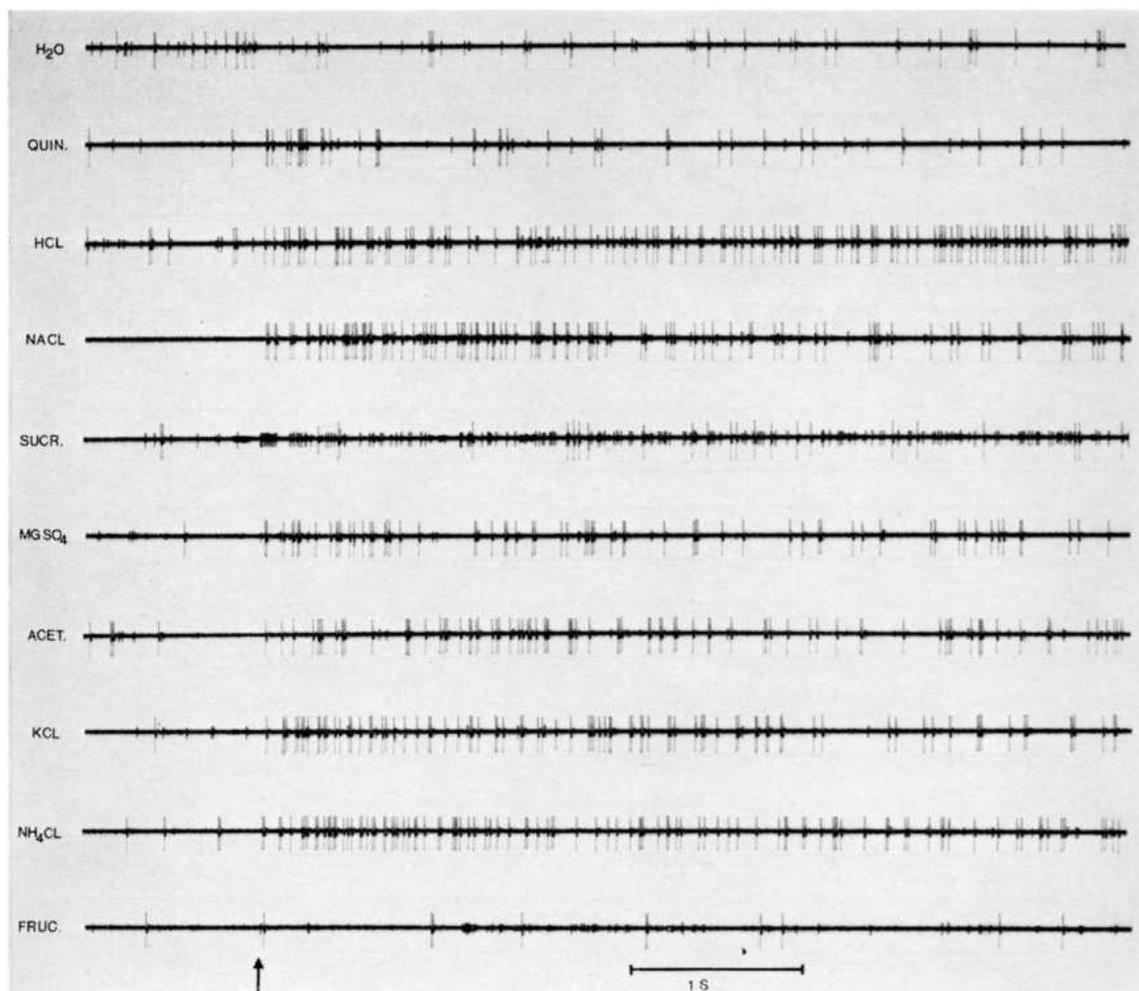


FIGURE 1. Photographs of oscillograph tracings of one hamster chorda tympani fiber's responses to water, 0.001 M quinine hydrochloride, 0.003 M HCl, 0.03 M NaCl, 0.1 M sucrose, 0.03 M MgSO₄, 0.003 M acetic acid, 0.1 M KCl, 0.03 M NH₄Cl, and 0.3 M fructose. The arrow indicates the beginning of the response. 6 s of record are shown in each tracing: 1 s before and 5 s of the response. Smaller impulses generated by other fibers can be seen in some of the tracings.

nerve summated response to a range of intensities of several compounds of each of the four taste quality classes. Stimulus compounds were chosen which stimulated the nerve and varied in taste, with some tasting more alike to man than others. Little is known about the taste of various compounds to hamsters; however, hamsters accept (or prefer) stimuli which are sweet (sucrose or sodium saccharin) to man and reject stimuli which are salty, sour, or bitter (sodium chloride, potassium chloride, citric acid, and quinine hydrochloride) to man (Carpenter, 1956; Harvey, 1970; and Faull and Halpern, 1971). Fig. 2 presents stimulus intensity-summated response functions (the means of responses of two preparations) for eight of the compounds. The response measure is the maximum deflection of the chart recorder pen (time constants: 0.6 s, rise; 2.6 s, fall) in response to a stimulus, the units are chart units, and the spontaneous response noise level is about ± 4 chart units. The encircled points

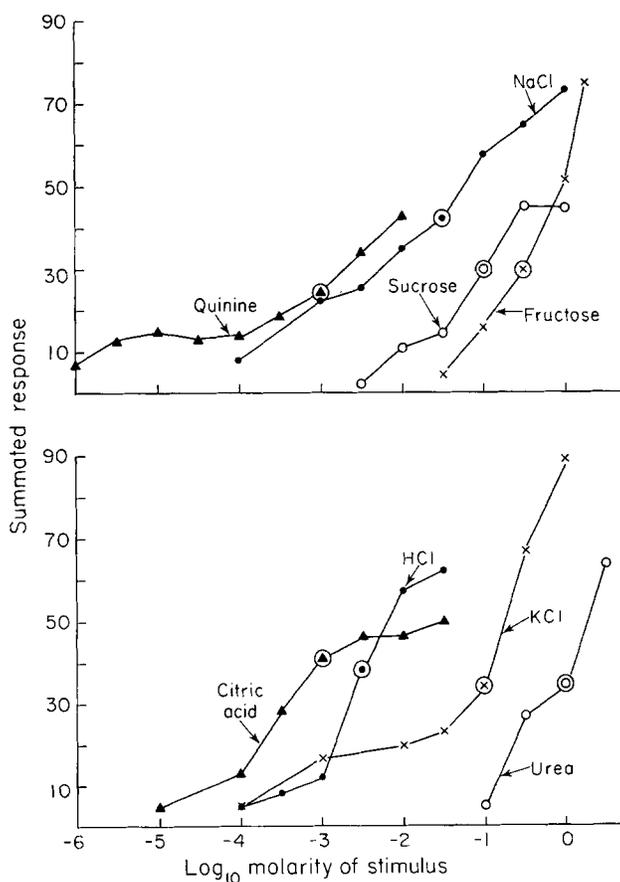


FIGURE 2. Stimulus intensity (\log_{10})—summated hamster chorda tympani nerve response functions for eight compounds: quinine hydrochloride, NaCl, sucrose, and fructose (upper set of axes), and citric acid, HCl, KCl, and urea (lower set of axes). The response measure was the maximum deflection of the chart recorder pen (time constants: 0.6 s, rise and 2.6 s, fall). The points for responses at intensities chosen as test stimuli are encircled for each compound.

are for responses at the intensities chosen to test a fiber's sensitivities. They were chosen because they evoked reasonably sized whole nerve responses and were in the middle of the range of concentrations limited by response threshold at the lower end and solubility or injury to the tongue at the upper end. It was reasoned that these test stimuli would give a less biased impression of the specificity of a hamster chorda tympani fiber's response than either weaker or stronger stimuli.

Table I presents the complete stimulation schedule which includes three stimulus groups. Solutions were made with reagent grade chemicals and distilled water (singly distilled in a Precision metal still, Precision Distillation Apparatus Co., Woodland Hills, Calif.). The Basic Taste stimuli are the most common representatives of the four classical taste qualities. The Other Taste stimuli, less commonly used in taste studies, include four salts, one sugar, sodium saccharin, two acids, and urea. The Concentration Series are for the Basic Tastes. Each of these stimuli is classified according to its predominant taste quality for man.

TABLE I
STIMULATION SCHEDULE

Taste quality	Basic tastes	Other tastes	Concentration series
Sweet	0.1 M sucrose	0.3 M fructose	0.003-1.0 M sucrose
Salty	0.03 M NaCl	0.001 M Na-saccharin	0.0001-1.0 M NaCl
		0.03 M NaNO ₃	
		0.03 M NH ₄ Cl	
Sour	0.003 M HCl	0.1 M KCl	0.0001-0.03 M HCl
		0.003 M acetic acid	
		0.001 M citric acid	
Bitter	0.001 M quinine-HCl	0.03 M MgSO ₄	0.000001-0.01 M quinine-HCl
		1.0 M urea	

The three stimulus groups were always presented in order, but the order of presentation of stimuli within a group was random. All of the stimuli in the first group were presented to 79 fibers, all the stimuli in the second group to 46 fibers, and the stimuli in the third to 5 fibers. The number of stimuli presented to a fiber and the number of times they were repeated depended upon the length of time the responses of that fiber were identifiable. This varied and averaged about 1 h.

RESULTS

The Distribution of Responses across Fibers: the Four Basic Tastes

Sensitivities to each of the four basic tastes (0.03 M sodium chloride, 0.1 M sucrose, 0.003 M hydrochloric acid, and 0.001 M quinine hydrochloride) do not occur in separate sets of hamster chorda tympani fibers, nor are they of a discrete number of sizes. Rather, the responses to each of these stimuli vary continuously in size (numbers of impulses elicited in 5 s) across fibers. The fibers were ordered four different times according to the size of the responses

to each stimulus and Fig. 3 presents these distributions of ordered response size.

There are differences in their sensitivity to the four tastes. The best stimulus is sodium chloride: it stimulates a greater number of fibers to a greater degree

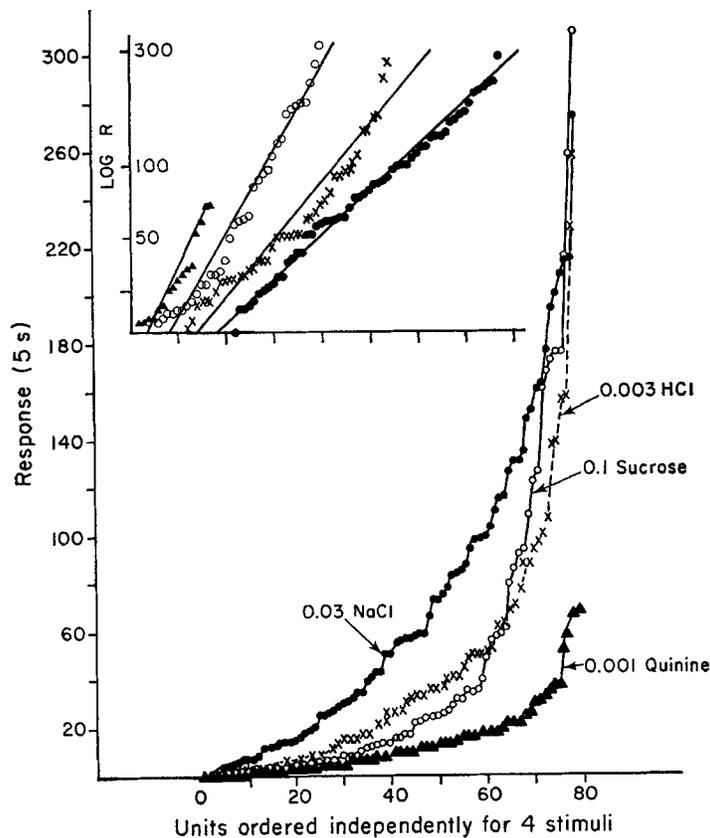


FIGURE 3. The distribution of responses of 79 hamster chorda tympani fibers to 0.3 M NaCl (●), 0.1 M sucrose (○), 0.003 M HCl (×), and 0.001 M quinine hydrochloride (▲) ordered four times according to the size of the responses to each of the stimuli. Response size (number of impulses in 5 s) is plotted on linear (main plot) and logarithmic (inset) scales. Fibers which responded at a level of less than 20 were excluded from the logarithmic plot, for which the least squares best fit straight line is drawn. The divisions on the abscissa are equal for both plots (10 fibers per division), but the logarithmic functions for sucrose, HCl, and NaCl are offset from the origin to allow for visibility.

than the other three basic tastes. For instance, it elicits at least 20 impulses during the 5 s stimulation period in 56 of the fibers, whereas, hydrochloric acid does in 43, and sucrose does in 35 fibers. Quinine is by far the poorest stimulus of the four: only 16 of the 79 fibers reach this level of response to quinine. Although fewer fibers respond to hydrochloric acid or sucrose than to sodium

chloride, some fibers respond as strongly to one of these two stimuli as those which respond most strongly to sodium chloride. For instance, 100 or more impulses are elicited in response to sodium chloride in 19 fibers, in response to sucrose in 11 fibers, and in response to hydrochloric acid in 8 fibers. But not one fiber responds this well to quinine.

Response magnitude increases approximately logarithmically across fibers which respond above an arbitrary "threshold." The inset in Fig. 3 is a plot of the logarithm of the responses for all fibers which respond with 20 impulses or more to each of the stimuli. The least squares best fit straight line is drawn for each set of ordered responses. The quinine function has the steepest slope and the sodium chloride function the shallowest. Quinine responses would increase 10 times in size across 24 quinine-sensitive fibers, sucrose responses across 29 sucrose-sensitive fibers, hydrochloric acid responses across 42 acid-sensitive fibers, and sodium chloride responses across 54 salt-sensitive fibers.² Thus, the salt and acid sensitivities occur at more finely graded levels in hamster chorda tympani fibers than the quinine or sucrose sensitivities. Although the sucrose sensitivity is not as finely graded, it covers about the same size range as the salt and acid sensitivities, whereas the quinine sensitivity does not.

Many taste fibers show a resting response before stimuli are applied to the tongue. However, this response is very small compared to the responses to at least one of the basic taste stimuli in most fibers. Fig. 4 shows the difference in magnitude of these "spontaneous" responses and responses to 0.03 M sodium chloride. The fibers have been ordered according to the size of the response to sodium chloride, and the spontaneous response of a fiber is given at the same point along the abscissa as its response to salt. The median spontaneous response is four impulses in 5 s, and it ranges from 0 to 26. It is 0 for 17 fibers and is greater than 20 for only 3 fibers. Because most responses to quinine are small, the spontaneous response is often a significant proportion of the quinine response: 63 fibers' responses to quinine are smaller than 20 impulses in 5 s. Also, spontaneous response size is statistically significantly correlated ($P < 0.01$, t test) across fibers with responses to quinine ($r_s = +0.60$), responses to hydrochloric acid ($r_s = +0.42$), responses to sodium chloride ($r_s = +0.39$), but not with responses to sucrose ($r_s = +0.08$).³ That is, there is some tend-

² The equations for the straight lines ($x =$ the ordered fiber number, $y =$ the response of that fiber), the average deviations of the observed responses from those lines (AD); and the probabilities (P) the observed and predicted points are from identical populations (calculated via the Wilk's Empty Cell Test [Bradley, 1968]) are:

- (a) for quinine: $x = 23.6 (\log y) - 27.6$, AD = 1.0, $P = 0.76$;
- (b) for sucrose: $x = 28.7 (\log y) - 33.8$, AD = 1.3, $P = 0.88$;
- (c) for HCl: $x = 41.6 (\log y) - 50.5$, AD = 2.6, $P = 0.59$; and
- (d) for NaCl: $x = 54.4 (\log y) - 73.4$, AD = 1.2, $P = 0.98$.

³ All reported correlations are Spearman rank-difference correlations: r_s , which are measures of how similarly different pairs of stimuli order the fibers' responses.

ency for fibers which respond better to quinine, or to a lesser extent to salt or acid, to have larger spontaneous responses; but the size of the response to sucrose is not at all related to the spontaneous response size.

Stimulus Intensity-Response Functions: the Four Basic Tastes

Although the main part of the data is a comparison of taste fiber responses to a variety of substances, each at one test concentration, some fibers were

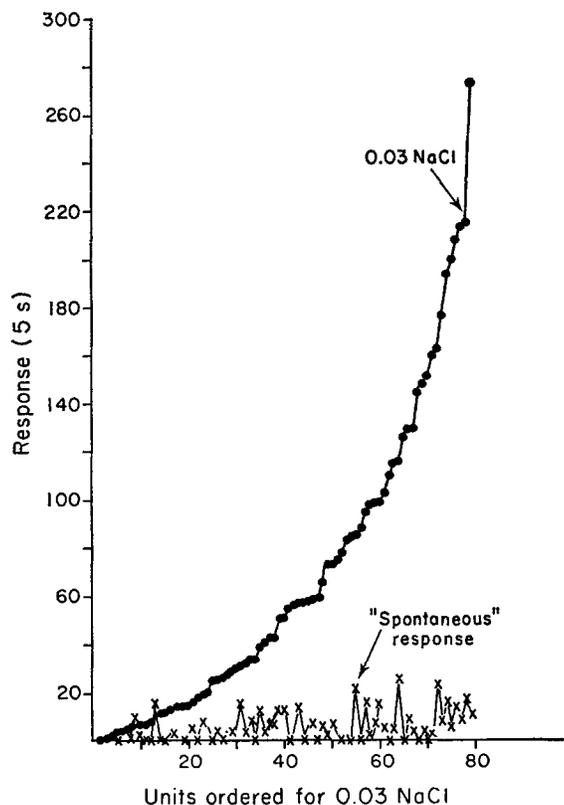


FIGURE 4. The distribution of the responses (number of impulses in 5 s) to 0.03 M NaCl of 79 hamster chorda tympani fibers, ordered according to their size; and the spontaneous responses of the fibers, not ordered but plotted at the same points along the abscissa as their responses to NaCl.

tested over a range of concentrations of the four basic tastes. Examination of stimulus-response functions for two fibers (Fig. 5) puts data taken across many fibers at only one concentration into perspective. Both fibers are insensitive to quinine. One fiber (A) is most sensitive to sodium chloride; both hydrochloric acid and sucrose elicit sizable responses which increase in size with concentration, but sodium chloride is certainly the best stimulus. The other fiber

(B), insensitive to hydrochloric acid, is highly sensitive to both sucrose and sodium chloride, however. The points for the responses at the test intensities used across all 79 fibers are encircled. The sucrose test stimulus (0.1 M) elicits a much greater response than the sodium chloride stimulus (0.03 M) in fiber B, but at higher stimulus intensities, the size of the salt response approaches the

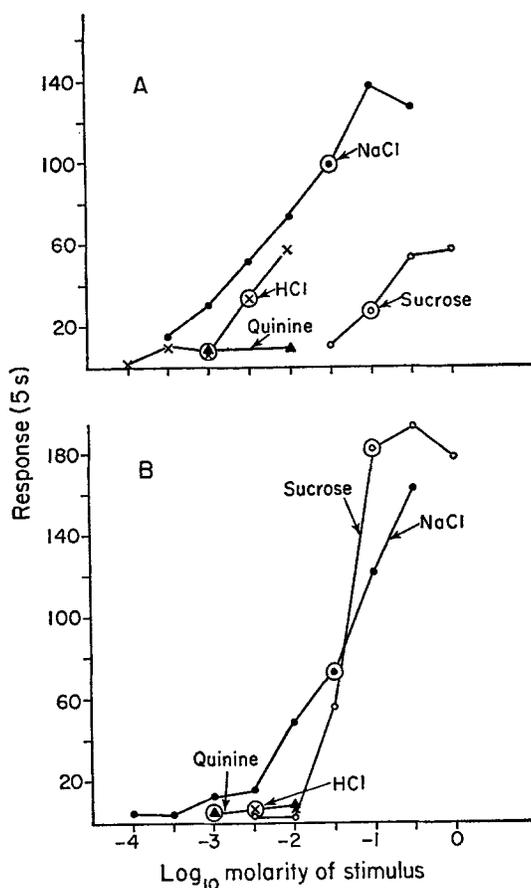


FIGURE 5. The response (number of impulses in 5 s) of two (A and B) hamster chorda tympani fibers as a function of the logarithm of the intensity of each of the four basic tastes: NaCl (●), sucrose (○), HCl (×), and quinine hydrochloride (▲). The points for responses to each of the test intensities are encircled.

size of the sugar response. Thus, for this fiber, although sucrose is the best stimulus, sodium chloride is nearly as effective.

The rate at which response size increases with increases in concentration varied for different fibers and different substances. For instance, the size of the sucrose response in fiber B increases at a greater rate than the sodium chloride response. However, fiber A response functions for sucrose, hydro-

chloric acid, and sodium chloride all have similar slopes. Therefore, when a fiber responds poorly to a test intensity, it may respond well at higher intensities of the same compound (Fig. 5 A); and a fiber which responds more to one compound (*a*), than to another (*b*) at test intensities, will not necessarily respond more to *a* than *b* at all proportional intensities (Fig. 5 B). The use of only one test intensity, then, puts some constraints on interpretation of the data.

Differential Response of Individual Fibers: the Four Basic Tastes

The extent to which individual fibers are differentially sensitive to three of the basic tastes at test concentrations is shown in Fig. 6. The 79 fibers have been ordered once: according to the size of the response to sodium chloride and their responses to sucrose (A) or hydrochloric acid (B) are placed at the appropriate points along the abscissa. A response to sucrose or hydrochloric acid may be either larger or smaller than a response to sodium chloride, de-

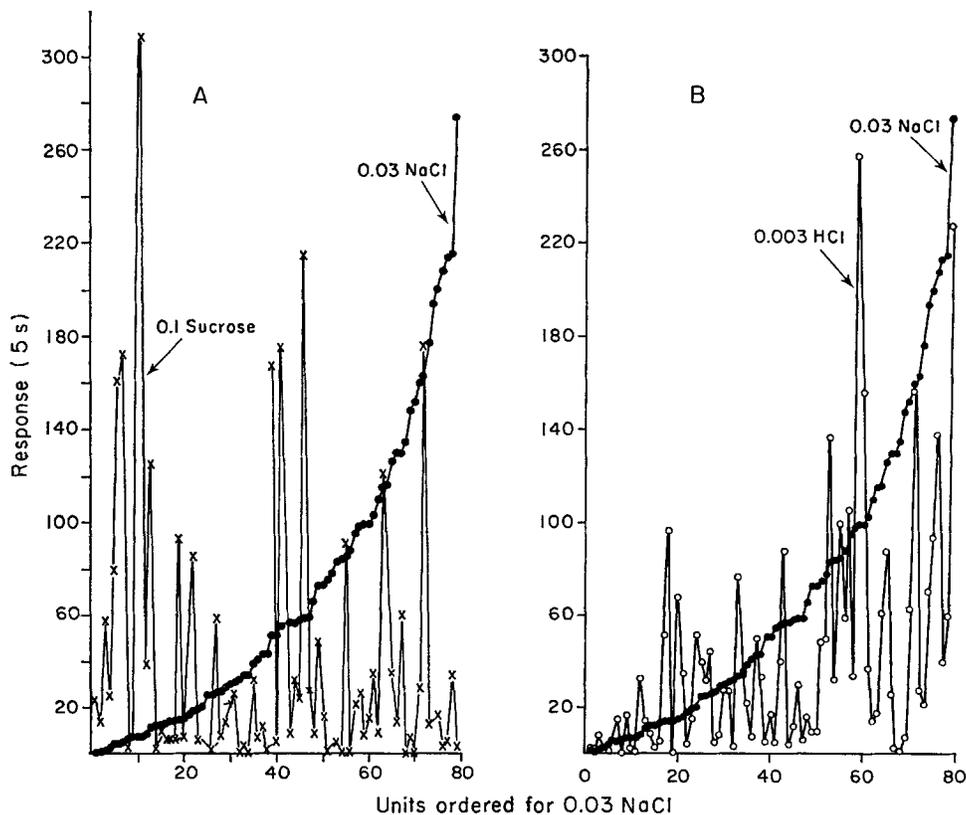


FIGURE 6. The distribution of responses (number of impulses in 5 s) of 79 hamster chorda tympani fibers to 0.03 M NaCl, ordered according to their size, and 0.1 M sucrose (A) and 0.003 M HCl (B), not ordered but plotted at the same points along the abscissa as their ordered NaCl responses.

pending upon the fiber considered. However, there are considerable differences in the distribution of sucrose and acid response size, given the ordering of fibers by sodium chloride response size. There are many more fibers which respond very strongly to sucrose in the lower half of the sodium chloride response ordered fibers, and more fibers which respond to acid in the upper half. This difference is reflected in the negative across-fiber correlation between sucrose and sodium chloride responses ($r_s = -0.12$) and the positive correlation between hydrochloric acid and sodium chloride responses ($r_s = +0.51$).

Rank-difference correlations between responses to the basic tastes across all 79 fibers are given in Table II. Responses to sucrose are negatively correlated with responses to each of the other three tastes, which are all positively correlated with each other. The three positive correlations are statistically significant ($P < 0.01$, t test). Fig. 7 presents the scatterplots. The negative correlations with sucrose reflect the occurrence of few fibers which respond strongly

TABLE II
RANK-DIFFERENCE CORRELATIONS BETWEEN RESPONSES TO
THE BASIC TASTES

	NaCl	HCl	Quinine
Sucrose	-0.12	-0.26	-0.11
NaCl	—	+0.51	+0.41
HCl	—	—	+0.58

$N = 79$, $r_s \geq \pm 0.30$, $P < 0.01$, t test.

to both sucrose and any one of the other three tastes. In all three sucrose scatterplots, few points occur above a diagonal line which might be drawn between the largest response to sucrose and the largest response to sodium chloride, hydrochloric acid, or quinine. There is a clustering of points along the axes. The positive correlations between responses to sodium chloride, hydrochloric acid, and quinine reflect the more frequent occurrence of larger responses to these three stimuli together in the same fibers, and the less frequent occurrence of fibers which respond strongly to one but not at all to the other two stimuli.

None of these correlations is very strong. The occurrence of a response of a certain size to one of the four stimuli only gives probabilistic information about the presence and size of a response to one of the other stimuli in the same fiber. For instance, the sensitivity to sucrose is not reciprocal to sensitivities to hydrochloric acid, sodium chloride, and quinine: responses to these three stimuli do not get proportionally smaller across fibers as sucrose responses get larger. The sucrose sensitivity does not occur in an exclusive set of fibers either: it is present in fibers with sensitivities to the other tastes. But it

does occur, frequently to its highest degree, in fibers with low sensitivities to hydrochloric acid, quinine, and sodium chloride. In this sense, the sucrose sensitivity is different and separate from sensitivities to the other basic tastes.

Specificities of Individual Fibers: the Four Basic Tastes

The degree to which the response of a hamster chorda tympani fiber is specific to one of the four basic tastes, at the test concentrations, varies considerably across fibers. Fig. 8 presents response profiles to the four tastes for 20 different

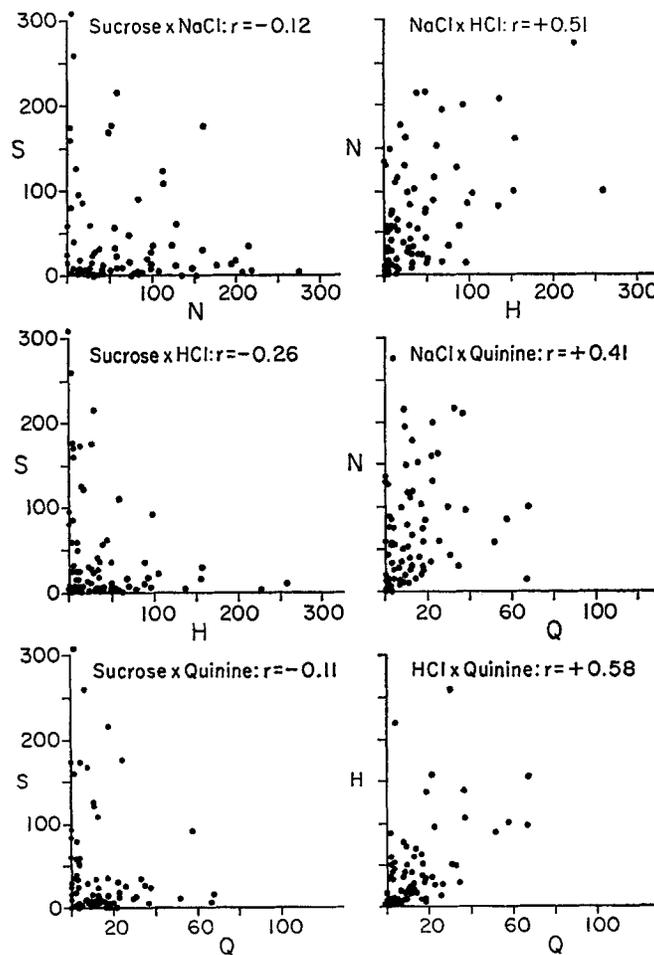


FIGURE 7. Scatterplots for responses (number of impulses in 5 s) of 79 hamster chorda tympani fibers to the basic taste stimuli: 0.1 M sucrose (S), 0.03 M NaCl (N), 0.003 M HCl (H), and 0.001 M quinine hydrochloride (Q). The six plots are for all possible pairings of the stimuli and the r 's are Spearman rank-difference correlation coefficients.

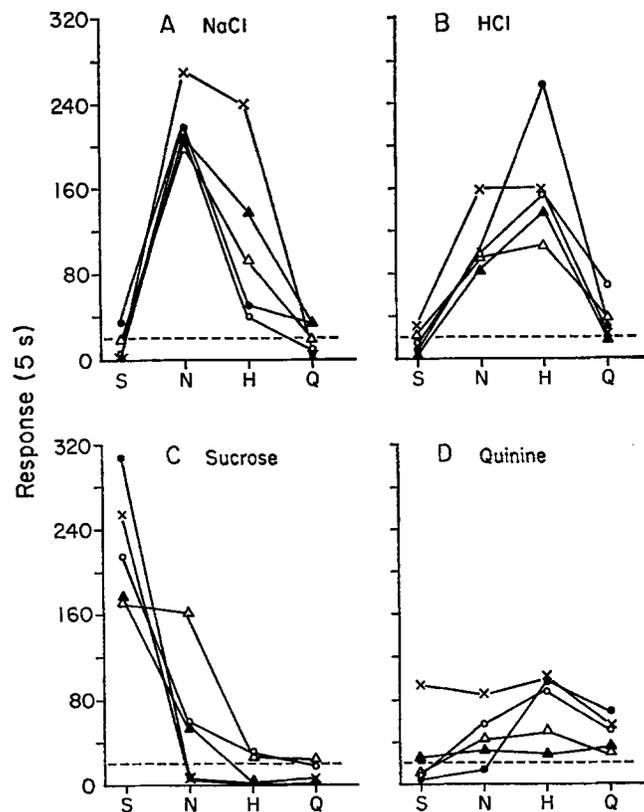


FIGURE 8. Response profiles across the basic tastes: 0.1 M sucrose (S), 0.03 M NaCl (N), 0.003 M HCl (H), and 0.001 M quinine hydrochloride (Q), of 20 hamster chorda tympani fibers. These profiles are for five fibers which respond most to NaCl (A), HCl (B), sucrose (C), or quinine (D). The response measure is the number of impulses in the first 5 s of the response. The dashed line at a response level of 20 represents an arbitrary threshold. The order of the stimuli along the abscissa, however, is not arbitrary (see text).

fibers. These include those which are most sensitive to sodium chloride (A), hydrochloric acid (B), sucrose (C), or quinine (D).⁴

None of the 10 fibers most sensitive to sodium chloride or hydrochloric acid is very sensitive to sucrose or quinine. Some of them are more sensitive to sodium chloride and some are more sensitive to hydrochloric acid, but the extent each fiber is specific to one of these two stimuli differs. For instance, the percentage the second-best response is of the best varies from 19 to 98. None of

⁴ In order that no response profile would be repeated, the five fibers which responded most to NaCl were chosen, then the five which responded most to HCl (except those included in the NaCl category), and then the five which responded most to quinine (not in the NaCl or HCl categories). There was no overlap of category for fibers which responded most to sucrose.

the fibers most sensitive to sucrose is very sensitive to hydrochloric acid or quinine, but some of them do respond well to sodium chloride: the percentage the salt response is of the sucrose response varies from 2 to 93. Not one fiber is very sensitive to quinine. In fact, the five largest responses to quinine occur in fibers which respond best to hydrochloric acid. There is only one fiber in the 79 which responds best to quinine and it responds at about the same low level to all four basic tastes (Fig. 8 D, filled triangles).

The most highly sensitive taste fibers, therefore, show patterns of sensitivity across taste quality. Their specificities vary from a strong sensitivity to one to strong sensitivities to two of the four basic tastes, and these two are always either hydrochloric acid and sodium chloride or sucrose and sodium chloride.

But the response profiles of only a minority of the taste fibers sampled (20/79), the most sensitive, have been described. Consideration of each fiber would be tedious, however, since each has a unique response profile as is seen in Fig. 8. A general description of the response profiles of all the fibers sampled is still possible. Of the 79 fibers, 42 responded best to sodium chloride, 20 best to sucrose, and 17 best to hydrochloric acid.⁵ If the second, third, and fourth largest responses are expressed as percentages of the largest response of each fiber, and these percentages averaged for all fibers in each group, mean response profiles for fibers which respond best to sodium chloride, sucrose, or hydrochloric acid are generated. These mean response profiles (Fig. 9 A) give each fiber equal weight whether it responds strongly or weakly to taste stimuli.

In the sucrose-best group of fibers, the average response to sodium chloride is $\frac{1}{4}$, to hydrochloric acid $\frac{1}{6}$, and to quinine $\frac{1}{25}$ of the size of the response to sucrose. This group of fibers is the most specific in that it has the smallest second, third, and fourth best responses. The fibers which respond best to sodium chloride are less specific. Their average hydrochloric acid response is $\frac{2}{5}$, sucrose response $\frac{1}{4}$, and quinine response $\frac{1}{5}$ the size of the response to sodium chloride. The hydrochloric acid-best fibers are the least specific: the average fractional relative responses being $\frac{1}{2}$ for sodium chloride, $\frac{1}{3}$ for quinine, and $\frac{1}{5}$ for sucrose. Thus, strikingly different mean relative response profiles are generated for the fibers which respond best to sucrose, sodium chloride, or hydrochloric acid.

In order to show the extent averaging may have obscured the nature of the relative specificity of individual fibers, the three groups of fibers have been further divided according to (a) which stimulus elicits the second-best response, and (b) the absolute size of the response to the best stimulus.

The sucrose-best fibers which respond second-best to sodium chloride have an average response to sodium chloride which is $\frac{1}{3}$, and a response to hydrochloric acid which is $\frac{1}{10}$ of the size of the sucrose response, whereas the other

⁵ One fiber responded best to quinine, and one fiber responded equally well to NaCl and sucrose and was placed in both categories; therefore, the total is 79.

sucrose-best fibers have averages of $\frac{1}{10}$ for sodium chloride and $\frac{1}{3}$ for hydrochloric acid (Fig. 9 B). However, it is a minority (7/20) of less sensitive sucrose-best fibers (Fig. 9 E) which respond relatively well to acid. All four divisions of sucrose-best fibers are insensitive to quinine and at least three times as sensitive to sucrose than either sodium chloride or hydrochloric acid.

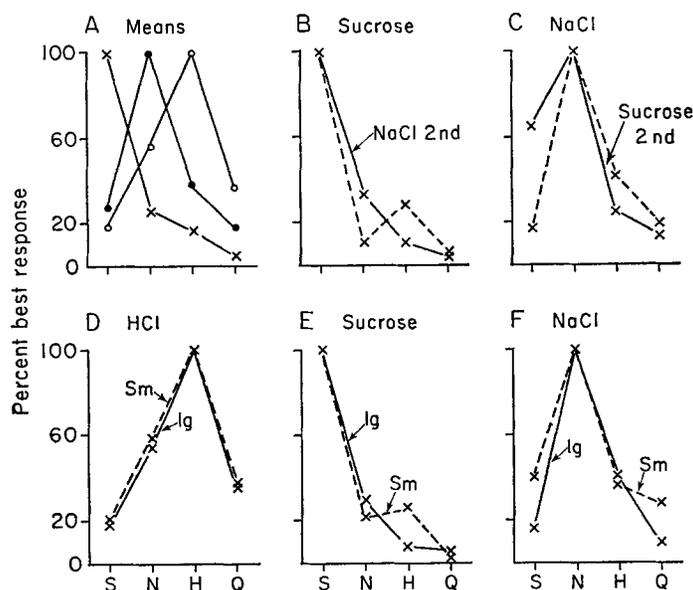


FIGURE 9. Mean relative response profiles of hamster chorda tympani fibers across the four basic tastes: 0.1 M sucrose (S), 0.03 M NaCl (N), 0.003 M HCl (H), and 0.001 M quinine hydrochloride (Q). The fibers were divided into three groups: those which responded best (largest number of impulses in 5 s) to sucrose ($n = 20$), NaCl ($n = 42$), or HCl ($n = 17$) of the four tastes. The responses of each fiber to the other three stimuli were expressed as percentages of the best response. The mean percentages for fibers which responded best to sucrose (\times), NaCl (\bullet), or HCl (\circ) are plotted in A. The sucrose-best fibers were divided (B) into those which responded second-best to NaCl (NaCl 2nd, $n = 13$) and those which did not (dashed line, $n = 7$). The NaCl-best fibers were divided into those which responded second-best to sucrose (sucrose 2nd, $n = 10$) and those which did not (dashed line, $n = 32$). Each of the three groups of fibers: HCl-best (D), sucrose-best (E), and NaCl-best (F) were divided into more and less sensitive halves, that is, into groups with the larger (lg) and smaller (Sm) best responses in the group. The order of the stimuli along the abscissa is not arbitrary (see text).

About $\frac{1}{4}$ (13/42) of the fibers which respond best to sodium chloride respond second-best to sucrose (Fig. 9 C). Their average response to sucrose is $\frac{2}{3}$ of the size of the sodium chloride response; the response to sucrose of the other sodium chloride-best fibers is only $\frac{1}{6}$. Most of the latter respond second-best to hydrochloric acid (25/29). Many sodium chloride-best fibers which respond second-best to sucrose or quinine are among the less sensitive (Fig.

9 F). However, some of the responses to sucrose are of considerable absolute magnitude, unlike any of the responses to quinine. Thus, fibers which respond best to sodium chloride can be divided in two: those which respond well to sucrose and those which do not.

Of the fibers which respond best to hydrochloric acid, most respond second-best to sodium chloride (15/17), third-best to quinine (13/17), and least to sucrose (14/17). Therefore, the hydrochloric acid-best fibers have not been divided on the basis of which stimulus elicits the second-best response. More and less sensitive fibers in this group also have very similar response profiles (Fig. 9 D). Fibers which respond best to acid are, then, the most homogeneous of all the groups of fibers.

These divisions of the best response groups of fibers show that the mean response profiles (Fig. 9 A) do not seriously distort the nature of individual fiber response profiles. But, although most sucrose-best and acid-best fibers are adequately described by their mean profiles, sodium chloride-best fibers may be better represented by two profiles: one showing a sensitivity to sucrose and the other a sensitivity to acid.

Both the response profiles of sensitive individual fibers (Fig. 8), and the average relative response profiles of best response fiber groups (Fig. 9) show the same patterns of differential response and allow the following general descriptions of hamster taste fiber sensitivities to the four basic tastes. First, fibers which respond best to sucrose are likely to respond second-best to sodium chloride, their responses to acid will be small and to quinine even smaller, and they will be relatively more specific than other fibers. Second, most fibers which respond best to sodium chloride will respond second-best to acid, a smaller group of them will respond much better to sucrose, but in either case, their responses to quinine will be small. Third, fibers which respond best to hydrochloric acid are likely to have a large second-best response to sodium chloride, and a larger response to quinine and smaller response to sucrose than other fibers. These are, of course, general descriptions which may not describe any particular fiber's response profile exactly.

Across-Fiber Correlations: Basic Tastes and Other Tastes

The probability is high that a hamster chorda tympani fiber will respond to all stimuli of the same quality or class. Responses to sodium chloride, hydrochloric acid, and sucrose are highly correlated with responses to stimuli which are of the same quality to man. Correlations between responses to the four basic tastes and all other stimuli, ordered from positive to negative and in size, are given in Table III. Sucrose responses correlate best with responses to fructose and saccharin; hydrochloric acid responses correlate best with responses to the other two acids; and sodium chloride responses correlate far better with responses to the other sodium salt than to any other stimulus.

Quinine responses, however, correlate best with responses to the organic acids, not the other bitter stimuli. Fig. 10 presents the scatterplots for responses to each basic stimulus and the stimulus most highly correlated with it. These correlations are stronger than correlations between responses to pairs of the basic taste stimuli which belong to different quality classes.

Sucrose responses are statistically significantly correlated ($P < 0.01$, t test) with responses to the other sweet stimuli only.⁶ Responses to the three bitter, four salt, and three acid stimuli are increasingly more negatively correlated with responses to sucrose. The sucrose-fructose and sucrose-citric acid interactions are the extremes (Fig. 10); most fibers which respond to sucrose respond proportionally to fructose, whereas most fibers which respond to su-

TABLE III
RANK-DIFFERENCE CORRELATIONS BETWEEN RESPONSES TO BASIC TASTES AND OTHER TASTES

Sucrose		NaCl		HCl		Quinine	
Fructose	+0.77	NaNO ₃	+0.94	Citric acid	+0.82	Acetic acid	+0.72
Saccharin	+0.61	KCl	+0.52	Acetic acid	+0.75	Citric acid	+0.66
Urea	+0.14	HCl	+0.51	KCl	+0.59	NH ₄ Cl	+0.66
MgSO ₄	-0.03	Citric acid	+0.48	NH ₄ Cl	+0.58	Urea	+0.61
Quinine	-0.11	Urea	+0.45	Quinine	+0.58	KCl	+0.58
NaCl	-0.12	Acetic acid	+0.43	MgSO ₄	+0.57	HCl	+0.58
KCl	-0.14	NH ₄ Cl	+0.43	NaCl	+0.51	MgSO ₄	+0.48
NaNO ₃	-0.19	Quinine	+0.41	NaNO ₃	+0.49	NaCl	+0.41
NH ₄ Cl	-0.21	MgSO ₄	+0.39	Urea	+0.47	NaNO ₃	+0.33
Acetic acid	-0.25	Saccharin	+0.12	Saccharin	-0.11	Fructose	+0.09
HCl	-0.26	Sucrose	-0.12	Fructose	-0.16	Saccharin	+0.06
Citric acid	-0.36	Fructose	-0.15	Sucrose	-0.26	Sucrose	-0.11

The N's for the Other Tastes vary between 46 and 49; $r_s \geq \pm 0.37$, $P < 0.01$, t test.

crose do not respond to citric acid and vice versa. Not only do sweet and acid responses correlate most negatively, the ordering of the stimuli by correlation size for sucrose, sweets > bitters > salts > acids, is nearly exactly opposite the ordering for hydrochloric acid: acids > salts = bitters > sweets.⁷ That is, the more alike the effects of sucrose and another stimulus, the less alike the effects of hydrochloric acid and that stimulus on the population of hamster chorda tympani fibers.

In contrast to sucrose, both sodium chloride and hydrochloric acid responses are statistically significantly correlated ($P < 0.01$, t test) with responses to all stimuli but the sweets, although the effects of sodium chloride and hydrochloric acid differ otherwise. Responses to the two sodium salts are the most

⁶ The terms *sweet*, *salty*, *sour*, and *bitter* are always meant only as labels for the particular compounds used in this study (see Table I) and refer to man's classification of the stimuli.

⁷ The correlation (r_s) between the two orderings is -0.90 , $P < 0.01$, t test.

highly correlated of all. However, correlations between responses to sodium chloride and potassium or ammonium chloride are not as high and are comparable in size to those for sodium chloride and acid or bitter responses. Many of the fibers respond well to both sodium salts, but few respond strongly to

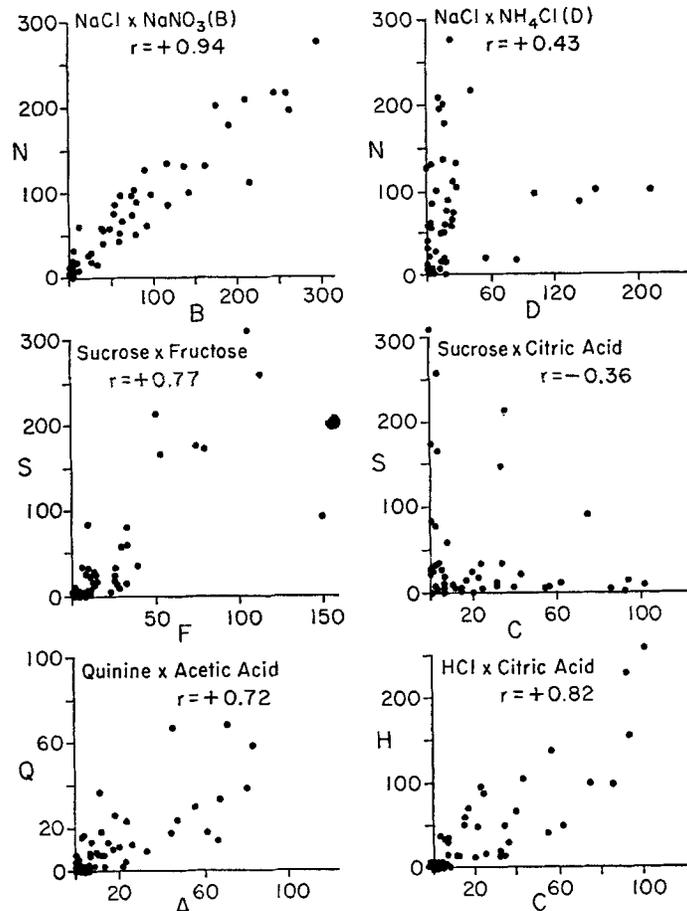


FIGURE 10. Scatterplots for responses (number of impulses in 5 s) of 46–49 hamster chorda tympani fibers to 0.03 M NaCl (N) and 0.03 M NaNO₃ (B) or 0.03 M NH₄Cl (D); to 0.1 M sucrose (S) and 0.3 M fructose (F) or 0.001 M citric acid (C); to 0.001 M quinine hydrochloride (Q) and 0.003 M acetic acid (A); and to 0.003 M HCl (H) and 0.001 M citric acid (C). The r 's are Spearman rank-difference correlation coefficients.

either ammonium or potassium chloride. In fact, fibers which respond to sodium chloride respond proportionally to sodium nitrate; but many fibers which respond to sodium chloride do not respond to ammonium or potassium chloride at all, and the fibers which respond most to ammonium and potassium chlorides respond only moderately to sodium chloride (Fig. 10). On the other hand, potassium and ammonium chloride responses are highly correlated across hamster chorda tympani fibers ($r_s = +0.77$).

Responses to hydrochloric acid are most highly correlated with responses to the other acids, and the effects of hydrochloric acid are less like the effects of the sodium salts than any of the other nonsweet stimuli. The order of correlation coefficient size is sodium salts > other salts (i.e. potassium and ammonium chlorides) > acids > bitters for sodium chloride, and acids > other salts > bitters > sodium salts for hydrochloric acid. Also, the correlations between responses to hydrochloric acid and all the nonsodium salts, bitters, and acids are higher than the correlations between responses to sodium chloride and the same stimuli. Correlations with the sweets, although negative for both hydrochloric acid and sodium chloride, are more strongly negative for the acid. Thus, the effects of hydrochloric acid on hamster chorda tympani fibers are more highly positively correlated with nonsweets and negatively correlated with sweets than the effects of sodium chloride.

The effects of quinine and hydrochloric acid, the most highly correlated of the basic tastes, are more alike. Quinine responses correlate best with organic acid and least with sodium salt responses of all the nonsweet stimuli. The quinine-organic acid correlations are some of the strongest observed, but do not indicate as close an approximation to proportionality of responses as correlations between stimuli of the same quality (Fig. 10). The ordering of the stimuli by correlation size for quinine, acids > other salts > bitters > sodium salts > sweets, is nearly the same as the ordering by hydrochloric acid.⁸ But, with the exception of urea and ammonium chloride, the responses to all stimuli are more highly correlated, either positively or negatively, with hydrochloric acid.

Therefore, the difference in distributions of sensitivities to the basic taste stimuli among hamster chorda tympani fibers has been generalized to other taste stimuli. Sucrose responses are not the only ones correlated negatively with responses to hydrochloric acid, sodium chloride, and quinine. Responses to other stimuli which taste sweet to man, and only other sweet stimuli, share this peculiarity with sucrose. The correlations between the effects of sweet and all nonsweet stimuli, the only negative or near-zero correlations observed, range from -0.36 to $+0.14$. It is also not just a characteristic of hydrochloric acid, sodium chloride, and quinine, but sensitivities to other stimuli which taste sour, salty, and bitter to man are distributed similarly among hamster chorda tympani fibers and differently from sweet sensitivities. The correlations between responses to all salty, sour, and bitter stimuli are never negative, ranging from $+0.94$ to $+0.33$, depending upon whether their qualities are more or less alike to man.

DISCUSSION

Many single hamster chorda tympani taste fibers do respond to stimuli which are of very different taste quality to man, as do the taste fibers of several other

⁸ The correlation (r_s) between the two orderings is $+0.86$, $P < 0.01$, t test.

mammals. This statement, however, must be tempered with consideration of exactly what is meant by "respond," "stimuli," and "different quality." Taste fibers vary in a number of ways. Some show substantial levels of spontaneous activity and others do not. Their absolute sensitivity to taste stimuli varies greatly. Some fibers do not respond very strongly to any taste quality, some respond well to several, and some respond much better to one than to any other quality. To say a fiber "responds" can mean there is less than a 2-fold or more than a 100-fold increase in an ongoing rate of response of less than 1 or more than 10 impulses per second.

Nearly every compound which has a taste, has a taste of a "different quality." For instance, all sweet compounds are supposedly distinct to man (Andersen, 1970). But some taste more alike than others; traditionally, sodium chloride, hydrochloric acid, quinine, and sucrose have been used to test for sensitivities to four classical taste quality categories: salty, sour, bitter, and sweet. But it is certainly possible that one of these compounds resembles another in quality more than the others (Morrison, 1967; Schiffman and Erickson, 1971). It is even possible one quality resembles some other quality more than others: for instance, sour may be more like bitter than sweet. Finally, the effectiveness of "stimuli" varies, both in the number of fibers they stimulate and the sizes of the responses they evoke, with changes in their intensity as well as their quality (Ogawa, Sato, and Yamashita, 1969; Ganchrow and Erickson, 1970). If the chosen test stimuli are all strong, or if some are strong and others weak, or if all are weak, different conceptions of how specific fibers are to a taste quality will result (see Fig. 5).

Is the Distribution of Sensitivities to the Four Taste Qualities Random?

In order to easily test the possibility that the presence or absence of sensitivities to stimuli of the four human taste qualities is generated by a random process, several assumptions have been made. They are: (a) there are four taste qualities equally different from each other; (b) these four qualities are represented in their purest form by sodium chloride, hydrochloric acid, quinine hydrochloride, and sucrose at moderate intensities; and (c) responses which reach a criterion, although they may differ greatly in size, are indistinguishable in import. These all-or-none sensitivities may be randomly associated in fibers in two taste nerves of the rat (Frank and Pfaffmann, 1968). That is, if the rat taste fiber responds to one quality, the probability of it responding to any of the other three qualities is the same as it would have been if it had not responded to that quality.

What about the fibers in the hamster chorda tympani nerve which differs from the rat chorda tympani nerve mainly in its more acute sensitivity to sweet compounds? With an arbitrary response criterion of 3 times the spon-

taneous response rate of the individual fiber,⁹ the proportion of fibers which "respond" to each of the basic tastes has been determined. If the four sensitivities are independently distributed among fibers, and these proportions are reasonable estimates of the probabilities that any fiber sampled would respond to the stimuli, the numbers of fibers which should respond to zero, one, two, three, or four of the tastes can be calculated from the multiplication and addition laws of probability for $P_{(i)} = 0.72$ (sodium chloride), 0.43 (hydrochloric acid), 0.39 (sucrose), and 0.18 (quinine).

Most hamster chorda tympani fibers respond to one, two, or three of the tastes, as do rat taste nerve fibers. There is little difference between the calculated number of fibers which should respond if the theory holds and the number of fibers which actually do respond to any number of tastes (Table IV A). However, unlike rat nerve fibers, there are consistent differences between the predicted and observed numbers of hamster fibers responding to the six possible stimulus pairs (Table IV B). Probabilities that pairs of independently distributed sensitivities would occur are given by the products of the probabilities for individual sensitivities. No one of the observed-predicted differences is very large, but there are too few fibers responding to both sucrose and any of the other three tastes, and too many fibers responding to pairs of the other three tastes. Some of these differences would rarely occur by chance if the stimuli did have independent effects (probabilities in Table IV B, determined by the Fisher exact method¹⁰).

The number of times each particular response profile occurs, and would occur if the stochastic-independence hypothesis holds, are given in Table V. Each theoretical probability for a response profile is the product of four probabilities: those appropriate for the occurrence (S, N, H, Q) or nonoccurrence ($\bar{\cdot}$, $Q_{(i)} = 1 - P_{(i)}$) of responses. The sucrose sensitivity occurs alone too often (predicted, 3.7; observed, 9) and is too few times combined with other sensitivities (predicted, 27.1; observed, 21). Sensitivities to sodium chloride, hydrochloric acid, and quinine (and not sucrose) are grouped together too often (predicted, 21.2; observed, 27), and occur alone too few times (predicted,

⁹ Since the spontaneous rate was very small for many fibers (47 had rates of less than one impulse per second) a lower cutoff for what would be called a response was established: 15 impulses in the 5 s stimulation period. A higher criterion was chosen than the one used for the rat nerve analysis to minimize the taking of small variations in a highly variable ongoing rate as responses. If the lower criterion (1.5 times the ongoing rate) is used, there are no major differences in the result.

¹⁰ These probabilities are given by the hypergeometric probability distribution (Bradley, 1968), for which extensive tables are available (Lieberman and Owen, 1961). Ogawa, Sato, and Yamashita (1968) also used this statistical method with 28 hamster chorda tympani fiber responses to 0.1 M NaCl, 0.5 M sucrose, 0.01 M HCl, and 0.02 M quinine and found two statistically significant ($P < 0.05$) differences between theory and observation: the NaCl-quinine pair occurred too frequently, and the NaCl-sucrose pair too infrequently.

21.4; observed, 14). In fact, the largest divergences of theory from observation are in the number of fibers which respond to sucrose alone and the number which respond to the other three stimuli, but not sucrose. There are too many in both classes. The observations of Ogawa, Sato, and Yamashita (1968) on 28 hamster chorda tympani fibers are the same: these two profiles occur too

TABLE IV
DISTRIBUTION OF SENSITIVITIES TO THE FOUR BASIC TASTES

A. Numbers of sensitivities			
Number of responses	Number of fibers		Predicted*
	Observed		
0	8		5.7
1	23		25.1
2	28		31.9
3	19		14.5
4	1		1.9

B. Pairs of sensitivities			
Response combination	Numbers of fibers		Probability it is chance difference‡
	Observed	Predicted	
Sucrose, NaCl	19	22.2	0.005
Sucrose, HCl	12	14.8	0.053
Sucrose, quinine	1	5.5	0.005
NaCl, HCl	34	27.3	0.231
NaCl, quinine	13	10.2	0.272
HCl, quinine	12	6.8	0.014

* The proportions of the fibers which responded to quinine, sucrose, HCl, and NaCl were 0.18, 0.39, 0.48, and 0.72, respectively, and there were 79 fibers.

‡ The 71 fibers which responded to at least one of the four stimuli were divided twice, depending upon whether they did or did not respond to each of the two stimuli in the combination. The probabilities were determined with Fisher's exact method; each is the sum of the probabilities for all outcomes as or more extreme in either direction.

frequently, and their numbers are also the greatest deviations from those predicted by stochastic-independence.

Actually, the difference between the distribution of these all-or-none sensitivities to the four taste qualities among hamster chorda tympani fibers, and what would be expected if it were random, is not very extreme. Most profiles occur, those which do not are not very probable, and those which occur most frequently are most probable according to the theory. The divergence from the theory is based on a relative isolation of sensitivities to the sweet quality, and association of sensitivities to the salty, sour, and bitter qualities which

would not be expected if sensitivities to four equally different qualities were independently distributed among the fibers.

Fiber Types, Fiber Specificities, and Stimulus Dimensions

If frequent combinations of all-or-none sensitivities were considered fiber types, the hamster chorda tympani would have six: a sensitivity to sucrose alone (S), or sucrose combined with sodium chloride (SN), or with both sodium chloride and hydrochloric acid (SNH), and a sensitivity to sodium

TABLE V
DISTRIBUTION OF RESPONSE PROFILES TO THE FOUR BASIC TASTES

Response profile	Number of fibers		Difference
	Observed	Predicted	
---	8	5.7	+2.3
S---	9	3.7	+5.3
-N--	12	14.8	-2.8
--H-	2	5.3	-3.3
---Q	0	1.3	-1.3
SN--	9	9.5	-0.5
S-H-	2	3.4	-1.4
S--Q	0	0.8	-0.8
-NH-	14	13.7	+0.3
-N-Q	2	3.3	-1.3
--HQ	1	1.2	-0.2
SNH-	9	8.7	+0.3
SN-Q	0	2.1	-2.1
S-HQ	0	0.7	-0.7
-NHQ	10	3.0	+7.0
SNHQ	1	1.9	-0.9

Response profiles: responses to sucrose, NaCl, HCl, or quinine are indicated by S, N, H, and Q, respectively; no response is indicated by -. The differences are plus (+) if the observed number of fibers exceeds the predicted number.

chloride alone (N), or combined with hydrochloric acid (NH), or with both hydrochloric acid and quinine (NHQ).¹¹ Each of these occur in more than 10% of the fibers sampled, whereas none of the other nine possible combinations occur in more than 3% (Table V). But the sizes of the responses to the two or three stimuli can vary tremendously (see Figs. 8 and 9) and other types do occur, although more rarely. The size of responses to the four tastes varies

¹¹ Ogawa, Sato, and Yamashita (1968) describe five types among 28 hamster chorda tympani fibers: S, SNH, SH, NHQ, and SNHQ. These are not strictly comparable, however, since they used a different response criterion: the mean plus one standard deviation of the spontaneous response, and the stimuli were all of greater intensity. See footnote 9.

continuously across fibers (Fig. 3) and their division into those which "respond" or do not is arbitrary. The absolute sensitivity to taste stimuli, judged by the size of the "best" response, varies more than 10-fold across the fibers sampled; the relative sensitivity to the best stimulus of the four might be more than 100 times as large as the second-best, or they might be nearly equal. These differences in the sizes of responses cannot be ignored. It may be necessary, rather than pointing to the six common fiber types, to note there is a multitude of types. But there is an order in the diversity.

When the four basic tastes are ordered along the abscissa as they are in Figs. 8 and 9 (sucrose—sodium chloride—hydrochloric acid—quinine) most fibers have response profiles with one peak. Only three fibers do not, if reasonable allowance is made for expected variation in response size with repeated stimulations.¹² One-peak response profiles result with this ordering of the basic tastes because of the common patterns of differential response described in the analyses of individual fiber and average relative response profiles. In fact, if all of the response profiles across the four tastes for mammalian taste fibers published are plotted in this way, although stimulus intensities and response measures vary widely, most of them also have one peak (Bartoshuk, 1965; Fishman, 1957; Frank, 1968; Marshall, 1968; Nagaki, Yamashita, and Sato, 1964; Ogawa, Sato, and Yamashita, 1968; Pfaffmann, 1955). Thus, with this particular ordering of the basic tastes along the abscissa, profiles show considerable regularity. This corresponds to man's hedonic ordering of the stimuli from good-tasting to bad-tasting or most acceptable to least acceptable (Pfaffmann, 1960).

This good-bad taste dimension may also help explain differences in the relative tuning of the average response profiles (Fig. 9 A). Fibers which peak at sucrose may appear more, and at hydrochloric acid less, specific because sucrose is located far from the other three tastes along the dimension, while hydrochloric acid is closely surrounded on both sides. That is, differences in the measured tuning of "neural responses functions"¹³ may indicate that the four taste qualities are not equally different from one another: sweet being less like salty, sour, or bitter than salty is like sour or bitter, or sour is like bitter in quality.

¹² Ogawa, Sato, and Yamashita (1969) report standard deviations for 5-s responses with five to six applications of the same six stimuli for two rat chorda tympani fibers. The percentages the standard deviations are of the mean responses are larger for smaller responses. These percentages for mean responses of 0-5, 6-30, and greater than 30 impulses are 45-182% (mean 95%), 15-65% (mean 35%), and 15-35% (mean 21%), respectively. Allowing for 100% variation in responses less than 6, 40% in responses from 6-30, and 20% in responses greater than 30 impulses, only three fibers have response profiles with more than one peak.

¹³ Erickson, Doetsch, and Marshall (1965) define "neural response function" as a "measure of neural activity as a function of a stimulus dimension." Since a stimulus dimension has been defined, the response profiles are also "neural response functions."

Differences in the tuning of individual fibers, in both the relative size of the second-best response and the absolute size of the response to the best stimulus, may also be considered in this vein. If there are truly only three peaks along a single dimension, the average response functions would have to be means of individual functions which vary in width and height. However, they could also be means of response functions which vary in the point along the axis at which they peak. For instance, there may be a response function which peaks between sucrose and sodium chloride, another between sodium chloride and hydrochloric acid, etc.¹⁴ This would imply that other stimuli, located at these intermediate points along the axis, would elicit greater responses than the basic four in some fibers. Yet, of the 49 fibers which were tested with 7–11 stimuli besides the basic four, 27 responded best to one of the two sodium salts (the responses to these two stimuli were usually of nearly equal size), 11 responded best to sucrose, and 9 responded best to either hydrochloric acid or ammonium chloride (in these fibers the responses to these two stimuli were usually nearly equal). Therefore, if the other stimuli were truly of comparable intensity, and a fair sample of the compounds which taste, it is not necessary to postulate many other points along this dimension at which neural response functions peak, if there is wide variation in the tuning of the functions.

Another notable aspect of the hamster chorda tympani fiber data: the negative correlations between sweet and nonsweet stimuli but positive correlations between nonsweet stimuli may also be explained.¹⁵ For example, taking the three mean response functions (Fig. 9 A) as functions for prototypic fibers, note that those fibers whose responses peak at sucrose respond worst to acid, those which peak at salt respond less to sucrose and more to acid, and those which peak at acid respond worst to sucrose. Therefore, if the responses to sucrose and acid are plotted against each other, the scatterplot generated looks like one generated by the real fibers' responses, and the calculated correlation coefficient is negative. The scatterplot for sodium chloride-hydrochloric acid generated by these prototypic fibers, on the other hand, would show a positive correlation. Stronger positive correlations would result for stimuli located closer to each other along the axis, and zero correlations for stimuli which are at intermediate distances from each other. Exact correlations generated by neural response functions would be dependent upon their shapes and how they are positioned along the dimension, as well as interstimulus distances.

Therefore, a simple ordering of taste stimuli along a dimension of human

¹⁴ Erickson, Doetsch, and Marshall (1965) have developed an ingenious multidimensional scheme based on rat chorda tympani fiber responses in which they limit the hypothetical response functions to one shape and postulate that there are many points at which these functions peak.

¹⁵ Ogawa, Sato, and Yamashita (1968, 1969) also obtained negative correlations between responses to both sucrose and saccharin and nonsweet stimuli for both hamster and rat chorda tympani fibers.

acceptance shows there is a tremendous amount of order in the highly varied response profiles of hamster chorda tympani fibers. Although there is a uniqueness to each fiber's response profile, graded sensitivities (when differences in the size of the sensitivities are considered) are not distributed randomly among fibers.

Discrimination of Taste Quality by Hamster Chorda Tympani Fibers

Different sets of fibers are strongly stimulated when the tongue is bathed with sucrose, sodium chloride, or hydrochloric acid at moderate intensities (see Fig. 9 A). This is not true for quinine which stimulates nearly the same set of fibers as the acid to a lesser extent, but a sensitivity to compounds which are bitter to man is not well represented at the front of the hamster tongue. Many of the fibers are stimulated to some degree by two or three of the stimuli to be sure, but the across-fiber patterns of response evoked in the nerve by sucrose, sodium chloride, or hydrochloric acid are very different and clearly a possible basis for their discrimination. The set of fibers activated by stimuli which are of the same quality to man, in contrast, are nearly identical and the evoked patterns of response nearly the same. They are not exactly the same, but neither are the tastes of the stimuli. In all, the responses of hamster chorda tympani fibers to sweet, salty, or sour stimuli and human judgments of their quality are highly consistent.

If the basic taste stimuli are considered quality prototypes, and correlations with responses to them and any stimulus across fibers measures of the extent that stimulus is of those qualities, correlation taste profiles for each stimulus can be generated (Fig. 11). Taste profiles for each of the basic tastes are very different. However, profiles for the three sweets are very much alike, as are those for the two sodium salts, ammonium and potassium chlorides, or the three acids. Fructose is the best match for sucrose in quality and saccharin is the second-best: fructose is more "sweet" than saccharin, which is more "salty" than fructose or sucrose. Sodium saccharin stimulates fibers which are not sensitive to sucrose but are very sensitive to sodium chloride, an effect of the sodium ion (Ogawa, Sato, and Yamashita, 1969). All three stimuli which are sweet to man have taste profiles which are very different from profiles for nonsweet stimuli.

Sodium nitrate mimics sodium chloride in effect, responses to the two sodium salts being highly correlated and having similar "sweet," "sour," and "bitter" parts. Ammonium and potassium chlorides are quite different from these, their "salty" components being smaller and their "sour" and "bitter" components larger than the sodium salts' profiles. Magnesium sulfate, a bitter-salty stimulus to man, actually falls closer to the other nonsodium salts in its taste profile than to the other bitter stimuli. Also, the correlation between responses to magnesium sulfate and quinine (+0.48) is much lower

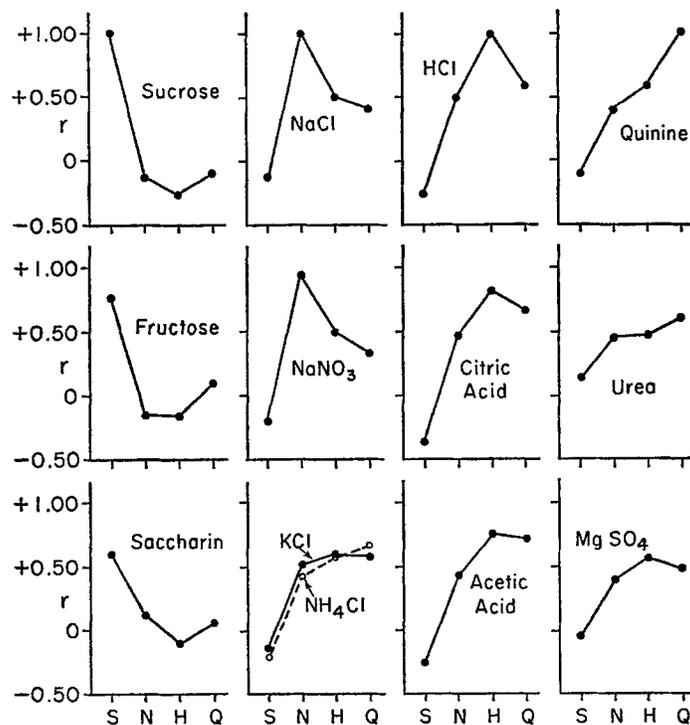


FIGURE 11. Correlation taste profiles across the four basic tastes: 0.1 M sucrose (S), 0.03 M NaCl (N), 0.003 M HCl (H), and 0.001 M quinine hydrochloride (Q) for the responses (number of impulses in 5 s) of 46–79 hamster chorda tympani fibers to these four stimuli and 0.3 M fructose, 0.001 M Na-saccharin, 0.03 M NaNO₃, 0.03 M NH₄Cl, 0.1 M KCl, 0.003 M acetic acid, 0.001 M citric acid, 1.0 M urea, and 0.03 M MgSO₄. The *r*'s plotted are Spearman rank-difference correlation coefficients. The correlation coefficients for sucrose and “sucrose” and each other basic taste and itself were assumed to be +1.00.

than their correlation with potassium and ammonium chloride responses (+0.80 and +0.74, respectively). This same distinction between sodium and nonsodium salts is made by rat chorda tympani fibers (Erickson, 1963; Ganchrow and Erickson, 1970) and in the cross adaptations of the transient phase of the summated whole rat chorda tympani nerve response (Smith and Frank, 1972).

The three acids are highly positively correlated in their effects and have similar taste profiles: they are not at all “sweet,” and are closer to being “bitter” than the salts or sweets are. Since there are no fibers with peak responses to quinine, the meaning of correlations with quinine is not clear. Urea and quinine responses are the most highly correlated of responses to stimuli which are bitter to man; but responses to quinine, the prototypic bitter, are

highly correlated with responses to acids. The response to quinine hydrochloride is not an acid response: 0.001 M quinine hydrochloride is slightly alkaline.

The bitter taste quality has certainly not been adequately studied. The response of the hamster chorda tympani to bitter is poor, and there are probably very few receptors which are most sensitive to the bitter quality on the front of the hamster tongue. Knowledge of the discriminative response of mammalian taste nerves to compounds categorized as bitter by man awaits work on the glossopharyngeal nerve or on the chorda tympani of a mammal with a greater bitter sensitivity at the front of the tongue.

It is reassuring to find that the frequently used stimuli: sucrose, sodium chloride, hydrochloric acid, and quinine are good choices as prototypes for the four taste qualities. Other stimuli said to be of the same qualities have highly similar effects on nerve fibers and none of them are more effective than the prototypes. That these other stimuli are not as effective, or more effective, for particular fibers, however, is not proven. Stimulus intensity was not varied, although the summated whole nerve response was consulted in the choice of comparable moderate intensities.

The problem of stimulus intensity variation needs study: a good number of stimulus intensity-taste fiber response functions for a variety of stimuli would allow for a more complete description of the discriminative abilities of peripheral taste nerves. However, a case can be made for using moderate intensity stimuli within the range a mammal might taste in life in the study of discrimination.

It is also reassuring to find that most taste fibers studied so far do not show drastic reductions in response size as stimulus intensities are increased, even to high values (Ganchrow and Erickson, 1970; Miller, 1971; Ogawa, Sato, and Yamashita, 1968, 1969; Pfaffmann, 1955; Wang and Bernard, 1969), although a number of small reductions at higher intensities have been reported (see Fig. 5).¹⁶ If they did, it would put severe limitations on interpretations of data taken across fibers at any one, though moderate, stimulus intensity.

Finally, the use of the 5 s response as the measure of taste sensitivities may not capture the more subtle discriminative powers of the nerve. It is a rather gross measure since mammals can discriminate taste stimuli after only a fraction of a second of stimulation (Halpern and Tapper, 1971). It is certainly possible that different parts of the response over time contain different kinds of information about the stimulus and this also awaits further study (Fishman, 1957; Marshall, 1968; Doetsch and Erickson, 1970; Smith and Frank, 1972; Faull and Halpern, 1972). However, in all, even with a simple and relatively

¹⁶ There is one notable exception: the response of sucrose sensitive fibers to sodium saccharin. The sodium saccharin concentration-response function of hamster and rat sucrose sensitive fibers is bell-shaped: it increases to a maximum at 0.03 M and decreases drastically thereafter, as concentration is increased (Ogawa, Sato, and Yamashita, 1969).

long response measure and only one moderate intensity of each compound, these data leave the impression that mammalian taste fibers, highly varied though they are in their sensitivities, are consistent in their response to quality and clearly discriminate between stimuli of positive and negative taste quality.

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