The Organization of Taste Sensibilities in Hamster Chorda Tympani Nerve Fibers

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ABSTRACT Electrophysiological measurements of nerve impulse frequencies were used to explore the organization of taste sensibilities in single fibers of the hamster chorda tympani nerve. Moderately intense taste solutions that are either very similar or easily discriminated were applied to the anterior lingual surface. 40 response profiles or 13 stimulus activation patterns were considered variables and examined with multivariate statistical techniques. Three kinds of response profiles were seen in fibers that varied in their overall sensitivity to taste solutions. One profile (*S*) showed selectivity for sweeteners, a second (*N*) showed selectivity for sodium salts, and a third (*H*) showed sensitivity to salts, acids, and other compounds. Hierarchical cluster analysis indicated that profiles fell into discrete classes. Responses to many pairs of effective stimuli were covariant across profiles within a class, but some acidic stimuli had more idiosyncratic effects. Factor analysis of profiles identified two common factors, accounting for 77% of the variance. A unipolar factor was identified with the *N* profile, and a bipolar factor was identified with the *S* profile and its opposite, the *H* profile. Three stimulus activation patterns were elicited by taste solutions that varied in intensity of effect. Hierarchical cluster analysis indicated that the patterns fell into discrete classes. Factor analysis of patterns identified three common unipolar factors accounting for 82% of the variance. Eight stimuli ($MgSO_4$, NH_4Cl, KCl, citric acid, acetic acid, urea, quinine HCl, HCl) selectively activated fibers with *H* profiles, three stimuli (fructose, Na saccharin, sucrose) selectively activated fibers with *S* profiles, and two stimuli ($NaNO_3$, NaCl) activated fibers with *N* profiles more strongly than fibers with *H* profiles. Stimuli that evoke different patterns taste distinct to hamsters. Stimuli that evoke the same pattern taste more similar. It was concluded that the hundreds of peripheral taste neurons that innervate the anterior tongue play one of three functional roles, providing information about one of three features that are shared by different chemical solutions.

INTRODUCTION

Agreement has not been reached on the manner in which information used to discriminate taste quality is coded in the mammalian nervous system (Erickson et al.,

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Volume 91 June 1988 861–896

1980; Boudreau et al., 1983; Frank et al., 1983; Smith et al., 1983*a*, *b*; Scott and Chang, 1984; Yamamoto et al., 1985*a*, *b*). An issue that is unsettled is whether it is meaningful to distinguish among peripheral neurons with discrete functions. If many neurons served one function, conceptualizations of coding would be restricted to hypotheses involving separate neural channels and redundant representation of information. Peripheral neurons can be "typed" very easily on the basis of measurements of their morphological, physiological, or signaling characteristics. Neurons can have thick or thin axons (Whitehead and Frank, 1983), or fast or slow conduction velocities (Boudreau and Alev, 1973), or small or large receptive fields (Boudreau et al., 1985; Nagai et al., 1985), or may respond best to sucrose or to NaCl (Frank, 1973). Although these distinguishing characteristics that define a type are precise, at issue is whether the definition is arbitrary. A neuron necessarily has either a thick or a thin axon, if "thick" is defined as greater than a particular diameter. A neuron necessarily responds best to some one of the stimuli applied (Erickson et al., 1980). However, evidence suggests that types of neurons are intrinsic within mammalian peripheral gustatory systems. Responses are covariant (Hyman and Frank, 1980*b*; Boudreau et al., 1982, 1985; Frank et al., 1983) or clustered (Ninomiya et al., 1984) for neurons of a type; measured characteristics for neurons of different types are not covariant (Boudreau et al., 1983) but are drawn from separate populations (Frank et al., 1983).

Also at issue is the nature of qualitative distinctions among the tastes of chemicals. Knowledge of which chemicals, on the basis of their taste quality, are discriminable is essential for the study of quality coding. The question reduces to: how many taste qualities are there? Whether there are very many (Schiffman and Erickson, 1980) or a few primary (Bartoshuk, 1978; McBurney and Gent, 1979; Bartoshuk and Gent, 1985) qualitative distinctions among the tastes of chemicals has not been unequivocally decided with psychophysical studies of human perception. What comprises a taste experience is a significant unresolved issue. Many chemicals in the oral cavity are potential activators of general sensory and olfactory neurons, which contribute to an oral sensation (Silver and Maruniak, 1981; Silver et al., 1985). It is generally accepted, however, that the division of qualitative taste experience into the familiar, primary—sweet, salty, sour, and bitter—although it may be incomplete, has been useful (Schiffman and Erickson, 1980). At least these adjectives describe very different taste experiences in humans. Discriminations among many sweet, salty, sour, and bitter chemicals made by other mammals are similar to those made by humans (Morrison, 1967; Smith et al., 1979; Nowlis et al., 1980; Jakinovich, 1982; Pritchard and Scott, 1982; Frank, 1985*b*).

Data have been accumulating on the peripheral and central neurophysiology (Frank, 1973; J. B. Travers and Smith, 1979; Hyman and Frank, 1980*a*, *b*; Van Buskirk and Smith, 1981; Hellekant and Roberts, 1983; S. P. Travers and Smith, 1984; Beidler and Nejad, 1985; Hanamori et al., 1987) and neuroanatomy (Whitehead and Frank, 1983; Miller and Smith, 1984; Whitehead, 1985, 1986; Whitehead et al., 1985; Davis and Jang, 1986; Hanamori and Smith, 1986; Jang and Davis, 1987) of the gustatory system of the hamster. These data, as well as detailed documentation of the ability of the hamster to discriminate among taste stimuli (Frank, 1985*b*), make it a choice species for an examination of taste information processing. The present report describes responses of fibers in the chorda tympani nerve, the peripheral

taste nerve for the anterior tongue in mammals. It conveys, in the coded signals of its hundreds of sensory neurons, information to the central nervous system regarding the taste of chemicals. Multivariate statistical techniques are used in the empirical demonstration of "natural" (Rodieck and Brening, 1983) types of peripheral taste nerve fibers of hamsters and in the demonstration of likenesses in the peripheral neural effects of 13 taste stimuli, which provide four distinct sensory cues (Nowlis and Frank, 1981; Frank, 1985*b*).

METHODS

Amplified responses of chorda tympani nerve fibers in 13 pentobarbital-anesthetized adult male golden hamsters (*Mesocricetus auratus*) were recorded. The surgery required and the recording techniques have been described in detail (Hyman and Frank, 1980*a*, *b*). The numbers of nerve impulses, judged to be from a single fiber on the basis of the amplitude and distribution in time of the recorded voltages, were counted from photographs of oscilloscope traces (Fig. 1). Counts were obtained for 2 s before and 5 s after initiation of a response,

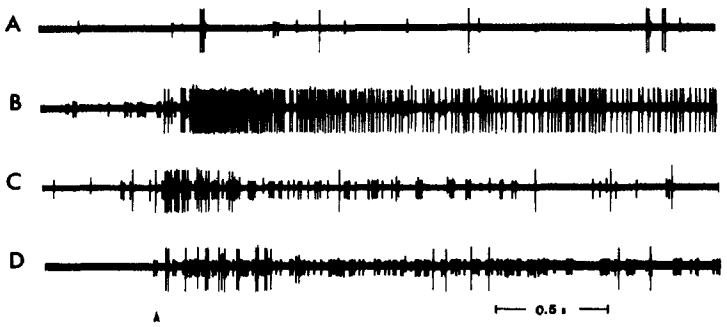

FIGURE 1. Responses of fibers in the hamster chorda tympani nerve. Photographs of oscilloscope traces of 3 s of neural activity are shown: 0.5 s before and 2.5 s after responses to 0.3 M fructose (*A*), 0.03 M $NaNO_3$ (*B*), 0.1 M KCl (*C*), and 0.03 M NH_4Cl (*D*) began (marked by arrowhead). The larger nerve impulses were recorded from a fiber (11; see below) that was highly responsive to sodium salts, and the smaller nerve impulses were recorded from a fiber (33; see below) that was highly responsive to salts and acids.

estimated after the solution contacted the tongue, and used as measures of a fiber's spontaneous and evoked response rates. 50 ml of a room temperature (23–25°C) stimulus solution, made with reagent-grade chemicals and singly distilled water, was applied in 15 s through a glass flow chamber that encased the animal's anterior tongue. The rinse was distilled water, flowed through the chamber for 20 s. The interstimulus interval was at least 1 min. Responses to 13 stimuli were recorded from each of 44 fibers.

The test stimuli (Table I) were neither equally effective (Hyman and Frank, 1980*a*) nor of equal molarity (Boudreau et al., 1983), but they were physiologically comparable (0.1 M sucrose, 0.3 M fructose, 0.001 M sodium saccharin, 0.03 M NaCl, 0.03 M $NaNO_3$, 0.03 M $MgSO_4$, 0.1 M KCl, 0.03 M NH_4Cl, 0.003 M HCl, 0.003 M citric acid, 0.003 M acetic acid, 1.0 M urea, and 0.001 M quinine HCl). Each evoked half the maximal effect of a compound from the whole chorda tympani nerve (Frank, 1973). Their differential effects approximate the intrinsic responsivity to the chemicals, within their individual concentration ranges.

Stimuli include prototypes (sucrose, NaCl, HCl, and quinine HCl), which were presented in random order, and other stimuli that elicit sweet, salty, sour, and bitter taste qualities in humans (McBurney and Shick, 1971), presented in random order thereafter. Stimuli within a

quality category are, to humans, discriminable (Schiffman et al., 1979, 1980; Murphy et al., 1981). All the stimuli tested have been categorized in terms of their qualitative similarities for hamsters by measuring generalizations of conditioned taste aversions (Smith et al., 1979; Nowlis et al., 1980; Frank, 1985*b*).

RESULTS

Neural Response Profiles

Data description and "best-stimulus" classification. Table I presents, for each fiber (1–44), numbers of nerve impulses in the initial 5 s of response to each stimulus as well as the mean spontaneous response rate per 5 s. Data from the most sensitive to the least sensitive "sucrose-best" (1–10), "NaCl-best" (11–32), and "HCl-best" (33–40) fibers, as defined by Frank (1973), are listed in order. Data from four of the fibers (41–44), which responded to no stimulus with a 5-impulse/s increase in the response rate, are not included in the analyses but are included in the table for completeness. These are the data from all of the recordings obtained in this series of experiments. All data analyses are derived from this data matrix.

The profiles for 40 of the 44 fibers' responses (the number of nerve impulses in 5 s above the spontaneous rate) across the 13 stimuli are presented in Fig. 2. The profiles are presented in two columns in numerical order. This figure simplifies comparisons across response profiles. For fibers 1–10, the most effective simulus of the quality prototypes was sucrose; for fibers 11–32, it was NaCl; and for fibers 33–40, it was HCl. Quinine HCl was never the most effective of the four prototypal stimuli. In Fig. 2, the bars, representing the response size by their heights (each successive short horizontal line segment crossing an ordinate marks an additional 60 impulses), are cross-hatched for responses to the prototypal stimuli but filled for responses to the other nine stimuli. Whether these profiles fall into "natural" classes (Rodieck and Brening, 1983) is the issue addressed in the following analyses.

The profiles within each group depicted in Fig. 2 are not identical. Most obviously, they differ in their absolute elicited response rates. However, some sucrose-best fibers respond relatively more than others to the sodium salts. Some NaCl-best fibers respond relatively more than others to HCl. Although, typically, HCl-best fibers respond to most of the ionic stimuli, some also respond relatively well to non-ionic stimuli. On the other hand, inspection of Fig. 2 gives the impression that there are essential similarities among profiles of fibers within a group, profound differences among profiles of fibers in different groups, and few obvious transitional profiles that show characteristics of two of the groups.

Hierarchical cluster analysis. The response profiles for fibers 1–40 presented in Table I were subjected to a hierarchical cluster analysis (BMDP2M). This analysis suggests whether it is reasonable to assume that the profiles are sampled from distinct subpopulations rather than from a single population. Pairs of profiles that are less and less similar, or more and more distant from one another, are sequentially clustered together. The distance between a pair of response profiles was defined as the square root of the χ^2 for neural impulse frequencies elicited by the 13 stimuli. This measure of distance is insensitive to the obvious differences in absolute impulse frequencies recorded from individual peripheral taste fibers (Frank, 1985*a*). However, it is sensitive to differences in the relative effects of the stimuli, including any overall parallel effect of all stimuli (Bieber and Smith, 1986). The centroid method of linking

TABLE I

The Data Matrix

Fiber	Sucrose	Fructose	Saccharin	NaCl	$NaNO_3$	$MgSO_4$	KCl	NH_4Cl	HCl	Citric	Acetic	Urea	Quinine	Spontaneous
1	309	105	115	7	2	27	26	2	1	0	3	5	2	1
2	258	112	108	7	9	14	16	5	2	4	0	23	7	3
3	215	51	70	59	12	58	39	17	30	36	63	12	18	7
4	176	74	57	55	40	0	8	4	5	1	1	23	5	1
5	173	78	107	5	2	47	16	4	15	34	1	8	0	0
6	168	53	44	51	62	11	30	15	5	4	11	5	8	12
7	86	9	5	18	10	3	2	2	4	1	2	9	0	0
8	80	33	35	4	1	0	0	1	1	3	0	1	3	0
9	58	29	17	1	2	3	3	0	8	0	1	2	2	1
10	25	8	4	2	0	2	0	3	2	0	0	0	0	0
11	3	9	4	274	295	33	30	23	228	93	24	15	4	11
12	35	26	34	215	245	60	35	42	50	34	69	47	33	18
13	4	4	17	208	211	48	22	12	138	57	12	31	37	15
14	17	14	8	200	175	39	28	15	94	23	49	15	23	6
15	14	26	30	194	262	19	28	13	71	17	18	64	10	17
16	13	13	53	177	189	17	48	18	21	32	8	38	13	8
17	0	0	36	135	118	10	30	16	1	1	5	0	0	0
18	61	32	44	130	137	7	12	4	2	8	5	20	0	4
19	36	6	12	126	90	7	3	0	88	24	9	0	2	0
20	9	0	0	110	216	32	16	23	14	32	27	68	12	0
21	35	38	33	103	78	9	25	28	37	4	4	24	17	6
22	27	13	2	98	98	8	11	9	34	6	7	25	8	3
23	2	3	12	88	79	17	30	19	59	15	23	3	2	1
24	1	0	0	84	55	10	21	5	32	7	6	1	3	0
25	1	0	0	75	53	11	13	18	49	21	5	2	2	2
26	9	27	10	66	63	25	21	24	16	11	16	20	13	6
27	25	8	14	59	87	5	2	3	6	0	5	4	0	0
28	24	24	25	58	48	9	5	23	12	20	19	7	26	6
29	32	10	11	57	38	5	2	1	4	2	2	1	3	0
30	6	22	23	51	77	23	26	12	17	25	21	18	11	13
31	7	1	4	41	40	0	2	1	7	2	3	4	16	4
32	5	10	1	19	21	24	20	55	15	12	34	18	9	8
33	9	9	11	99	70	90	112	212	258	102	57	74	30	8
34	16	32	14	99	143	129	121	161	156	94	73	112	68	16
35	22	10	28	95	61	65	88	102	106	43	82	38	38	16
36	92	149	99	85	117	144	116	145	100	75	85	166	58	22
37	6	1	0	14	5	11	17	17	97	86	47	2	67	2
38	7	0	14	15	33	56	39	85	68	40	68	21	14	3
39	6	7	6	20	2	5	22	15	52	15	46	5	17	6
40	17	24	10	16	22	11	4	13	35	7	14	16	2	6
41	24	13	3	0	6	12	13	17	1	1	0	6	3	0
42	8	3	6	27	24	19	21	8	5	7	13	10	7	4
43	6	9	1	13	5	0	3	0	5	4	7	1	7	3
44	7	10	9	7	4	8	15	11	17	7	14	9	7	10

The response rates (number of impulses in 5 s) of fibers 1–44 to the stimuli indicated, and before stimuli were applied (spontaneous rate), are given.

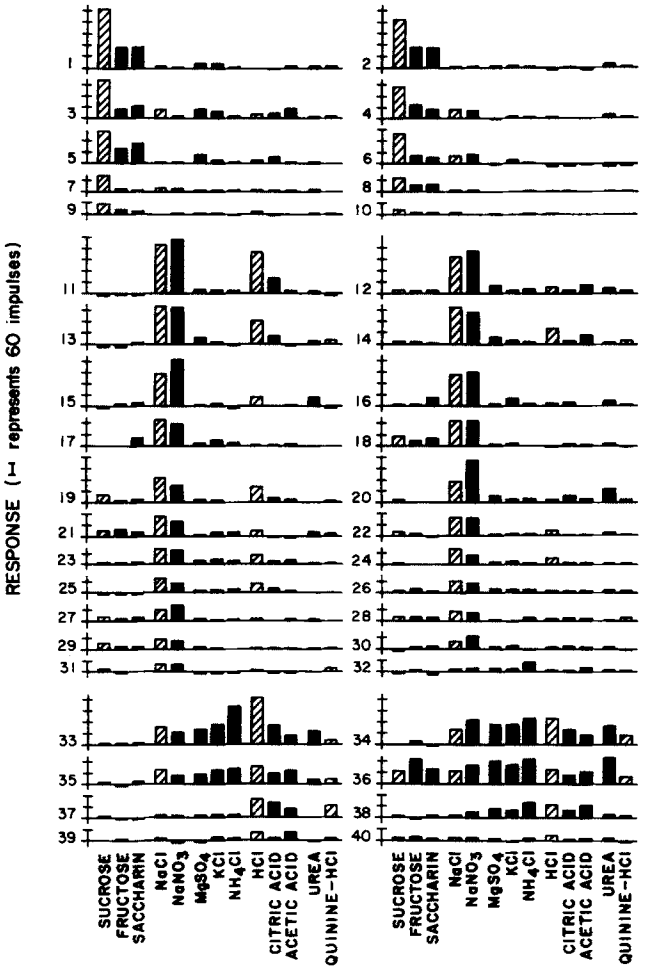

FIGURE 2. Response profiles of hamster chorda tympani nerve fibers. The numbers to the left of each profile identify the fibers (Table I). The left-hand column shows profiles for odd-numbered fibers and the right-hand column shows profiles for even-numbered fibers. Fibers 1–10 are sucrose-best, fibers 11–32 are NaCl-best, and fibers 33–40 are HCl-best. Test stimuli (see text) are listed along the abscissa, beneath bars whose heights represent response rates. The response (nerve impulse) rates for 5 s are indicated. The long horizontal lines from which the bars project represent a rate of zero. Each short horizontal line sequentially crossing the profile's ordinate represents an additional rate increase of 60 impulses above the spontaneous rate. Response rates that are lower than the spontaneous rate are seen as bars extending below the horizontal zero line. The cross-hatched bars represent responses to prototypal stimuli and the filled bars represent responses to other stimuli.

elements that was used combines the two closest (most similar) of the 40 (n) profiles to form a cluster. The cluster's profile (centroid) is then added to the pool of profiles, reduced by 1 to 39 ($n - 1$). This process is repeated until all the profiles are joined. With this truly sequential linking process, a given profile irretrievably loses its individuality once it is included in a centroid. With single linkage, a given profile main-

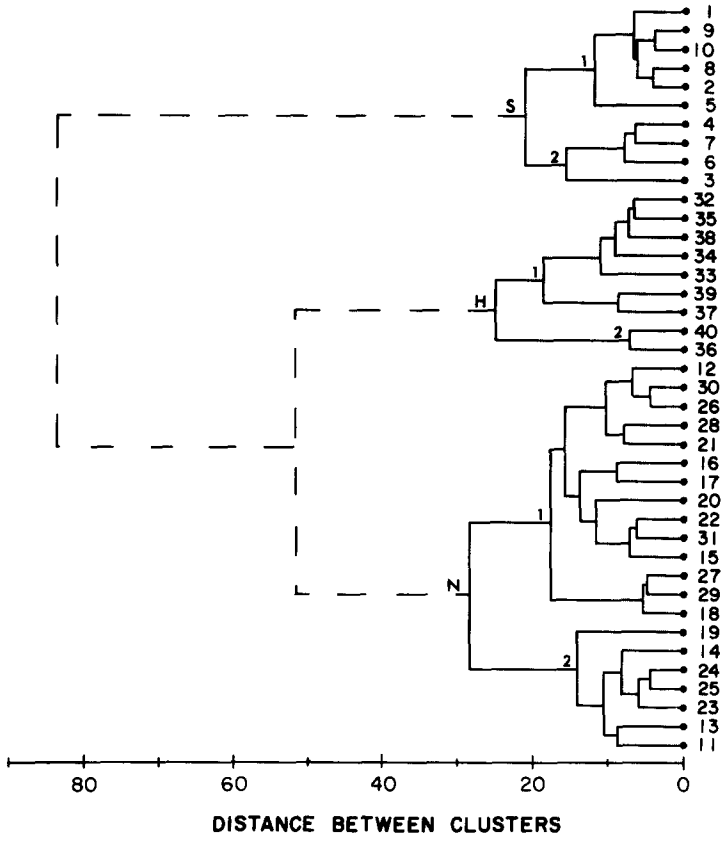

FIGURE 3. Cluster analysis of response profiles. The parallel horizontal lines of the dendogram represent profiles, or groups of profiles, of fibers indicated at the right and numbered as in Table I. The major profile clusters (*S, N, H*) and subclusters (1, 2) are identified to the left of the defining vertical lines. The amalgamation of the major clusters is indicated with dashed lines. The distances $[(\chi^2)^{1/2}]$ between profiles (or groups of profiles) are obtained by projecting the vertical lines that tie the horizontal lines together to the distance scale below.

tains its individuality after joining a cluster, allowing amalgamation of two quite different clusters based on a pair of profiles with low absolute frequencies (and a relatively low χ^2).

The hierarchical tree (dendogram) resulting from cluster analysis is shown in Fig. 3. At the right of the figure, the fiber numbers are indicated as they are specified in Table I and Fig. 2. The analysis divided the chorda tympani profiles, represented by the numbers at the right, into three major classes, members of which are connected by solid lines in Fig. 2. This conclusion is based on a regular, stepwise increase in the intercluster distance as the linking proceeds, until, in moving from three clusters to two clusters, a dramatic increase in the intercluster distance occurs.[1]

[1] The BMDP2M program summed the frequencies but did not divide by the number of profiles combined in calculating centroids. If the centroid used in the linking process is the mean of the combined profiles, the scale of intercluster distances is compressed but the conclusion is identical.

The classes defined by the cluster analysis are labeled "*S*", "*H*, and "*N*" in Fig. 3. Fibers with the *S* profile are identical to the sucrose-best fibers. Fibers with the *N* and *H* profiles are nearly identical to the NaCl-best and HCl-best fibers, respectively. One weakly responsive fiber (32), which is NaCl-best, has an *H* profile. Although this fiber responds slightly more to NaCl than HCl, making it NaCl-best, it is generally responsive to all ionic stimuli, as are fibers with an *H* profile. The cluster analysis, considering relative responsiveness to 13 stimuli, should identify class membership more reliably than does identification of the best stimulus, considering responses to four prototypal stimuli (Maes, 1985). The fact that the profiles are classed virtually identically by the two methods suggests that many of the tested stimuli are superfluous for a distinction among profile types (cf. Hyman and Frank, 1980*b*). How this finding relates to primary or elementary tastes will be addressed below.

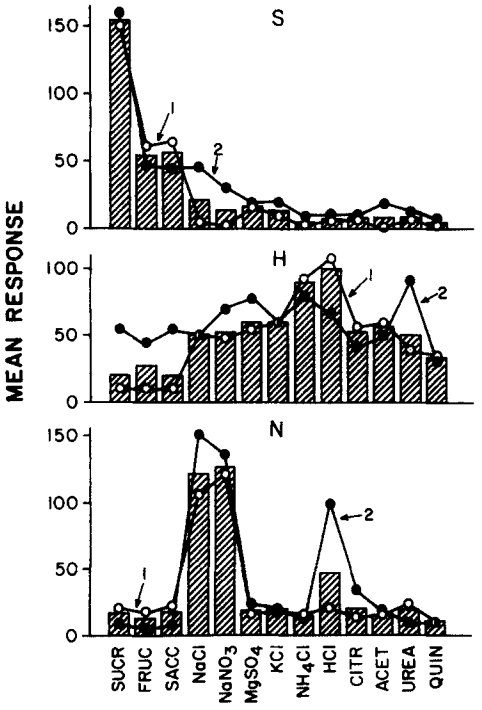

FIGURE 4. Response profiles for clusters and subclusters. The mean response profiles for each major profile cluster (*S*, *N*, *H*; Fig. 3) are indicated with bars in the three sets of axes. These are simple averages of elicited response rates, and highly reactive fibers are most influential (see Discussion). Two subclusters (1 and 2; Fig. 3) of each major cluster are shown as points (1: open; 2: filled) connected by lines. Stimuli (see text) are listed beneath bars representing the mean nerve impulse rates for 5 s. Of the 10 *S* profiles, 6 belong to S_1 and 4 to S_2. Of the 21 *N* profiles, 14 belong to N_1 and 7 to N_2. Of the nine *H* profiles, seven belong to H_1 and two to H_2.

In Fig. 4, mean response profiles for the three clusters are presented as bar graphs. *S* profiles show sizeable responses to sucrose, fructose, and saccharin. *N* profiles show sizeable responses to the two sodium salts and to HCl. *H* profiles show sizeable responses to the acids, salts, quinine, and urea. Thus, within the chorda tympani nerve, fibers that are "specialists," responding to few of the stimuli, and "generalists," responding to most of the tested stimuli, are found. This result is, of course, influenced by the set of test stimuli used. The specialists outnumber the generalists by more than three to one. Fig. 1 presents photographs of the recorded neural responses of one highly reactive generalist (fiber 33) and one highly reactive specialist (fiber 11).

The structure of the dendogram (Fig. 3) suggests that subgroups of profiles within

each of the major clusters may share distinctive characteristics. The profiles of the subgroups that were the last to be joined, all at distances of >20, in the formation of each major cluster (note numbers 1 and 2 in Fig. 3) are shown as line profiles superimposed over the bars in Fig. 4. Fibers with profile S_2 ($n = 4$) show a notable response to sodium salts absent in those with the S_1 profile ($n = 6$).[2] The mean NaCl-sucrose response ratio is 0.03 for S_1 and 0.26 for S_2 profiles. All S_1 ratios were <0.10, but all S_2 ratios were >0.20 (Mann-Whitney $U = 0$; $p = 0.01$). H_2 profiles occurred for two fibers that showed rather equal sensibilities to all 13 stimuli, whereas the seven H_1 profiles do not show responses to sucrose, fructose, and saccharin.[2] The responses of a fiber (33) with an H_1 profile are shown in Fig. 1. N_2 profiles in seven fibers show a sizeable response to HCl that is absent in the 14 N_1 profiles.[2] The responses of a fiber (11) with an N_2 profile are shown in Fig. 1. The mean HCl-NaCl response ratio is 0.12 for N_1 and 0.64 for N_2 profiles (Mann-Whitney $U = 0$; $p < 0.01$).

The hierarchical cluster analysis reinforces the impression obtained from inspection of Fig. 2. The response profiles of peripheral taste neurons segregate into one of three clusters that frequently can be identified by a "best" stimulus (Frank, 1973). Although it had been thought that the distinction between HCl-best and NaCl-best fibers might be arbitrary, since NaCl and HCl are effective stimuli for both classes, the current result suggests the distinction is meaningful. The general relative insensitivity of fibers with the *N* profile to all non-sodium ionic stimuli except HCl (with the possible exception of citric acid) contrasts with the sensitivity of fibers with the *H* profile to many ionic stimuli. The cluster analysis also suggests that there may be subgroups of profiles within the major clusters. Because of the greater number of NaCl-best fibers sampled, the N_1 and N_2 profiles are of greatest interest. One-third of the *N* profiles show a relatively larger response to HCl than the other two-thirds do.

Graded covariant responses to pairs of stimuli. Peripheral mammalian taste nerve fibers show highly varied absolute response levels (Frank, 1973, 1985*a*), and fibers with distinctly different relative response profiles are activated by some of the very same stimuli (Frank et al., 1983). These attributes make it possible to discern characteristic relative effects in sets of profiles by plotting responses to pairs of effective stimuli against one another (Boudreau et al., 1983; Frank et al., 1983). If pairs of stimuli have similar ratios of effect across profiles showing graded absolute sensitivities, the responses will be covariant and highly correlated. Responses to effective pairs of stimuli that have dissimilar ratios of effect in different profiles would not be highly correlated. A single or a few distinct ratios (Frank et al., 1983), described by separate regression lines (Frank, 1985*c*), or a continuous spectrum of ratios (Beidler and Tonosaki, 1985) may be observed within a profile cluster. Whether a distinct ratio of effect for a stimulus pair is associated with a profile cluster will be explored.

[2] As seen in the dendogram in Fig. 3 or a scree plot of distance vs. number of clusters, S_1 and S_2 profiles are both comprised of a subcluster and a single outlier (Bieber and Smith, 1986). The outliers show moderate relative sensibilities to stimuli besides the sweeteners and sodium salts, particularly $MgSO_4$, KCl, and the organic acids. H_1 profiles are comprised of subclusters of five and two profiles. The subcluster of two profiles shows lesser relative sensibilities to salts than the subcluster of five profiles. N_1 and N_2 are seen as subclusters.

TABLE II

Correlations between Responses in Sets of Fibers

Stimulus pair	*S*	*N*	*H*	"*H*"	S + *N* + *H*	*N* + *H*
Sucrose, fructose	+0.89*	+0.66*	+0.97*	+0.23	+0.82*	+0.75*
Sucrose, saccharin	+0.89*	+0.42	+0.98*	+0.61	+0.89*	+0.68*
Fructose, saccharin	+0.95*	+0.47‡	+0.94*	−0.35	+0.89*	+0.74*
NaCl, $NaNO_3$	+0.70‡	+0.90*	+0.80*	+0.80‡	+0.93*	+0.91*
NaCl, KCl	+0.43	+0.41	+0.95*	+0.96*	+0.13	+0.01
NaCl, NH_4Cl	+0.65‡	+0.07	+0.87*	+0.86*	+0.01	−0.16
NaCl, HCl	+0.25	+0.73*	+0.77‡	+0.80‡	+0.47*	+0.35
KCl, NH_4Cl	+0.65‡	+0.45‡	+0.93*	+0.93*	+0.91*	+0.92*
HCl, KCl	+0.39	+0.10	+0.75‡	+0.84*	+0.60*	+0.58*
HCl, NH_4Cl	+0.68‡	−0.06	+0.83*	+0.87*	+0.64*	+0.60*
Number of fibers	10	21	9	8	40	30

Pearson *r*'s were calculated for responses (elicited minus spontaneous activity). Fiber set "*H*" contains the fibers in *H* minus fiber 36. Coefficients with <0.01* and <0.05‡ probabilities of chance occurrence are identified.

The responses to sucrose, fructose, and saccharin are highly correlated (Table II, column *S*) and covariant across *S* profiles, as illustrated by the scatter plots in Fig. 5. The points, indicating the responses of individual nerve fibers to pairs of stimuli, are open circles for *N* profiles, half-filled circles for *S* profiles, and filled circles for *H* profiles. Three "orthogonal" regression lines[3] suggest the relative effects of sucrose and fructose (*A*) or sucrose and Na saccharin (*B*) for the three clusters of profiles. The

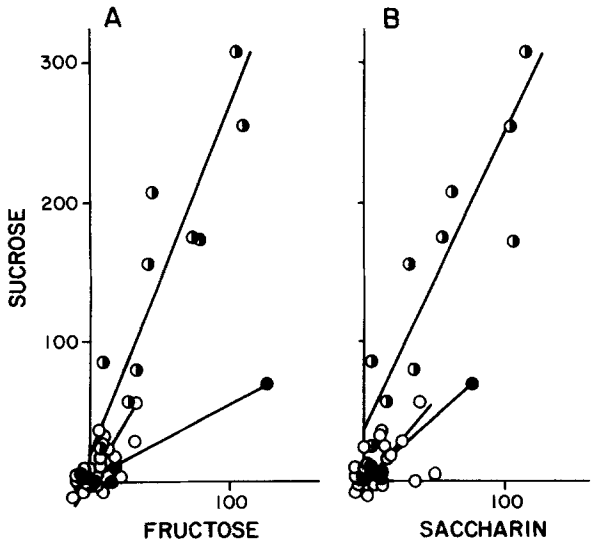

FIGURE 5. Scatter diagrams for sucrose-fructose (*A*) and sucrose-saccharin (*B*) responses. The points within each set of axes represent responses (numbers of nerve impulses in 5 s) in individual *S* (half-filled), *N* (open), and *H* profiles (filled) to the two stimuli indicated for the ordinates and abscissas. The regressions shown are the average of *X* on *Y* and *Y* on *X* because neither responses to sucrose nor responses to fructose or saccharin can be considered independent variables.

[3] Since neither response can be considered an independent variable, an "orthogonal" regression line is shown. It is the average of the two least-squares regressions of *X* on *Y* and *Y* on *X*, minimizing deviations for both *X* and *Y*. The slopes of the least-squares regressions differ from the orthogonal regression by a factor equal to the correlation coefficient. Another name for "orthogonal regression line" is "principal axis" (Kim and Mueller, 1978, p. 16). Deviations "orthogonal" to the regression line are minimized.

graded covariant responses indicate that the stimuli have similar relative effects in different *S* profiles. In all cases, the responses to sucrose are larger than the responses to fructose or saccharin. The average sucrose/fructose and sucrose/saccharin response ratios do not differ (Mann-Whitney $U = 42$; $p \gg 0.1$). The responses to sucrose are typically two to three times as large as the responses to fructose or saccharin. The responses to pairs of these three compounds across *N* and *H* profiles are also correlated (Table II, columns *N* and *H*). However, graded covariant responses were not seen. For example, the high correlation between the responses to sucrose, fructose, and saccharin across *H* profiles is dependent upon the point for fiber 36. In Table II, the "*H*" set of profiles excludes fiber 36. Moderate-sized responses to sucrose, fructose, and saccharin occurred sporadically in *H* and *N* profiles.

The responses to the two inorganic sodium salts are highly correlated (Table II, column *N*), graded, and covariant across *N* profiles. They are, in fact, equivalent stimuli. The mean difference in their effects on *N* profiles is only 1 impulse/s. The responses to NaCl and $NaNO_3$ are correlated, graded, covariant, and also correlated with responses to other effective stimuli across *H* profiles (Table II, column *H*). However, although the NaCl and $NaNO_3$ responses are correlated, they are neither graded nor positively correlated (*r* values range from $+0.25$ to -0.40), with the responses to sucrose, fructose, or saccharin across *S* profiles. Rather, moderate-sized responses are typically seen to both salts in some, but not in other, *S* profiles (Table I). The mean difference in the effects of NaCl and $NaNO_3$ in *S* profiles is only 1.4, and in *H* profiles it is only 0.26 impulses/s. These two sodium salts appear to be providing an identical stimulus to receptors innervated by the chorda tympani.

In Fig. 6, responses to NaCl and HCl (*A*), NaCl and KCl (*B*), NH_4Cl and HCl (*C*), and NH_4Cl and KCl (*D*) are plotted against each other. Separate orthogonal regression lines are drawn for the points from *N* (open) and *H* (filled) profiles. The responses to both NaCl and HCl occur in many *N* and *H* profiles (Table I and Fig. 6 *A*). 15 of the 30 profiles (11 of 21 *N* and 4 of 9 *H*) show responses that exceed 5 impulses/s to both stimuli. However, the responses to HCl and NaCl are not correlated across *N* and *H* profiles, which are lumped together (Table II, column $N + H$).

N profiles show NaCl/HCl response ratios that range from 0.01 to 0.83. Responses to HCl and NaCl are not covariant, although they are moderately correlated.[4] Points are scattered through the space between the *Y* axis above a diagonal at $X = Y$, which separates points for *N* and *H* profiles. It appears that N_2 profiles (open points with diagonals) show the high extreme of relative HCl/NaCl effect on *N* profiles. Since HCl/NaCl ratios of *N* profiles in the rat chorda tympani increase significantly with a second presentation of the stimuli to the tongue (Frank et al., 1983), we considered

[4] A correlation coefficient of about $+0.50$ would result if points were randomly distributed throughout the area of the scattergram between the *Y* axis and a line denoting equal relative values for the two variables. That line would separate points for *N* profiles from points for *H* profiles. Without the point for fiber 11 (Table I), the correlation coefficient for NaCl and HCl responses is $+0.58$ for *N* profiles. Profiles that show responses to distinct sets of stimuli are negatively correlated. The negative correlation is highest when responses to stimuli within the two stimulus sets are equal and large but the negative correlation is lower when responses are unequal and small.

the hypothesis that the HCl/NaCl ratio increases with the order in which profiles were sampled from the hamster chorda tympani. Profiles sampled later in the recording session were for fibers innervating a tongue that had been stimulated many times. 6 of the 7 fibers with N_2 profiles, but only 3 of the 14 fibers with N_1 profiles, were isolated "late" in a 6-h recording session. N_2 profiles were more likely to be among the second half isolated ($\chi^2 = 7.88$; $p < 0.01$). The mean HCl/NaCl response ratio was 0.20 for "early" fibers but was 0.42 for "late" fibers (Mann Whitney $U = 26$; $p \leq 0.05$). Sensitivity to HCl in N profiles increases as the preparation "ages." Responses

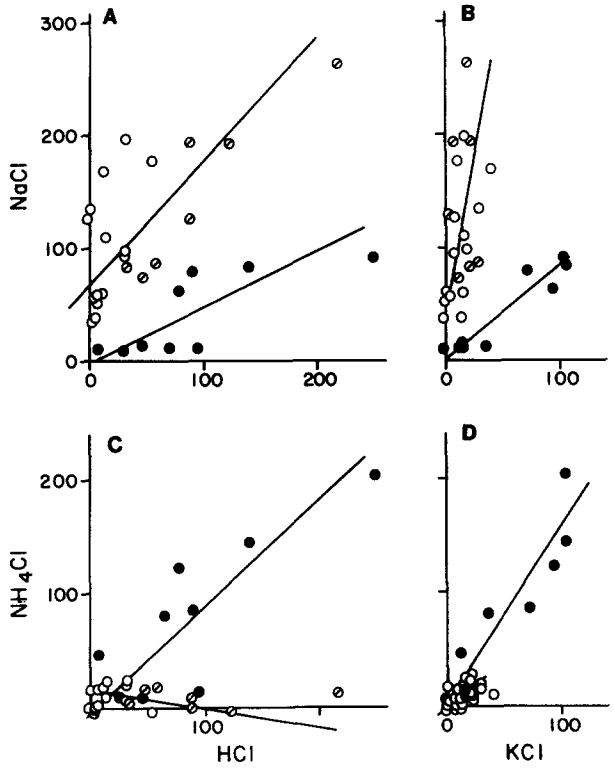

FIGURE 6. Scatter diagrams for NaCl-HCl, (*A*), NaCl-KCl, (*B*), NH_4Cl-HCl (*C*), and NH_4Cl-KCl (*D*) responses. The points within each set of axes represent responses (number of nerve impulses in 5 s) of individual N (open: N_1; open with diagonal line: N_2) and H profiles (filled) to the two stimuli indicated for the ordinates and abscissas. The regressions shown are the average of X on Y and Y on X because neither of the sets of responses can be considered an independent variable.

to KCl or NH_4Cl are small and are not covariant with responses to NaCl (Fig. 6 *B* and Table II, column N) or to HCl (Fig. 6 *C* and Table II, column N) in N profiles.

The moderate correlation coefficients in Table II (column H) and scatter plots (Fig. 6, *A* and *C*) indicate that NaCl or NH_4Cl responses are not clearly covariant with HCl responses in H profiles either. However, some profiles showing high rates of responding to one stimulus show high rates to the other. KCl and NH_4Cl responses are more clearly covariant across H profiles (Fig. 6 *D*). In fact, responses to all pairs of salts (e.g., Fig. 6 *B*) tend to be more highly correlated than responses to pairs of acids

TABLE III

Factor Structure Matrix (Varimax-rotated): Response Profiles

Profile	Factor I	Factor II	Communality
1	−0.161	+0.964	0.955
2	−0.162	+0.977	0.980
3	−0.090	+0.852	0.733
4	+0.164	+0.973	0.973
5	−0.238	+0.911	0.887
6	+0.246	+0.915	0.898
7	+0.102	+0.853	0.738
8	−0.138	+0.974	0.968
9	−0.150	+0.936	0.899
10	−0.103	+0.899	0.819
S			0.885
11	+0.887	−0.262	0.856
12	+0.967	−0.102	0.946
13	+0.922	−0.249	0.913
14	+0.961	−0.182	0.956
15	+0.966	−0.091	0.941
16	+0.957	−0.043	0.918
17	+0.941	−0.039	0.888
18	+0.924	+0.340	0.969
19	+0.881	−0.003	0.776
20	+0.849	−0.151	0.743
21	+0.920	+0.169	0.875
22	+0.985	+0.029	0.971
23	+0.897	−0.306	0.898
24	+0.932	−0.198	0.908
25	+0.865	−0.309	0.844
26	+0.921	−0.139	0.867
27	+0.945	+0.195	0.931
28	+0.831	+0.185	0.725
29	+0.875	+0.428	0.949
30	+0.874	−0.158	0.789
31	+0.944	−0.010	0.891
N			0.884
32	−0.004	−0.541	0.293
33	+0.069	−0.636	0.409
34	+0.260	−0.765	0.653
35	+0.285	−0.661	0.518
36	−0.121	−0.073	0.020
37	−0.186	−0.446	0.234
38	−0.162	−0.672	0.478
39	−0.080	−0.449	0.208
40	+0.329	+0.051	0.111
H			0.325

The entries under factors are correlation coefficients between profiles and factors; communality is the percent variance of a profile accounted for by the two factors. The underlined values are mean communalities for *S*, *N*, and *H* profiles.

or salts and acids (Mann-Whitney $U = 6$; $p < 0.001$) across *H* profiles. The mean salt-salt correlation coefficient is +0.87, but the acid-acid and salt-acid correlations average +0.62. A comparable difference in correlations (+0.85/0.55) is seen if urea is grouped with the salts and quinine HCl is grouped with the acids. Thus, although

salt responses appear to be covariant across *H* profiles, as would be expected for profiles that differ mostly in reactiveness, acids and quinine have more idiosyncratic effects.

In summary, the responses to many pairs of effective stimuli are clearly covariant in fibers with a type of profile, which suggests that fibers having one type of profile are activated by a population of receptors with similar relative sensibilities to these compounds. However, some (particularly acidic stimuli) have more idiosyncratic effects on chorda tympani fibers with *N* or *H* profiles. In *N* profiles, the effect of HCl is associated with preparation age.

Exploratory factor analysis. In an attempt to discover sources contributing to the organization of the response profiles of the hamster chorda tympani, the data presented for fibers 1–40 in Table I were factor-analyzed. Table III presents the results of an exploratory *Q*-factor analysis (SPSS). A scree analysis (Bieber and Smith, 1986) suggested that there were two major factors, which accounted for 47 and 30% of the data variance. The initial least-squares, principal-axis factor solution (PA2) was simplified using an orthogonal rotation that maximizes the variance accounted for by each factor (Varimax). This method is designed to simplify interpretation of factors. Nonetheless, the communality (the variance in profiles accounted for by the two common factors) of every *S* profile and *N* profile is largely due to the high correlation of a profile with a single factor: factor II for *S* profiles and factor I for *N* profiles (Table III). This suggests that the factors (hypothetical profiles) are nearly identical to some of the observed profiles. *N* profiles in the N_1 subcluster correlate strongly and specifically with factor I. *S* profiles in the S_1 subcluster correlate very strongly and specifically with factor II. This is demonstrated in Fig. 7, *A* and *B*. The mean profiles for the three fibers (12, 15, and 22; variance accounted for 93–97%) with the highest correlations with factor I (bars) and the mean N_1 profile (points) are shown in *A*. The profiles most highly correlated with factor I are representative of N_1 profiles. In *B*, the mean profiles for the three fibers (2, 4, and 8; variance accounted for 95%) with the strongest correlations with factor II (bars) and the mean S_1 profile (points) are shown. The profiles most highly correlated with factor II are representative of S_1 profiles.

Neither of the major common factors accounts well for the varied *H* profiles. *H* profiles show an average communality of 32%, whereas the percentage of the variance in *N* or *S* profiles accounted for by the two factors is 88% (Table III). *H* profiles correlate most strongly and negatively with factor II. The negative correlations of *H* profiles with factor II derive from the *H* profile being, in a way, the opposite of an *S* profile. *H* and *S* profiles do not truly show inverse sensitivities to the stimuli. As seen in Fig. 4, S_1 profiles show responses to three stimuli that are the only ones to which H_1 profiles do not show responses.[4] In Fig. 7 *C*, the mean of three profiles (34, 35, and 38; variance accounted for 45–59%) correlating most strongly negatively with factor II (bars) and, for reference, the mean H_1 profile (points) are shown. The profiles most strongly negatively correlated with factor II are representative of H_1 profiles.

In Fig. 8, the correlations of each response profile with the two factors is represented by a point within two-dimensional space. Correlations with factor I are represented by the horizontal distance of a point from the origin. Correlations with factor II are represented by the vertical distance of a point from the origin. A point would fall on the circumference of the drawn circle if 100% of the variance of

a profile were accounted for by the two factors. The points for N profiles (N_1: filled; N_2: half-filled) are distributed about the positive end of the axis for factor I, close to the circle. The points for S profiles (S_1: filled; S_2: half-filled) are near the circle at the positive end of the axis for factor II. The points for H profiles do not fall near the perimeter of the circle. The solid points for H_1 profiles are at some distance from the negative pole of the axis for factor II, but the half-filled points for H_2 profiles fall close to the origin.

The two factors can be thought of as elementary response profiles. Factor I is a profile with responses to only NaCl and $NaNO_3$. N_1 profiles (Fig. 4) are all highly

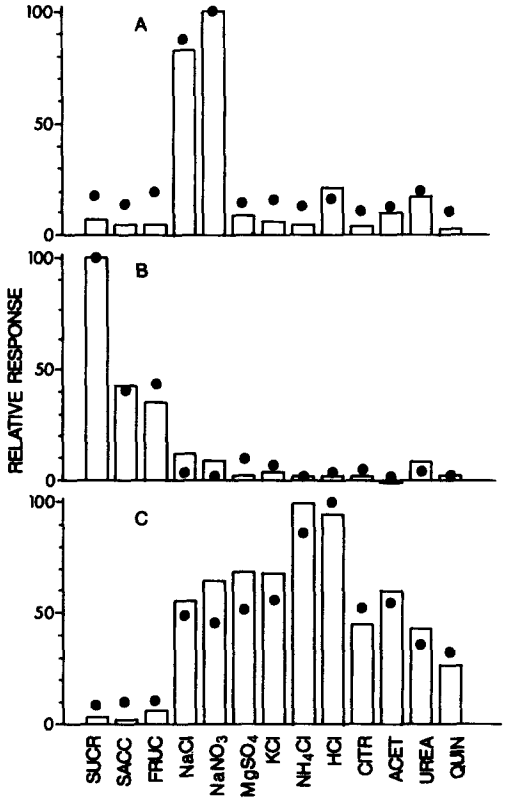

FIGURE 7. Relative response profiles demonstrating the relationship between clusters and factors. The means (normalized so that the largest mean equals 100) of the three profiles with the highest positive correlations with factors I (*A*) and II (*B*), and the highest negative correlations with factor II (*C*) are represented by bars. The points represent the relative mean profiles for subclusters N_1 (*A*), S_1 (*B*), and H_1 (*C*). The mean correlations with factors I and II for three profiles with the highest positive correlations with factor I are $+0.97/-0.05$; those for the three profiles with the highest positive correlations with factor II are $-0.05/+0.98$; and those for the three profiles with the highest negative correlations with factor II are $+0.13/-0.70$.

correlated with factor I, as indicated by the points for them in Fig. 8, far out along axis I. Similarly, factor II is a profile showing a high sensibility only to sucrose, fructose, and saccharin. S profiles (Fig. 4) are all highly correlated with factor II, as indicated by the positions of their points in Fig. 8. The profiles, including all H_1 profiles (Fig. 4), showing responses to all stimuli except sucrose, saccharin, and fructose, are negatively correlated with factor II, as their points indicate. A few N_1 profiles show minor responses to sucrose, fructose, and saccharin and are weakly correlated with factor II. Some N_2 profiles, showing a sensibility to HCl that is not seen in N_1 profiles (Fig. 4), are somewhat negatively correlated with factor II. A few S_2 profiles (Fig. 4) show small responses to the sodium salts and weak correlations

with factor I. *H* profiles are the most individualistic and least well accounted for by the common factors, with the H_2 profiles for fibers 36 and 40 being the extreme cases.

In summary, two common factors can be identified with N_1 and S_1 (and their mirror image, H_1) response profiles. The individual profiles in these subclusters show sensitivities to sodium salts, sweeteners, or all stimuli but sweeteners. More than seven-eighths of the observed variance for all of the *N* and *S* profiles but only about one-third of the variance for all of the *H* profiles could be accounted for by two factors.

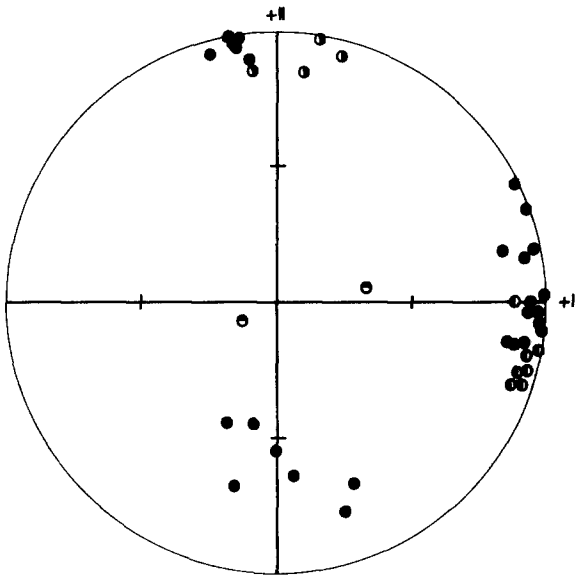

FIGURE 8. Two-dimensional representation of correlations of response profiles with two profile factors. Each point in the space represents the correlation of one response profile with two factors. Zero is at the origin, where the axes cross, and ±0.50 is marked on each axis by crossing line segments. The filled points are for profiles that belong to subcluster 1, and the half-filled points are for profiles that belong to subcluster 2. A point would fall on the circumference of the circle if 100% of the variance of a profile were accounted for by the two factors. The points for *S* profiles are close to the positive extreme of the axis for factor II, where it intersects the circle. The points for H_1 profiles are scattered about the axis for factor II at some distance from its negative extreme. The points for the two H_2 profiles lie closest to the origin. The points for *N* profiles are clustered near the positive extreme of the axis for factor I, where it intersects the circle.

Stimulus Activation Patterns

The response profiles of 40 individual hamster chorda tympani fibers across 13 stimuli have been described above. The distinctiveness of the peripheral neural effects of each of the 13 test stimuli across these fibers is explored below. As pointed out by Erickson (1984), the information that the central nervous system receives about taste stimuli is comprised of a distribution of responses across neural elements. The nervous system never "sees" the differential response (response profile) of a given element to various stimuli at the time a stimulus is recognized. Rather, all elements see the same stimulus (stimuli) simultaneously. An examination of these stimulus patterns may provide insight into the functioning of the gustatory system during a behavioral discrimination.

The stimulus activation patterns to 13 stimuli across 40 peripheral taste neurons are given in Fig. 9. Each row depicts one pattern. The effect of a stimulus, noted at

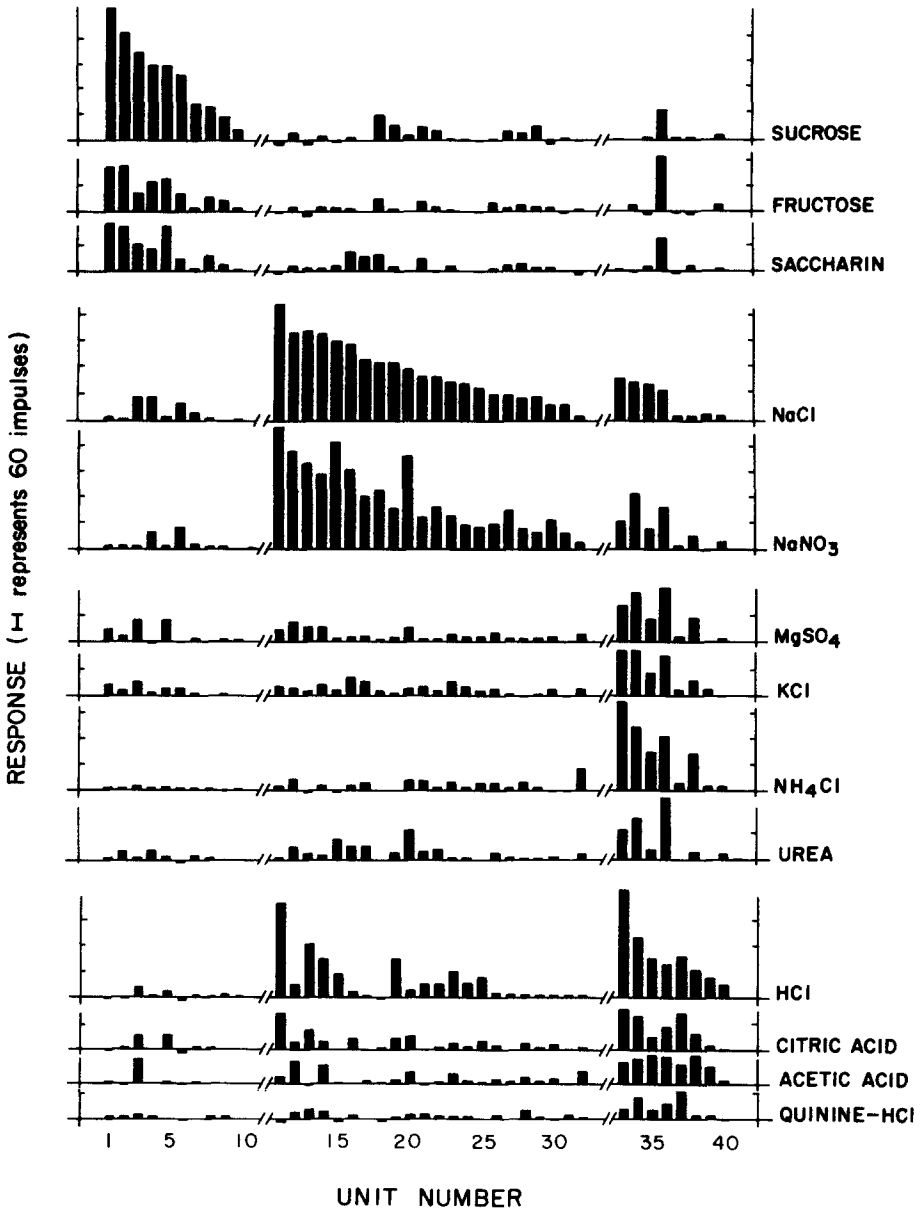

FIGURE 9. Stimulus activation patterns for chorda tympani fibers. The response rates elicited for 5 s in chorda tympani fibers 1–40 (Table I) are represented by consecutive filled bars from left to right. Each row depicts the activation pattern elicited by the stimulus indicated to the right of the horizontal line representing the zero-response rate. These horizontal lines are broken twice with two short parallel diagonals at the transitions between sucrose-best and NaCl-best (between fibers 10 and 11) and NaCl-best and HCl-best (between fibers 32 and 33) fibers. Fiber numbers are indicated along the abscissa. The short horizontal lines parallel to the zero-rate line interrupting the ordinates indicate successive increases in the response rate of 60 nerve impulses. The bars extending below the zero line indicate response rates lower than the spontaneous rate.

the right in the figure, on the most to least responsive sucrose-best fiber (1–10, which show *S* profiles), the most to least responsive NaCl-best fiber (11–31, which show *N* profiles, and 32, which shows an *H* profile), and the most to least responsive HCl-best fiber (33–40, which show *H* profiles), is indicated sequentially from the left to the right by the heights of successive bars in a row. This figure simplifies visual comparisons across patterns. Inspection of this figure clearly suggests that some of the stimuli produce quite similar patterns of activity across chorda tympani nerve fibers. Disregarding differences in the overall effect of stimuli (Table IV), three distinctly different patterns are seen. One is elicited by sucrose, fructose, and saccharin. A second pattern is elicited by NaCl and $NaNO_3$. A third, more variable pattern is elicited by $MgSO_4$, KCl, NH_4Cl, urea, HCl, citric acid, acetic acid, and quinine.

Table IV compares the efficacy of the test stimuli. Just as the different fibers

TABLE IV

Efficacy of the Stimuli

Stimulus	Mean responses			
	All (40)	*S* (10)	*N* (21)	*H* (9)
0.1 M sucrose	46.4	152.3	11.5	10.3
0.3 M fructose	21.0	52.7	7.4	17.2
0.001 M Na saccharin	22.1	53.7	12.0	10.7
B	29.8	86.2	10.3	12.7
0.03 M NaCl	74.7	18.4	115.7	41.7
0.03 M $NaNO_3$	75.9	11.5	120.7	43.0
A	75.3	15.0	118.2	42.4
0.03 M $MgSO_4$	21.6	14.0	13.0	49.8
0.1 M KCl	21.5	11.5	13.8	50.2
0.03 M NH_4Cl	23.4	2.8	9.8	79.8
0.003 M HCl	42.7	4.8	41.0	88.9
0.001 M citric acid	19.0	5.8	15.0	43.0
0.003 M acetic acid	17.4	5.7	10.3	46.6
1.0 M urea	17.9	6.3	13.7	40.6
0.001 M quinine HCl	8.8	2.0	5.5	24.0
C	21.5	6.6	15.3	52.9

The underlined values are means for stimuli, whose individual effects are shown immediately above, eliciting the three across-neuron patterns: *A*, *B*, and *C*. The number of fibers in the All, *S*, *N* and *H* categories are given in parentheses.

showed varied reactiveness, the stimuli showed widely varied efficacy in activating the fibers. The first column of numbers in Table IV presents the mean effect of the different stimuli for the 40 fibers studied. The second, third, and fourth columns present the mean effects of the stimuli on fibers with *S*, *N*, and *H* profiles, respectively.

For fibers with *S* profiles, sucrose was the most effective stimulus. Fructose and saccharin had lesser, comparable overall effects. The relative stimulus activation patterns for these three stimuli across all fibers are quite similar (Fig. 9), as indicated by the correlation coefficients given in the $S + N + H$ column in Table II. The evoked patterns for NaCl and $NaNO_3$ are quite similar to each other but differ from the patterns to sucrose, fructose, and saccharin. These two inorganic sodium salts have about the same absolute (Table IV) and relative (Table II) effects across fibers. Pat-

terns evoked by non-sodium salts ($MgSO_4$, KCl, and NH_4Cl) differ from the sodium salt patterns but are similar to each other, as are patterns for hydrochloric, acetic, and citric acids. The patterns for the salts and acids are somewhat different. NH_4Cl was the most effective non-sodium salt. It was slightly more effective, overall, but much more effective on fibers with *H* profiles (Table IV) than were the other two non-sodium salts. HCl was the most effective of the acids, activating fibers with *H* profiles and some fibers with *N* profiles. Bitter quinine HCl and urea, both weakly effective stimuli, elicit patterns of activity that show some similarity to patterns for the non-sodium salts and acids. Quinine HCl was the least effective stimulus overall and it was the least effective stimulus for fibers with *H* profiles, the group it activated most strongly (Table IV).

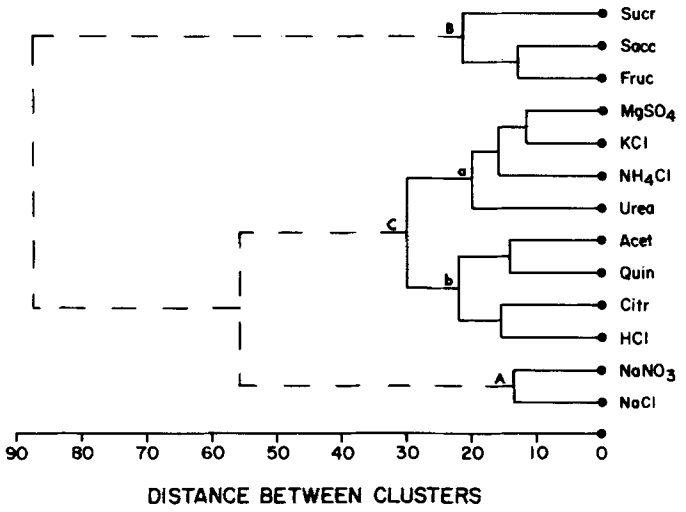

FIGURE 10. Cluster analysis of stimulus activation patterns. The parallel horizontal lines of the dendogram represent the patterns evoked by the stimuli, or groups of stimuli, indicated at the right. The major clusters of the stimulus patterns (*A*, *B*, and *C*) and the subclusters of patterns *C* (*a* and *b*) are identified to the left of defining vertical lines. The amalgamation of major clusters is indicated with dashed lines. The distances $[(\chi^2)^{1/2}]$ between the patterns (or groups of patterns) are obtained by projecting the vertical lines that tie horizontal lines together to the distance scale below.

The results of hierarchical cluster analysis (BMDP2M, centroid linkage) of the patterns elicited by the stimuli are shown in Fig. 10. The cluster analysis procedures used for the stimulus patterns were identical to those used for the response profiles described above. Distance, in this case between patterns, is quantified by calculating the χ^2 for pairs of patterns. This method is insensitive to absolute differences between patterns but sensitive to relative differences, including overall parallel effects of stimuli on all fibers. Three clusters of patterns for stimuli (named at the right) across chorda tympani fibers, with members connected by solid lines, are indicated by the resulting dendogram (Fig. 10). This conclusion is based on regular increases in the inter-cluster distance until an inordinately large increase occurs when the linking moves from three to two clusters.

Pattern *A* is elicited by the two inorganic sodium salts, which activate fibers with *N* and *H* profiles in a highly correlated fashion (Table II). Pattern *B* is evoked by sucrose, fructose, and saccharin, which have highly correlated effects (Table II) on fibers with *S* profiles and activate fiber 36 (Fig. 9). Pattern *C* is elicited by the remaining eight stimuli, which activate fibers with *H* profiles most strongly. Pattern *C* may be composed of two somewhat different evoked patterns (Fig. 9). Pattern C_a is evoked by $MgSO_4$, KCl, NH_4Cl, and urea. Pattern C_b is evoked by HCl, citric acid, acetic acid, and quinine HCl, stimuli that sporadically strongly activate fibers with *N* profiles. In addition, the stimuli that evoke pattern C_a have more highly correlated effects on fibers with *H* profiles than do the stimuli that evoke pattern C_b, which have more idiosyncratic effects on these fibers (see above).

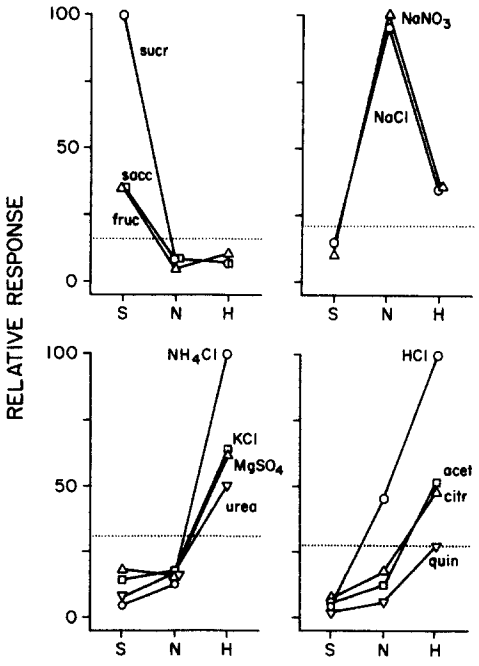

FIGURE 11. Stimulus activation patterns across fibers showing *S*, *N*, and *H* profiles. The mean response (numbers of nerve impulses in 5 s) to each stimulus is normalized by setting the largest mean response plotted within a set of axes equal to 100. The three points for each stimulus, which represent the response rates for fibers showing *S*, *N*, and *H* profiles, are connected by lines to ease identification. The horizontal dotted line demarks the absolute response rate of 5 impulses/s.

The mean patterns evoked across fibers with *S*, *N*, and *H* profiles by the 13 stimuli are presented in Table IV and Fig. 11. In Fig. 11, responses have been normalized so that the largest response to the most effective stimulus in each set of axes equals 100. The dotted horizontal lines mark a response rate of five impulses/s to anchor the absolute response levels that are being considered. The relative effectiveness of each stimulus in a set and the absolute levels of response being considered are evident. In the upper right-hand quadrant of Fig. 11, the *A* patterns for NaCl and $NaNO_3$ are shown. In the upper left-hand quadrant, the *B* patterns for sucrose, fructose, and saccharin are shown. In the lower left-hand quadrant, the C_a patterns for NH_4Cl, KCl, $MgSO_4$, and urea are shown. In the lower right-hand quadrant, the C_b patterns for HCl, acetic acid, citric acid, and quinine HCl are shown. On the average, all but four of the stimuli activate fibers with one of the identified profiles above the response criterion (5 impulses/s). Sucrose, fructose, and saccharin activate fibers

with *S* profiles. NH_4Cl, KCl, $MgSO_4$, urea, acetic acid, and citric acid activate fibers with *H* profiles. Quinine HCl does not, on the average, activate any of the three groups of fibers, although it weakly activates five fibers with *H* profiles and three fibers with *N* profiles. The two inorganic sodium salts and HCl activate fibers with *N* and *H* profiles.

Several chemical stimuli elicit very similar common response patterns across chorda tympani neurons. Such stimuli differ largely in the intensity of their effects. Fig. 1 presents responses of two such stimuli, KCl and NH_4Cl. The pattern is comprised of activation of neurons showing one or two of three identified response profiles.

An *R*-factor analysis (SPSS) identified sources contributing to the stimulus activation patterns across these 40 fibers. A scree analysis suggested that three common factors were extracted from the correlation matrix (principal-axis factoring as

TABLE V

Factor Structure Matrix (Varimax-rotated): Stimulus Activation Patterns

Pattern	Factor 1	Factor 2	Factor 3	Communality
Sucrose	−0.148	+0.829	−0.233	0.764
Fructose	+0.095	+0.951	−0.142	0.933
Na saccharin	−0.028	+0.947	−0.078	0.903
B				0.867
NaCl	+0.065	−0.218	+0.927	0.912
$NaNO_3$	+0.089	−0.166	+0.966	0.968
A				0.940
$MgSO_4$	+0.927	+0.215	+0.113	0.919
KCl	+0.913	+0.110	+0.082	0.853
NH_4Cl	+0.916	−0.063	−0.049	0.845
Urea	+0.725	+0.220	+0.233	0.628
C_a				0.812
HCl	+0.660	−0.296	+0.339	0.638
Citric acid	+0.776	−0.173	+0.206	0.675
Acetic acid	+0.774	−0.131	−0.056	0.620
Quinine HCl	+0.684	−0.118	−0.093	0.490
C_b				0.606

The entries under factors are correlation coefficients between patterns and factors; communality is the percent variance of a pattern accounted for by the three factors. The underlined values are means for patterns *A*, *B*, C_a, and C_b.

described above for fiber profiles), accounting for 82% of the data variance (factor 1: 44%; factor 2: 25.5%; factor 3: 12.5%). The structure matrix for the Varimax-rotated solution is given in Table V.

The stimulus patterns (observed variables) for $MgSO_4$, KCl, and NH_4Cl (members of subcluster C_a) correlate ($r = +0.91$ to $+0.93$) most highly with the hypothetical variable, factor 1. Of the 13 stimuli, they activate fibers with *H* profiles most exclusively (Fig. 11). The patterns for fructose and saccharin (members of cluster *B*) are strongly related ($r = +0.95$) to factor 2. These stimuli predominantly activate the fibers with *S* profiles and fiber 36. Fructose and saccharin activate fiber 36 about as strongly as they activate the most reactive fiber with an *S* profile. The two inorganic sodium salts evoke highly similar patterns (members of cluster *A*), activating fibers

with *N* more than fibers with *H* profiles. The patterns to these sodium salts correlate highly ($r = +0.93$ and $+0.96$) with factor 3. By examining the observed patterns of activation that correlate most highly with the common factors, factor 1 can be identified with a stimulus activation pattern involving mainly fibers with *H* profiles, factor 2 with a pattern involving fibers with *S* profiles and fiber 36, and factor 3 with a pattern in which fibers with *N* profiles are activated more than twice as strongly as fibers with *H* profiles.

The patterns for a number of stimuli show moderate communalities (Table V). More than 20% of the variance in patterns for sucrose and HCl, two very effective stimuli (Table IV), is not accounted for by the factors. The pattern for sucrose differs from those for fructose and saccharin (factor 2) in its relatively weak activation of fiber 36 (Fig. 9). The pattern for HCl, which correlates with factors 1 (+0.66) and 3 (+0.34), is unique in its considerable effect on some, but not all, *N* profiles (cf. Fig. 6 *A*). That unique effect of HCl has been associated with the age of the physiological preparation (see above). Other stimuli evoking patterns with communalities ranging from 0.49 to 0.68 were relatively weak stimuli overall (Figs. 9 and 11). In fact, there is a direct relationship between communality (Table V) and the overall effect of stimuli eliciting fewer than 20 impulses/5 s across all fibers (Table IV). The lesser effects of weaker stimuli overall allow low variable response rates to affect the relative pattern across neurons inordinately. Sporadic activation contributes more to a pattern for a less effective than to a more effective stimulus.

The factor analysis of evoked stimulus patterns suggests, as did the cluster analysis, that there is a considerable similarity in the effects of a number of compounds. This is clear in the three-dimensional representation of correlations with the three major factors in Fig. 12. The patterns for most stimuli lie close to the axis for one factor, which indicates that each stimulus primarily evokes one of the three common patterns.

In Fig. 12, a point would fall on the surface of the sphere if 100% of the variance of a profile were accounted for by the three factors. Correlations with factors 1 and 3 are represented by the position of an × within the circular plane through the center of the sphere defined by the ellipse with a long horizontal axis. Correlations with factor 2 are indicated by the lengths of the vertical dashed line segments projecting from the × in that plane and topped by a point. Circular planes defined by axes for factors 2 and 3 and for factors 2 and 1 are also drawn.

The positions of points for patterns evoked by NH_4Cl, KCl, $MgSO_4$, acetic acid, quinine HCl, members of cluster *C*, are closely apposed to the axis for factor 1. The points for patterns for urea (filled circle) and citric acid (half-filled circle) are those a short distance from the axis. The point for the HCl pattern shows the greatest deviation from an axis for a single factor. C_a patterns are indicated by filled points; C_b patterns are indicated by half-filled points. The three points (filled circles) for *B* patterns hover above the plane defined by the axes for factors 1 and 3 and close to the axis for factor 2. The points (filled circles) for *A* patterns for the inorganic sodium salts lie close to the axis for factor 3. This result suggests, as far as the taste receptors on the anterior tongue are concerned, that 3 of the 13 stimuli, such as sucrose, NaCl, and acetic acid, or fructose, $NaNO_3$, and KCl, or saccharin, NaCl, and NH_4Cl, would elicit all of the common distinguishable patterns elicited by the 13 stimuli. In this

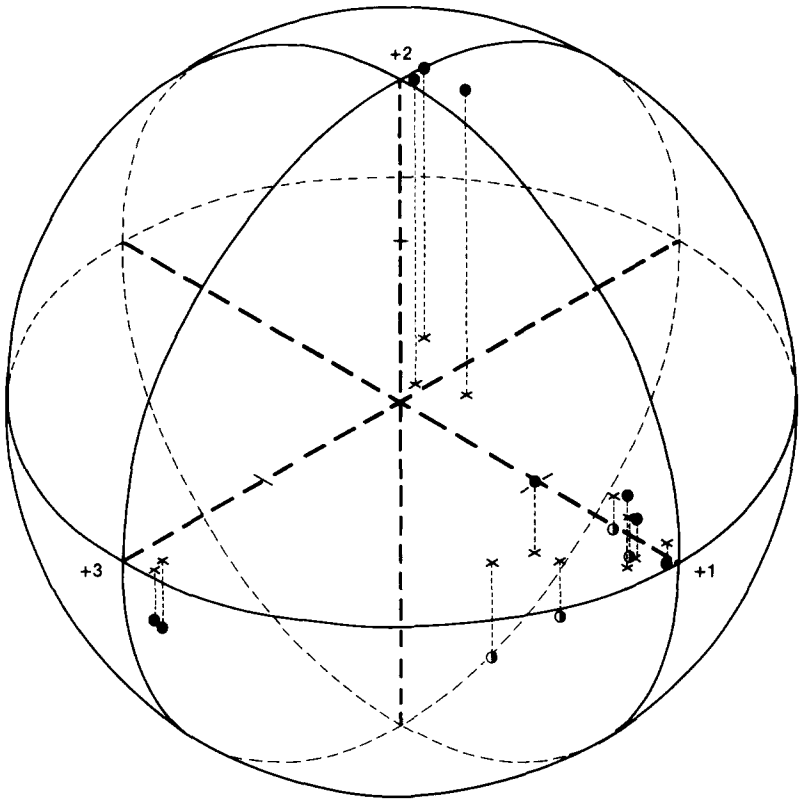

FIGURE 12. Three-dimensional representation of correlations of stimulus patterns with three pattern factors. Each point in the space represents the correlation of one response pattern with each of the three factors. The points for profiles with 100% of their variance accounted for by the factors would fall on the surface of the sphere. The semi-circles projecting in front of the plane are solid lines; the semi-circles projecting behind that plane are dashed lines. The three axes are the heavier dashed lines. Zero is the origin, where the three axes cross, and +0.50 is marked on each axis by a crossing line segment. The filled circles are for patterns that belong to cluster *A*, cluster *B*, and cluster C_a; the half-filled circles are for patterns that belong to cluster C_b. The three patterns in cluster *B*, which were elicited by sucrose, fructose, and saccharin, are highly positively correlated with factor 2. The two patterns in cluster *A*, which were elicited by NaCl and $NaNO_3$, are highly correlated with factor 3. The nine patterns in cluster *C* are correlated with factor 1. Of the three points that are some distance in front of the axis for factor 1, the point representing the correlation of the pattern elicited by HCl is most distant because of a moderate correlation with factor 3. The two points that lie slightly in front of axis 1 are for patterns elicited by citric acid (half-filled) and urea (filled).

sense, they are equivalent sets of primary stimuli. The responses to one of these sets of three primary stimuli are seen in Fig. 1.

In conclusion, a factor analysis of the stimulus activation patterns indicates that a number of compounds elicit common patterns across chorda tympani fibers, differing predominantly in overall level. Some of the unique effects of stimuli are tied to

a single, highly active, nonspecific fiber (36), the age of the physiological preparation, or the effect of sporadic, low-level responses on patterns for weak stimuli.

DISCUSSION

Three Characteristic Neural Response Profiles

A summary of the primary stimulus selectivities of hamster chorda tympani fibers (Table VI) is seen in the three average response profiles shown in Fig. 13 *A*. These are the mean *S*, *N*, and *H* response profiles across the groups of stimuli that elicit patterns *A*, *B*, and *C*. Fibers with *S* profiles respond eight times more strongly to pattern *B* compounds than to other compounds. Fibers with *N* profiles respond nine times more strongly to pattern *A* compounds than to others. The sharp tuning of *N* profiles seen in Fig. 13 *A* results from the very strong effect of both sodium salts (Table IV) and the general ineffectiveness of compounds that elicit *B* and *C* patterns on these fibers. The relatively large effect of HCl, a pattern *C* compound, on one-third of the fibers does not offset the typical ineffectiveness of stimuli that elicit pattern *C* (Fig. 4). Fibers with *H* profiles show comparable sensibilities to compounds eliciting patterns *A* and *C* (all salts and acids; cf. Fig. 4). A general effect of salts on fibers with *H* profiles is also seen in the rat chorda tympani (Boudreau et al., 1983; Frank et al., 1983). Sodium and nonsodium salts are not distinguished by these fibers, which are sensitive to many electrolytes. They contrast with fibers with *N* profiles, which clearly distinguish between sodium and nonsodium salts. The average profiles shown in Fig. 13 *A* depict the mean selectivity of three groups of peripheral taste neurons that have distinctly different sensibilities to stimuli with sweet, salty, sour, and bitter tastes for humans. Fibers within a group differ most obviously in their ability to respond to any of the stimuli (Table VI).

The Varied Reactiveness of Nerve Fibers

Hamster chorda tympani fibers show highly varied abilities to respond to taste stimuli that are sweet, salty, sour, or bitter to humans. In the sample reported here, individual afferents ranged from being barely reactive (fibers 41–44 in Table I) to responding at sustained rates of >50 impulses/s for 5s to a most effective stimulus (fibers 1, 2, 11, and 33 in Table I). The average ability of fibers to respond to the 13 stimuli used in this study ranged >20-fold (Table IV). However, the relative response profiles across the stimuli could be highly similar for fibers with very different reactiveness. The highly characteristic varied reactiveness of taste afferents (Frank, 1985*a*) invites speculation concerning its origin.

Taste bud cells turn over (Beidler and Smallman, 1965; Conger and Wells, 1969; Cheal and Oakley, 1977; Farbman, 1980; Delay et al., 1986). More reactive fibers may be those that contact a larger number of fully developed receptor cells. Younger receptor cells, which may not yet have developed a full receptive microvillar surface or may not be completely innervated by a fiber's endings (Cheal et al., 1977), and degenerating old cells, which may have lost their ability to generate a receptor potential or may have lost some of their functional contacts with nerve endings, may provide input to the continuum of less reactive fibers.

TABLE VI

Reactiveness of the Nerve Fibers

Fiber	Mean response			
	All (13)	*A* (2)	*B* (3)	*C* (8)
1	45.5	3.5	175.3	7.2
2	40.5	5.0	156.3	5.9
3	45.3	28.5	105.0	27.1
4	33.5	46.5	101.3	4.9
5	37.7	3.5	119.3	15.6
6	23.9	44.5	76.3	−0.9
7	11.6	14.0	33.3	2.9
8	12.5	2.5	49.3	1.1
9	8.7	1.0	33.7	1.4
10	3.5	1.0	12.3	0.9
S	26.3	15.0	86.2	6.6
11	68.6	273.5	−5.7	45.2
12	53.1	212.0	13.7	28.2
13	46.6	194.5	−6.7	29.6
14	47.8	181.5	7.0	29.8
15	41.9	211.0	6.3	13.0
16	41.2	175.0	18.3	16.4
17	27.1	126.5	12.0	7.9
18	31.5	129.5	41.7	3.2
19	31.0	108.0	18.0	16.6
20	43.0	163.0	3.0	28.0
21	27.5	84.5	29.3	12.5
22	23.6	95.0	11.0	10.5
23	26.1	82.5	4.7	20.0
24	17.3	69.5	0.3	10.6
25	17.2	62.0	−1.7	13.1
26	18.7	58.5	9.3	12.2
27	16.8	73.0	15.7	3.1
28	17.1	47.0	18.3	9.1
29	12.9	47.5	17.7	2.5
30	12.5	51.0	4.0	6.1
31	5.8	36.5	0.0	0.4
N	29.9	118.2	10.3	15.1
32	10.7	12.0	−2.7	15.4
33	79.2	76.5	1.7	108.9
34	77.7	105.0	4.7	98.2
35	43.8	62.0	4.0	54.2
36	88.1	79.0	91.3	89.1
37	26.5	7.5	0.3	41.0
38	32.4	21.0	4.0	45.9
39	10.8	5.0	0.3	16.1
40	8.7	13.0	11.0	6.8
H	42.0	42.3	12.7	52.8

The underlined values are means for fibers showing *S*, *N*, and *H* profiles. The numbers of stimuli in the All, *A*, *B*, and *C* categories are given in parentheses.

Individual chorda tympani fibers can be activated by stimulating a single or many papillae (Pfaffmann, 1970; Miller, 1971; Boudreau et al., 1971; Oakley, 1975; Nagai et al., 1985; Mistretta et al., 1987), which may be related to their reactiveness. In the rat, a single nerve fiber may be activated by stimulation of as few as one or as many as 14 fungiform papillae, each of which contains a single taste bud. The number of taste buds showing functional interaction with a fiber could be a consequence of the turnover of receptor cells or it may be inherent in the innervation pattern laid down during ontogenetic development. However, neurons of a type tend to develop com-

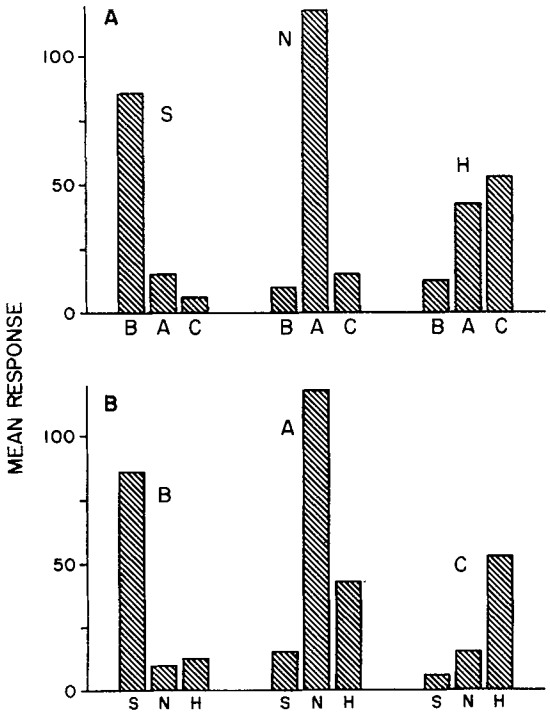

FIGURE 13. Response profiles across stimuli that elicit patterns *A*, *B*, and *C*, and stimulus patterns across fibers that show *S*, *N*, and *H* profiles. In *A*, the mean effect of stimuli that elicit the common patterns *A*, *B*, and *C* on fibers that show *S*, *N*, and *H* response profiles are represented. The profiles across 13 compounds have been condensed to profiles across three "stimuli" because a number of compounds have very similar relative effects across fibers, which suggests they are stimuli differing largely in intensity. Each set of three bars is a response profile comprised of the mean responses to all stimuli that evoke patterns *A*, *B*, and *C*. In *B*, the mean patterns across fibers showing *S*, *N*, and *H* response profiles elicited by stimuli that evoke common patterns *A*, *B*, and *C* are represented. The patterns across 40 fibers have been condensed to patterns across three "fibers" because many fibers have very similar relative response profiles, which suggests that they distinguish similarly among chemical stimuli. Each set of three bars is a stimulus activation pattern comprised of mean responses of all fibers with *S*, *N*, and *H* profiles.

parable fields of innervation in other systems (Purves and Lichtman, 1984). In accordance with this general principle, types of chorda tympani fibers innervate characteristic average numbers of papillae in sheep (Nagai et al., 1985; Mistretta et al., 1987).

A severed nerve fiber's ability to respond to the receptor potential provided by taste receptor cells deteriorates in time. The recordings reported here were from nerve fibers severed from their somas, which may contribute to their varied reactiveness. Multiunit responses recorded from the chorda tympani nerve grow smaller with

hours after nerve severance (Hellekant et al., 1979). However, this reduction in response size is not large after a few hours (Kitada et al., 1984). Also, a full range of reactiveness can be recorded from fibers immediately after nerve severance or from taste neuron cell bodies from which the fiber is not severed (Boudreau et al., 1983). In fact, the loss of the ability to react is not due to the fiber's inability to generate action potentials, but to a deterioration of the interaction between the fiber and the receptor cells (Oakley et al., 1981; Sloan et al., 1983; Oakley, 1985).

An individual nerve fiber, during the course of time, might be more or less reactive depending upon the number of mature receptor cells it innervates. However, the response profile of an individual nerve fiber does not seem to change systematically as sites on receptor cells develop, although there is a sequential development of chemical sensibilities during ontogeny (Hill et al., 1982; Mistretta and Bradley, 1983). If an individual fiber maintained functional contact with receptor cells as they developed different membrane-bound receptor sites, or if an individual fiber developed functional connections with a series of different receptor cells as they migrated through the taste bud (Beidler and Smallman, 1965), it might be expected that more response profiles that were transitional between the three profiles depicted in Fig. 13 *A* would exist.

Profile Variability

Although the response profiles within a group differ most obviously in absolute reactiveness, there are smaller differences in the relative effect of the stimuli (Table VI). The clearest difference is seen for the most numerous *N* profiles. Two-thirds of these profiles (N_1) show minimal sensitivity to HCl, but one-third (N_2) show larger responses to HCl (Fig. 4). The scatter of points for responses of fibers with *N* profiles in Fig. 6 *A* suggests that these are not two types of *N* profiles. HCl/NaCl response ratios are not clearly bimodal; transitional ratios occur. Some N_1 profiles show relatively large HCl/NaCl response ratios (range, 0.01–0.45) and some N_2 profiles show relatively small HCl/NaCl response ratios (range, 0.17–0.83). The relative effect of HCl ranges from 1 to 83% of the effect of NaCl in fibers with *N* profiles. Also, the N_2 profile is not transitional between *N* and *H* profiles. N_2 profiles show clear responses only to the strong acid, HCl (Fig. 3), and perhaps slight responses to the organic citric acid. *H* profiles show responses to non-sodium salts, quinine, and urea as well as to sodium salts and HCl.

The fact that most of the chorda tympani fibers with N_2 profiles were recorded late in a recording session suggests that fibers with *N* profiles can exist in several functional states. It is possible that the N_2 profile is the response profile of an *N* fiber with sensitized receptors. Whether the sensitization is a precursor of deterioration of the receptors owing to failing trophic effects, direct chemical injury, or a functional, reversible alteration in transduction is a matter of speculation. Individual rat chorda tympani fibers with *N* profiles responded more strongly to HCl on a second, later presentation (Frank et al., 1983). The recorded whole rat chorda tympani nerve does not show an increase in the relative effect of HCl as time progresses (Hellekant et al., 1979; Kitada et al., 1984). Rather, an initial increase in overall reactiveness is followed by a slow decline. However, the responses to HCl of fibers with *H* profiles in the rat decrease in that time (Frank et al., 1983). This decrease

would mask any increase in the HCl responses of fibers with *N* profiles in whole-nerve recordings.

The small number (10) of *S* profiles sampled makes detailed analysis of the two subgroups in this cluster foolish. However, a few comments can be made. S_2 profiles show a more notable sensibility to NaCl (and perhaps $NaNO_3$) than do S_1 profiles. In fact, the distribution of NaCl-sucrose response ratios for *S* profiles is bimodal. S_1 ratios range from 0.02 to 0.08 and S_2 ratios range from 0.21 to 0.31. This suggests that there are two kinds of *S* profiles, each showing a discrete, consistent, relative sensibility to NaCl-sucrose. All four of the fibers showing S_2 profiles were isolated from the chorda tympani nerve during the later part of a recording session. On the other hand, three of the six fibers showing S_1 profiles and low NaCl-sucrose response ratios were isolated early and three were isolated late in the session. S_2 profiles are not more likely to be sampled in older preparations ($\chi^2 = 2.85$; $0.10 > p > 0.05$). The suggestion is that either the fibers exist in two discrete states or there are two kinds of fibers. In the process of attempting to isolate fibers for the length of time required to apply 13 stimuli, some fibers were isolated for a shorter period. Eight of these were sucrose-best fibers. These short-lived fibers showed a range of NaCl-sucrose response ratios of 0.02 to 1.00. The isolation of a recorded fiber may be lost either when nerve impulses of other recorded fibers obscure its nerve impulses or its nerve impulses decrease progressively in size and disappear. It is possible that *S* profiles with high NaCl-sucrose response ratios are seen in fibers whose function is waning since they are more frequently seen in short-lived fibers.

Nine of the fibers sampled had *H* profiles. The diverse *H* profiles are generally characterized by a lack of relative selectivity. In fact, the two fibers with the H_2 profile respond indiscriminately to all 13 stimuli. Most of the seven fibers with the H-1 profile respond to all stimuli except the "sweets," but a few less reactive fibers (37 and 39) respond more selectively to acidic stimuli. The response ratios for salts and urea are relatively constant, whereas the response ratios for acids and quinine vary drastically across *H* profiles. These results suggest that there may be several types of profiles included in this category: one that is responsive to all stimuli (H_2, $n = 2$), one that is sensitive to salts, acids, urea, and quinine (H_1, except for profiles for fibers 37 and 39, $n = 5$), and one that is more specifically sensitive to acids and quinine (H_1 profiles 37 and 39, $n = 2$). There is an alternative that should be considered, however. Sources of varied profiles for HCl-best fibers of the rat chorda tympani include a post-stimulation depression that dissipates in minutes and a decreased reactivity that develops with time after fiber isolation (Frank et al., 1983). HCl-best fibers of the rat chorda tympani also had more varied response profiles than other types of fibers, but repeated measurements from a single HCl-best fiber yielded quite different profiles. Unfortunately, stimulus sequences were not routinely repeated in the present experiments on the hamster. It is not known how each of the nine *H* profiles might look if measured again.

Fibers showing low elicited response rates (a <5 impulse/s increase above the spontaneous response rate) to all of the test stimuli were not considered in the analyses. This decision was based on the inherent unreliability in measuring small numbers of impulses that are randomly distributed in time (Harper, 1985), as are impulses elicited by many taste stimuli (Nagai and Ueda, 1981). If the impulses are not randomly

distributed in time, this argument does not hold. A mean impulse rate of <25 randomly distributed impulses has a standard deviation of >20% of its value. If the mean response rate is 10 impulses, the standard deviation is >30%. On the other hand, a mean rate of 300 impulses has a standard deviation that is 6% of its value. Relative response profiles are critical in multivariate statistical techniques. Profiles that are based on small numbers of impulses will fluctuate widely with repeated sampling, whereas relative response profiles based on larger numbers of impulses are more stable.

Moderate responses (25–82 impulses/5 s) occurred sporadically to stimuli that did not consistently activate fibers with a given type of response profile. Such responses occurred in more reactive fibers (with maximum elicited rates of ≥100). For example, 24 of 25 occasional moderate responses to pattern *C* stimuli are seen in more reactive *S* and *N* profiles ($\chi^2 = 19.02$; $p < 0.001$). They were also elicited more frequently by particular pattern *C* stimuli. $MgSO_4$, KCl, citric acid, and acetic acid elicited moderate responses in some more reactive *S* profiles, but NH_4Cl, HCl, urea, and quinine never did (Table I). A χ^2 of 7.35 ($p < 0.01$) suggests that the moderate responses in the more reactive fibers were not randomly elicited by any pattern *C* stimulus. In *N* profiles, moderate responses occurred to $MgSO_4$, KCl, citric acid, acetic acid, and urea, but never to NH_4Cl or quinine. Again, this distribution is probably not random for more reactive *N* profiles ($\chi^2 = 6.41$; $p < 0.02$). These regularities suggest that some pattern *C* stimuli may have a reliable effect on fibers with *S* and *N* profiles. A more accurate appraisal of the true effect of weaker stimuli could be obtained by sampling responses for longer periods of time, during which more impulses would accumulate.

The foregoing suggests that each of the hundreds of peripheral neurons devoted to taste on the anterior tongue in the hamster (Whitehead and Frank, 1983; Jang and Davis, 1987) have one of three functions. Three distinct sets of chemicals that interact differentially with associated transductive events in taste buds are detected. According to this model, the taste system is organized in a highly redundant way, providing the animal with essentially the same three pieces of information from all parts of the anterior tongue, an expanse of epithelium over which endings of neurons with different functions intermingle (Boudreau et al., 1985). Besides indicating the general location of the taste stimulus, this organization can be likened to a redundant technology in which alternative elements are provided to take over in case of failure, but it is more dynamic than that. In this model, individual peripheral neurons sequentially play the role of failed and functioning elements because their links with the environment, the cells of the taste bud, are regularly replaced, as are olfactory receptors (Graziadei and Monti Graziadei, 1979), perhaps especially after injury (Hinds et al., 1984). The capacity of a given neuron at a given time is evident in its ability to react to the stimuli to which it is tuned. This part of the model provides a raison d'etre (Erickson, 1985*a*, *b*) for the highly variable overall activity levels seen in the peripheral gustatory system. In the model, consistent information is provided by neurons with a given function because, although a neuron at a given time may react weakly or strongly, it and all of its kind have the same differential sensibilities across chemicals. However, looking at the gustatory system from the point of view of the receiver, weak signals (e.g., 5–10 impulses/5 s) from weakly reactive neurons may not influence the

information transferred as much as strong signals (e.g., 100–300 impulses/5 s) from highly reactive neurons (Gill and Erickson, 1985). The outputs of these anterior lingual afferent gustatory systems apparently interact at their central neural target, the nucleus of the solitary tract (Smith et al., 1983*a*; S. P. Travers et al., 1986), but continue to function as parallel systems in the gustatory central nervous system (Smith, 1985).

Three Prototypal Activation Patterns for Sweet, Salty, Sour, and Bitter Stimuli

Most of the information about the 13 stimuli that is made available to the central nervous system from fibers of the chorda tympani nerve can be reduced to the stimulus activation patterns shown in Fig. 13 *B*. Pattern *B* is elicited by three stimuli that predominantly activate fibers with *S* profiles. The responses to sucrose, fructose, and saccharin are, respectively, 13.7, 5.1, and 4.6 times larger in these fibers than in other fibers. Pattern *A* is elicited by two stimuli that activate fibers with *N* profiles 2.8 times more strongly than they activate those with *H* profiles. The responses to $NaNO_3$ and NaCl are, respectively, 4.6 and 3.9 times larger in fibers with *N* profiles than other fibers. These two sodium salts are the only stimuli that consistently activate fibers with two types of profiles. Pattern *C* is elicited by eight stimuli that predominantly activate fibers with *H* profiles. The responses to NH_4Cl, quinine, acetic acid, KCl, $MgSO_4$, citric acid, urea, and HCl are, respectively, 10.6, 5.5, 5.3, 3.8, 3.7, 3.6, 3.6, and 3.0 times larger in fibers with *H* profiles than in other fibers.

The relatively greater activation of fibers with *S* profiles by sucrose, compared with fructose or saccharin, is largely attributable to the greater effectiveness of sucrose (Table IV and Fig. 11). The test stimuli elicited half-maximal responses from the chorda tympani nerve. Their concentrations, therefore, would approximate the dissociation constants of the chemicals' interactions with taste receptors (Beidler, 1954), and the different-sized responses should relate directly to intrinsic activities. Sucrose elicits a stronger reaction than does either fructose or saccharin.

It is a common assumption that differences in the absolute evoked response rates code for differences in stimulus intensity rather than quality. There is a simple relationship between the maintained response rates in many peripheral afferents and perceived intensity (Mountcastle, 1974). Sucrose may have a taste quality very similar to fructose and saccharin but a taste intensity that is perhaps two or three times stronger. Generalizations of aversions established to sucrose, fructose, or saccharin in hamsters cross-generalize to one another. Cross-generalizations are not seen among aversions established to these compounds and the other 10 test stimuli (Frank, 1985*b*). The generalizations were strongest to sucrose even if fructose or saccharin were the conditional stimulus. Since it has been shown (Nowlis, 1974) that a stronger test stimulus elicits a stronger conditioned response than a weaker test stimulus of the same quality, sucrose may actually have a stronger taste to these animals.

At 30 mM, NaCl and $NaNO_3$ elicit similar versions of pattern *A*, which suggests that the sodium ion is the common stimulus. Both sodium salts activate fibers with *N* and *H* profiles (two-thirds of the sampled fibers) to degrees related to the overall reactiveness of the individual fibers. Both activate fibers with *N* profiles about three times more strongly than those with *H* profiles. Both stimuli are about equally effective for chorda tympani fibers (Table IV and Fig. 11).

Behavioral discriminations made by hamsters suggest that NaCl and $NaNO_3$ have a common taste, distinct from the taste of non-sodium salts and acids. The patterns of cross-generalization of aversions are identical. The aversions established to NaCl or $NaNO_3$ generalize to each other but to none of the other 11 test stimuli (Frank, 1985*b*). Among those 11 stimuli to which the aversions do not generalize are all the other salts and acids that activate fibers with *H* profiles in common with the two sodium salts. Sodium salts differ from these other stimuli in that they strongly activate fibers with *N* profiles. The distinctiveness in taste of sodium salts may be coded in a pattern of relative effect on two populations of afferent neurons (Fig. 13 *B*). It is possible that the activation of the more than twice as many specific fibers with *N* profiles dominates the pattern received by the central nervous system concerning these stimuli (Gill and Erickson, 1985). En masse, fibers of the chorda tympani with *N* profiles are activated 6.5 times more strongly than are fibers with *H* profiles by NaCl or $NaNO_3$.

It is also possible that strong input from fibers with *N* profiles reduces the central neural effect of simultaneous, weak input from fibers with *H* profiles. Interactions have been suggested by behavioral studies of mixtures of NaCl (a strong activator of fibers with *N* profiles) and quinine (a weak but specific activator of fibers with *H* profiles). Rats behave as if quinine were weakened in mixtures with NaCl (Mason et al., 1985). Also, the taste of NaCl more readily supports a generalization of an aversion to an NaCl-HCl mixture than the taste of HCl supports a generalization of an aversion to HCl mixed with NaCl. Rats show a 32% aversion learned to 0.1 M NaCl to the mixture of 0.05 M NaCl and 0.0015 M HCl. They show only an 8% aversion learned to 0.003 M HCl to the mixture of 0.05 M NaCl and 0.0015 M HCl (Smith and Theodore, 1984). Recordings from brain stem nuclei in the hamster that receive gustatory input, however, do not show an overall sharpening of the response to NaCl in the nucleus of the solitary tract (J. B. Travers and Smith, 1979; Smith et al., 1983*a*; Smith and Sweazey, 1984). Nor was sharpening evident for neurons in the pontine parabrachial nuclei (Van Buskirk and Smith, 1981; Smith et al., 1983*a*; S. P. Travers and Smith, 1984). Finally, it is possible that the behavioral generalizations are specific for the sodium salts, although there is an element of their taste that is held in common with non-sodium salts and acids. That element could have been less salient because of the distinct taste owing to strong activation of the specific fibers with *N* profiles. Such "overshadowing" in conditioned taste aversion learning has been shown for compounds with multifaceted tastes (Nowlis et al., 1980).

Among stimuli that elicit pattern *C*, NH_4Cl most exclusively activates fibers with *H* profiles. It is a very effective stimulus for the chorda tympani that does not activate other fibers (cf. Table IV and Fig. 11), as do other stimuli that elicit pattern *C*. Quinine, the least effective chorda tympani stimulus tested, also showed a relatively exclusive *H* profile activation. Other pattern *C* stimuli did show weak ($MgSO_4$, KCl, citric and acetic acids of some *S* and *N* profiles; urea of some *N* profiles) or strong (HCl of some *N* profiles) activation in other than *H* profiles, however. The pattern for HCl deviates the most from the general trend (Fig. 11). HCl, uncharacteristically, shows a considerable activation in one-third of the *N* profiles. Several lines of evidence suggest that receptors innervated by fibers with *N* profiles can be sensitized to HCl.

In contrast to the distinctiveness of stimuli that elicit either pattern *A* or *B*, behavioral analyses have shown that hamsters distinguish between at least two classes of stimuli that elicit pattern *C*. Aversions to NH_4Cl, KCl, quinine HCl, and $MgSO_4$ cross-generalize, as do aversions to citric, acetic, and hydrochloric acids (Frank, 1985*b*). Although there are some interclass generalizations among HCl, NH_4Cl, and quinine, the animals clearly distinguish among sets of these stimuli. Several explanations come to mind. First, it is possible that afferents with an additional type of profile, which provide the cue, exist in very small numbers in the chorda tympani. In the rat and hamster, nerve fibers with four types of profile have been described for lingual taste afferents. One of them, the quinine-best, does not occur frequently in the chorda tympani but does in the glossopharyngeal nerve (Nowlis and Frank, 1981; Hamamori et al., 1987). Interestingly, the quinine-sensitive afferents in the catfish also are segregated in the glossopharyngeal and vagus nerves (Kanwal and Caprio, 1983). On the other hand, *H* profiles may truly be of two types. They had the most diverse profiles and a few of them responded specifically, though weakly, to the acids.

In conclusion, not every chemical compound that has a taste evokes a unique activation pattern in the chorda tympani. Taste stimuli that are distinct to the animals establish unique patterns, but many compounds establish similar patterns. These patterns are often an activation of peripheral afferents that show one of three types of response profile but they can be the activation of afferents showing two types of profile. These results suggest that the gustatory system recognizes discrete features of chemicals in the oral cavity, although specific chemical compounds may have several features. Furthermore, each feature may be detected by receptors associated with a single chorda tympani neuron.

M. E. Frank thanks T. P. Hettinger for his thoughtful assistance in analyzing the data.

This work was supported by National Science Foundation grant BNS-8519638 to M. E. Frank.

Original version received 12 August 1987 and accepted version received 22 January 1988.

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