

Response Properties of Macaque Monkey Chorda Tympani Fibers

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ABSTRACT Many of the chorda tympani fibers of crab-eating monkeys respond to more than one of the four basic stimuli (NaCl, sucrose, HCl, and quinine hydrochloride) as well as cooling or warming of the tongue. Fibers could be classified into four categories depending on their best sensitivity to any one of the four basic stimuli. Sucrose-best and quinine-best fibers are rather specifically sensitive to sucrose and quinine, respectively, while salt-best and acid-best fibers respond relatively well to HCl and NaCl, respectively. Saccharin, dulcin, and Pb acetate produce a good response in sucrose-best fibers, but quinine-best and salt-best fibers also respond to saccharin. Highly significant positive correlations exist between amounts of responses to sucrose and those to saccharin, dulcin, and Pb acetate, indicating that these substances produce in the monkey a taste quality similar to that produced by sucrose. Compared with chorda tympani fibers of rats, hamsters, and squirrel monkeys, macaque monkey taste fibers are more narrowly tuned to one of the four basic taste stimuli and more highly developed in sensitivity to various sweet-tasting substances. Also LiCl and NaCl are more effective stimuli for gustatory receptors in macaque monkeys than NH_4Cl and KCl. This contrasts with a higher sensitivity to KCl and NH_4Cl than to NaCl in chorda tympani fibers of squirrel monkeys.

INTRODUCTION

Certain differences in taste responses have been indicated by behavioral experiments between rodents such as rats, hamsters, and squirrel monkeys on the one hand, and between squirrel and macaque monkeys on the other. For example, hamsters and rats prefer sucrose and saccharin to water but do not respond to dulcin (Carpenter, 1956; Fisher et al., 1965), while squirrel monkeys (*Saimiri sciureus*) prefer sucrose and dulcin but reject saccharin (Fisher et al., 1965), or reject both dulcin and saccharin (Glaser, 1972). On the other hand, rhesus monkeys (*Macaca mulatta*) show preference for saccharin at concentrations between 0.4 and 10 mM (Weiskrantz, 1960). Electrophysiological experiments have also demonstrated differences in taste

responses in the chorda tympani between rodents and squirrel monkeys, and between the two kinds of monkeys. Snell (1965) reported a response to NH_4Cl and KCl greater than that to NaCl in squirrel monkeys, while the reverse is true for rats, hamsters, and guinea pigs (Beidler et al., 1955). Also in the white-faced ringtail monkey (*Cebus capucinus*) the magnitude of response to KCl is greater than that for equimolar NaCl solution (Fishman, 1959). On the other hand, Ogawa et al. (1972) have revealed in a recent study that the order of the magnitudes of the chorda tympani nerve responses to chloride salts with varying cations in rhesus and crab-eating monkeys is $\text{LiCl} \geq \text{NaCl} \geq \text{CaCl}_2 \geq \text{MgCl}_2 \geq \text{SrCl}_2 > \text{NH}_4\text{Cl} \geq \text{KCl}$, thus indicating difference in response to salts between macaque and squirrel monkeys. They also demonstrated good neural responses to saccharin, dulcin, and Na cyclamate in macaque monkeys. In keeping with the above reports Brouwer et al. (1973) have recently shown that sweet-tasting proteins, Monellin and Thaumatin, elicited a significant response in the green monkey (*Cercopithecus aethiops*) which showed several characteristics that could be related to psychophysical observations in man, while in the guinea pig and rat little or no response could be obtained.

It has been known that single gustatory nerve fibers in mammals respond to a variety of substances of different quality (Pfaffmann, 1955; Ogawa et al., 1968; Frank, 1973), and consequently it has been proposed by a number of investigators that coding of taste quality may be made by an across-fiber response pattern specific to a stimulus (Erickson et al., 1965; Marshall, 1968; Ganchrow and Erickson, 1970). On the other hand, recent electrophysiological studies on chorda tympani fiber responses in hamsters and squirrel monkeys (Frank, 1973, 1974; Pfaffmann, 1974) have indicated that, although most taste nerve fibers are broadly tuned to the so-called four basic stimuli, individual fibers are categorized into three groups which yield a best response to either sucrose, NaCl , or HCl with side response to three other stimuli and that there are species-specific classes of taste fibers, each with its cluster of sensitivities.

Although Gordon et al. (1959) recorded responses to a variety of stimuli from a few nerve fibers of the rhesus monkey and reported the presence of fibers rather specifically sensitive to one of the four stimuli representing the four basic tastes, no detailed study of response properties of single chorda tympani fibers in macaque monkeys has been made. Therefore, in the present study impulse discharges in single nerve fibers of crab-eating monkeys elicited by various stimuli were recorded, and their response properties for the stimuli representing the four basic tastes and other various substances were examined. Finally, the results obtained were compared with those obtained by other investigators on rats, hamsters, and squirrel monkeys in order to see differences in taste sensitivity between these animal species and macaque monkeys.

MATERIALS AND METHODS

Animals

Thirty crab-eating monkeys (*Macaca fascicularis*) of both sexes weighing 2.5–3.5 kg were used in the experiments.

Experimental Procedure

Induction of anesthesia in the monkey was carried out with ether. The monkey was laid in a supine position, the trachea cannulated and the head clamped by ear bars, while the animal was anesthetized with ether. Anesthesia was maintained by subsequent intravenous injection of sodium amobarbitone of about 3 mg/kg body weight.

Sixty-seven single taste nerve fibers were functionally isolated from chorda tympani nerves. The chorda tympani on both sides were used for the experiment, the one on the left side on the first experimental day and the other on the next day. The chorda tympani was exposed from the point where it leaves the bulla until it enters the tongue muscle after joining with the lingual nerve, and the proximal end of the nerve was cut. The sheath which surrounds the nerve was removed and a few fibers were isolated from the nerve with a pair of needles. The proximal end of the nerve was suspended in mineral oil on a pair of Ag-AgCl electrodes. Impulse discharges resulting from gustatory and thermal stimulations of the tongue were recorded with conventional electrophysiological equipment consisting of a preamplifier, dual-beam oscilloscope, and kymographic camera. Spikes of uniform size were a criterion for a single unit. The output of the preamplifier was recorded on magnetic tape with an FM tape recorder. The data stored on magnetic tape were later displayed on the oscilloscope, if necessary.

Gustatory stimulation of the tongue was carried out by continuously passing 150 ml of solution at 25°C for 10–12 s over the tongue, the anterior two-thirds of which had been enclosed in a chamber made of glass. The flow chamber was essentially similar to that described earlier (Nagaki et al., 1964). After stimulation the tongue was rinsed for more than 20 s with 300 ml of tap water at 25°C. For thermal stimulation of the tongue, tap water at 5–45°C was passed through the chamber. Thermal sensitivities of all the units isolated were examined by applying water at 20°C to the tongue which had been preadapted to 40°C water (cooling) as well as by applying water at 40°C to the tongue preadapted to 20°C (warming). In every experiment sensitivities of all the units to the four basic taste stimuli representing salty, sweet, sour, and bitter tastes (0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, and 0.003 M quinine hydrochloride) were examined. Integrated responses of the whole chorda tympani nerve to the basic stimuli are shown in Fig. 1. Responses to NaCl and HCl attained a peak immediately after stimulation, while those to sucrose and quinine reached a steady magnitude gradually. A sudden increase in response appeared after water rinse of sucrose and HCl. As shown in the figure, 0.3 M NaCl elicited the greatest magnitude of response among the four basic stimuli, while 0.003 M quinine produced the smallest magnitude of response.

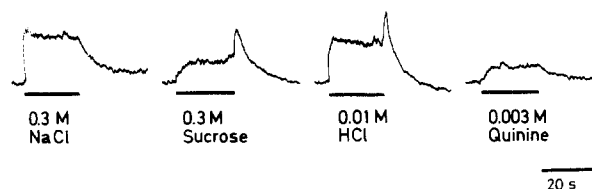


FIGURE 1. Integrated responses to the four basic stimuli in the chorda tympani nerve of a crab-eating monkey. Horizontal bars underneath individual records indicate period of application of stimulus.

Test Solutions

Test stimuli employed in the experiments are indicated in Table I. They consisted of the four basic stimuli, six common salts, five sweet-tasting substances, two acids, and strychnine nitrate. However, after the experiments, 0.001 M strychnine was found to be too weak to be an effective stimulus because responses to strychnine in a majority of units examined were nearly equal or smaller than the spontaneous discharge rate. Therefore, the data were discarded.

In several experiments responses to series of concentrations of NaCl, sucrose, HCl, quinine hydrochloride, and Na saccharin were recorded, and those to dulcin and sodium cyclamate were examined in one experiment. The stimuli were presented mostly in an ascending order of concentration. All the chemicals used were of reagent grade and dissolved in deionized water, its specific resistance being greater than 5 M Ω and pH about 5.7.

Data Processing

The number of impulses in each second during 10 s of stimulation in each unit were counted successively on the photographed record. The magnitude of response was represented usually by the number of impulses during the initial 5-s period, because the time-course of impulse discharges in chorda tympani fibers of macaque monkeys was relatively slow, especially when sucrose and quinine were employed as stimuli (see Fig. 1 and Results).

Statistical calculations for obtaining across-fiber correlations (Pearson product-moment correlations) were made on numbers of impulses during the initial and second 5-s periods, although the results based on the numbers during the latter period were reported in the paper only when it was considered necessary. Significance of all correlation coefficients was tested by the Student *t* test at 5% level, and, when a higher significant level (1%, 0.1%) was attained, the level was stated.

Most of the chorda tympani fibers were found to be spontaneously active. Therefore, the rate of the spontaneous impulse discharges in each unit was determined by counting impulses during 5 s without applying any stimulus to the tongue after its preadaptation to 25°C water for more than 2 min, and the average rate was obtained by calculating the mean of several determinations distributed throughout the study of a unit.

Since most chorda tympani fibers of macaque monkeys show a relatively high rate of spontaneous discharge (see Results), their responsiveness to the stimuli should

TABLE I
TASTE STIMULI USED IN THE EXPERIMENTS

Basic stimuli	Other stimuli	Numbers of fibers
0.3 M NaCl	0.3 M LiCl	30
	0.3 M KCl	30
	0.3 M NH ₄ Cl	30
	0.3 M CaCl ₂	30
	0.3 M MgCl ₂	30
	0.3 M SrCl ₂	30
0.3 M Sucrose	0.01 M Na saccharin	38
	0.01 M Insoluble saccharin	41
	0.003 M Dulcin	34
	0.1 M Pb acetate	31
	0.1 M Na cyclamate	34
	0.3 M Na saccharin	35
0.01 M HCl	0.01 M Tartaric acid	27
	0.02 M Acetic acid	30
0.003 M Quinine hydrochloride	0.001 M Strychnine nitrate	31

Basic stimuli were used for 67 fibers, and other stimuli for the numbers of fibers indicated.

be determined using a certain criterion. The criterion is rather arbitrary. In the present study in order to determine responsiveness of units to gustatory (and also thermal) stimuli, the 5% tolerance limits (Johnson, 1949) of the spontaneous impulse discharges in each unit were calculated, and, when the magnitude of response to a particular stimulus in a unit exceeded the limit, the unit was assumed to be responsive to a given stimulus. The tolerance limits are given by $\bar{X} \pm t_{\alpha} \{(n+1)/n\}^{1/2} \cdot s$ where \bar{X} is the sample mean and $s^2 = \sum_i^n (X_i - \bar{X})^2 / (n-1)$ the sample variance estimate in a sample size n with individual response value X_i . The value of t_{α} can be obtained from the table of t distribution when the value of α (level of significance) has been specified. When α is 0.05, t_{α} is greater than 2 for a small number of n .

Random distribution of responsiveness to four basic taste stimuli was tested by means of the Chi-square test for a 2×2 case which has been described in detail elsewhere (Ogawa et al., 1968, Siegel, 1956).

RESULTS

Sensitivities to the Four Basic Stimuli

Sensitivities of 67 chorda tympani fibers to each of the four basic stimuli are shown in Fig. 2, where the numbers of impulses during the first 5 s after stimulation were plotted against units ordered independently for the four stimuli. As expected from the integrated responses obtained from the whole chorda tympani (Fig. 1), 0.3 M NaCl is the strongest stimulus among the

four basic stimuli. It stimulated a greater number of fibers to a greater degree than the other three stimuli: During the first 5 s of stimulation NaCl elicited more than 10 impulses in 54 fibers, HCl in 42 fibers, sucrose in 38 fibers. One hundred or more impulses are elicited in response to NaCl in 10 fibers, in response to sucrose in 5 fibers, and in response to HCl and quinine in 4 fibers.

Sensitivity to NaCl is distributed continuously across fibers, and the magnitude of response increases approximately logarithmically with the ordered number. The inset in Fig. 2 is a plot of the logarithm of the response magnitude for all the fibers, and indicates that the logarithm of the response magnitude

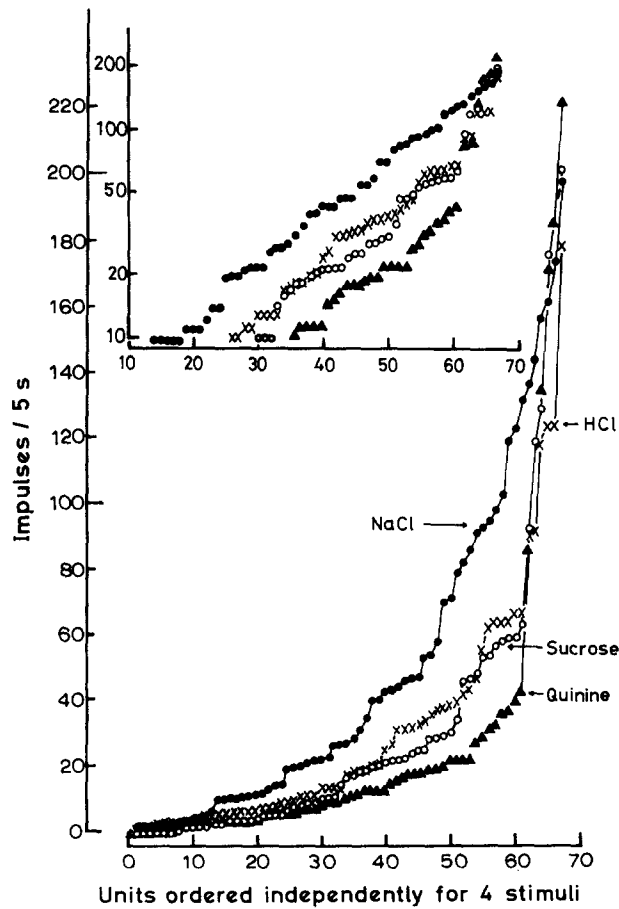


FIGURE 2. Responses of 67 monkey chorda tympani fibers to 0.3 M NaCl (●), 0.3 M sucrose (○), 0.01 M HCl (×), and 0.003 M quinine hydrochloride (▲), ordered according to the amount of the response to each of the stimuli. Number of impulses during the initial 5 s is plotted on linear and logarithmic scales in the abscissa. Fibers which responded with less than 10 impulses/5 s were excluded from the logarithmic plot.

for NaCl is linearly related to the ordered number for fibers which responded with 10 impulses or more. The response magnitudes for the other three stimuli also increase linearly with the ordered number in a majority of fibers, but they do so more steeply above the firing rate of 60 impulses.

Spontaneous Discharges

Sixty-three out of 67 macaque monkey chorda tympani fibers showed a resting discharge without application of stimuli. The mean (\pm SD) rate of the "spontaneous discharges" in these fibers is 9.8 ± 8.8 impulses/5 s. This rate is high compared with that in rats and hamsters (Ogawa et al., 1968; Sato et al., 1969; Frank, 1973). Fig. 3 shows the difference in magnitude of the spontaneous discharges and responses to 0.3 M NaCl. The spontaneous discharge rate ranged from 0 to 45 impulses/5 s, while the amount of response to 0.3 M NaCl ranged from 0 to 198 impulses during the initial 5 s. Therefore, the spontaneous discharge rate is significantly small compared with the magnitude of response to 0.3 M NaCl, but is often a significant proportion of the quinine response, which is the smallest among responses to the four basic stimuli: Fibers whose response magnitude for quinine is 10 impulses or more and is greater than the spontaneous discharge rate are only 23 in number.

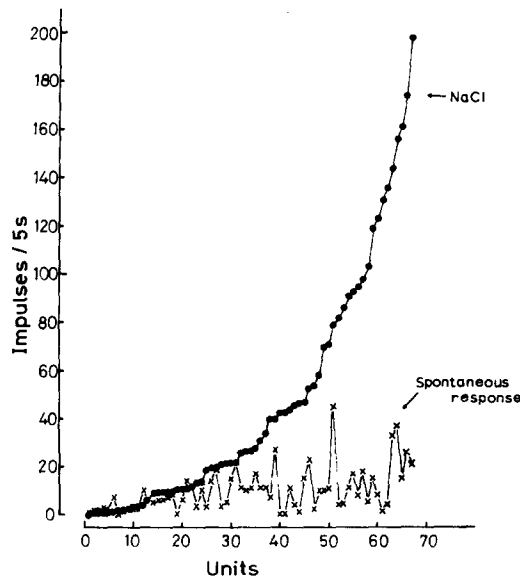


FIGURE 3. Responses to 0.3 M NaCl and spontaneous discharges of 67 monkey chorda tympani fibers, ordered according to the amount of response to NaCl. The spontaneous responses of the fibers are plotted at the same points along the abscissa as their responses to NaCl. Responses to NaCl are expressed by the number of impulses during the initial 5 s.

Spontaneous response magnitude is statistically significantly correlated across fibers with responses to HCl ($r = 0.41$, $P < 0.001$, t test), but not with those to NaCl ($r = 0.20$), sucrose ($r = -0.02$), and quinine ($r = 0.23$). Thus there is some tendency for fibers, which respond well to HCl, to show a large spontaneous discharge rate.

Time-Course of Impulse Discharges

In a majority of the chorda tympani fibers impulse discharges produced by NaCl attained a maximum within a few seconds after stimulation, and subsequently decayed to a plateau level. However, in some fibers impulse discharges were slowly built up after stimulation, reaching a maximum response at several seconds after stimulation. Impulse discharges by the other three stimuli were in general slow in time-course compared with those elicited by NaCl. In order to see the approximate time-course of impulse discharges elicited by the four basic stimuli, the numbers of impulses in individual fibers during the first 5 s after stimulation and the second 5 s are compared with each other. As indicated in Table II, the mean number of impulses elicited by NaCl is much greater during the first than during the second 5 s, but for sucrose and HCl it is only a little greater, and for quinine, a little smaller, during the first 5 s. When the numbers of fibers responding to each stimulus with 20 impulses or more are compared for the initial and second 5-s periods, a greater number of fibers elicited a stronger response to NaCl during the first 5 s, but the numbers of fibers showing a greater response magnitude for sucrose, HCl, and quinine are nearly equal for both 5-s periods.

Differential Sensitivity to the Four Basic Stimuli

As in other mammals, many chorda tympani fibers of macaque monkeys responded to more than one of the four basic taste stimuli. For example many fibers sensitive to NaCl responded well to HCl and sometimes to su-

TABLE 11
COMPARISON OF THE MAGNITUDES OF RESPONSES TO THE FOUR
BASIC STIMULI BETWEEN THE FIRST AND SECOND 5-S PERIODS

	Mean numbers of impulses in 67 fibers		Numbers of fibers responding to one of the four basic stimuli with 20 impulses or more		
	N_{1-5}	N_{6-10}	$N_{1-5} > N_{6-10}$	$N_{1-5} < N_{6-10}$	$N_{1-5} = N_{6-10}$
0.3 M NaCl	47.8±49.8	36.2±40.8	31	12	
0.3 M Sucrose	29.7±43.4	26.8±32.2	17	15	
0.01 M HCl	29.8±35.5	27.3±27.2	18	17	
0.003 M Quinine	23.5±43.1	26.6±57.0	10	11	1

N_{1-5} and N_{6-10} represent the numbers of impulses elicited during the first and second 5-s periods after stimulation, respectively.

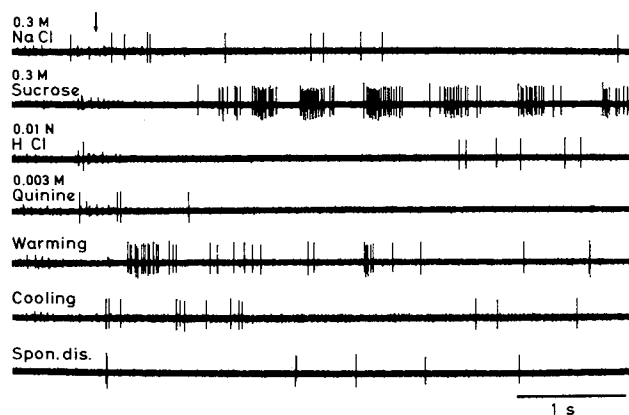


FIGURE 4. Impulse discharges in a single chorda tympani fiber of a crab-eating monkey, produced by 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, 0.003 M quinine hydrochloride, 20°C warming, and 20°C cooling. The bottom trace indicates spontaneous discharges. The arrow represents time of application of stimuli.

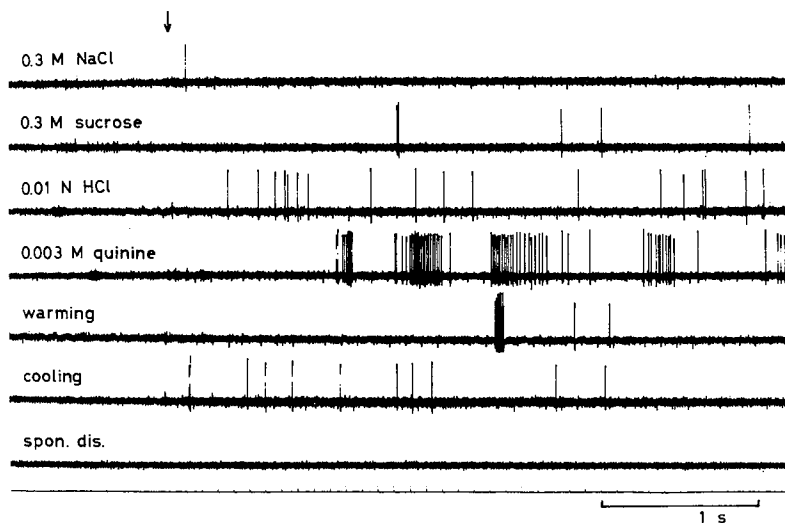


FIGURE 5. Impulse discharges in a single chorda tympani fiber of a crab-eating monkey, produced by 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, 0.003 M quinine hydrochloride, 20°C warming, and 20°C cooling. The bottom trace indicates spontaneous discharges. The arrow represents time of application of stimuli.

crose and quinine. However, most fibers highly responsive to either sucrose or quinine responded poorly to the remaining three stimuli. Examples of impulse discharges elicited by the four basic taste stimuli and thermal stimuli in two fibers are shown in Figs. 4 and 5. The unit shown in Fig. 4 responded highly to sucrose with a regular bursting impulse pattern, which had often been observed in impulse discharges by sucrose and saccharin in chorda

tympani fibers of rats and hamsters (Sato et al., 1969; Ogawa et al., 1974), but far less to the other three taste stimuli. The unit shown in Fig. 5 responded massively to quinine with bursts of impulses but far less to the other three stimuli. Both units responded also to thermal change.

Response profiles of 67 fibers for the four basic stimuli are presented in Fig. 6. As shown in the figure, most of the units sensitive to NaCl responded to HCl as well but poorly to sucrose and quinine. On the other hand, units sensitive to sucrose or quinine responded little to the other three stimuli. Such differential sensitivity to sucrose or quinine in monkey taste fibers can be quantitatively demonstrated in Table III by the correlation coefficients between amounts of responses to the four basic stimuli across 67 fibers. Although there is a statistically significant positive correlation between responses to NaCl and HCl, no significant correlation exists between other pairs of the four basic stimuli. Sucrose response is negatively correlated with

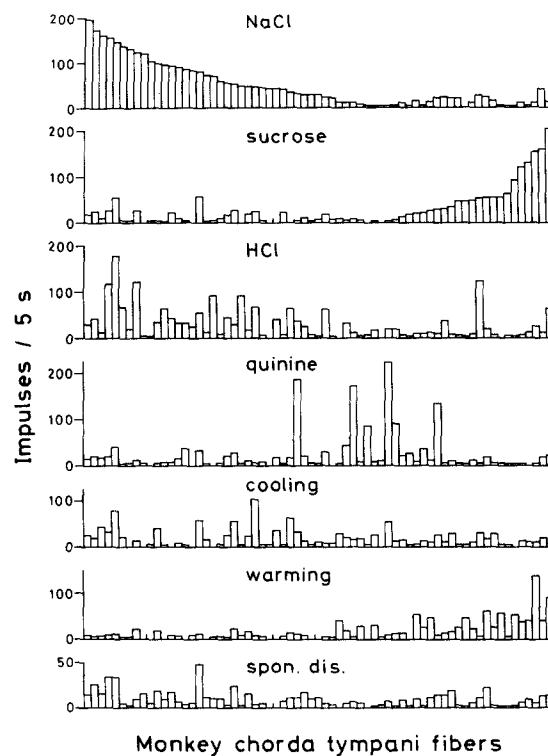


FIGURE 6. Response profiles of 67 monkey chorda tympani fibers for 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, 0.003 M quinine, cooling (20°C water to 40°C tongue) and warming (40°C water to 20°C tongue). Each block represents the number of impulses elicited during the initial 5 s of stimulation in an individual fiber. Fibers were arranged approximately in the order of responsiveness to NaCl in the left-hand side and in the order of responsiveness to sucrose in the right-hand side. Bottom, spontaneous discharge.

TABLE III
CORRELATION COEFFICIENTS BETWEEN AMOUNTS OF RESPONSES TO
THE FOUR BASIC STIMULI ACROSS 67 FIBERS

	NaCl	HCl	Quinine	Spontaneous discharge
0.3 M Sucrose	-0.23	0.04	-0.13	-0.02
0.3 M NaCl		0.45*	-0.18	0.20
0.01 M HCl			-0.02	0.41*
0.003 M Quinine				0.23

* $P < 0.001$ (t test).

Correlations were based on the numbers of impulses during first 5 s of stimulation.

NaCl and quinine responses, and quinine response is also negatively correlated with NaCl and sucrose responses, though none of these correlations is high and statistically significant.

Responsiveness of Chorda Tympani Fibers to the Four Basic Stimuli

According to the criterion described in the Methods, i.e. 5% tolerance limit, responsiveness of individual chorda tympani fibers of macaque monkey to the four basic stimuli was determined and distribution of the sensitivities among 67 fibers was examined. The number of fibers thus assumed to be responsive to either one of the four basic stimuli is shown in Table IV: The largest number of fibers, i.e. 66% of the total population, was responsive to NaCl, 55% to HCl, 48% to sucrose, and the smallest number (33%) to quinine. Also using the above criterion, 23 fibers out of 67 were found to be responsive to one, 24 to two, 16 to three, and 4 to all the four basic stimuli.¹

The number of fibers responding to pairs of the four basic stimuli is shown in Table V. As indicated in the table, 29 fibers among 67, which is about twice the number of fibers responsive to the other pairs, respond to both NaCl and HCl. This is consistent with the finding described in the preceding section that responses to NaCl and HCl across fibers are correlated significantly with each other.

Classification of Fibers According to Their Highest Responsiveness

Since most fibers responded best with higher frequency of response to one of the four basic stimuli, 67 fibers were classified into four classes, depending

¹ When responsiveness of individual fibers to the four basic stimuli was determined by the 1% tolerance limit, the number of NaCl-, sucrose-, HCl-, and quinine-sensitive fibers is 47, 37, 40, and 27, respectively, and the number of fibers responsive to one, two, three, and four kinds of stimuli becomes 16, 26, 17, 8. Alternatively, one may determine responsiveness of fibers by using as a criterion the mean + SD, as was done by Ogawa et al. (1968). In this case the number of NaCl-, sucrose-, HCl-, and quinine-sensitive fibers is 55, 41, 47, and 31, respectively, and the number of fibers responsive to one, two, three, and four kinds of stimuli becomes, 12, 18, 22, and 15, respectively, thus giving less specific sensitivity to fibers.

TABLE IV
NUMBER OF UNITS RESPONDING TO EACH OF SIX KINDS OF TASTE
AND THERMAL STIMULI IN 67 UNITS

Stimuli	Number*	Proportion
0.3 M NaCl	44	0.657
0.3 M Sucrose	32	0.478
0.01 M HCl	37	0.552
0.003 M Quinine	22	0.328
40°C water to 20°C tongue	28	0.418
20°C water to 40°C tongue	20	0.299

* Responsiveness of units to a given stimulus was determined by the criterion: When the magnitude of response to a particular stimulus exceeded the 5% tolerance limit, the unit was assumed to be responsive to a given stimulus.

TABLE V
NUMBERS OF UNITS RESPONSIVE TO PAIRS OF STIMULI AND
PROBABILITY OF INDEPENDENT OCCURRENCE OF RESPONSES
TO A PAIR OF STIMULI

Stimuli	Observed numbers	Expected numbers	Chi-square test*
NaCl, sucrose	16	21.0	0.01 < P < 0.05 †
NaCl, HCl	29	24.3	0.01 < P < 0.05 §
NaCl, quinine	11	14.4	0.05 < P
Sucrose, HCl	15	17.7	0.05 < P
Sucrose, quinine	10	10.5	0.05 < P
HCl, quinine	15	12.2	0.05 < P
Cooling, NaCl	21	18.4	0.05 < P
Cooling, sucrose	12	13.4	0.05 < P
Cooling, HCl	17	15.5	0.05 < P
Cooling, quinine	15	15.5	0.05 < P
Cooling, warming	9	8.4	0.05 < P
Warming, NaCl	7	13.1	P < 0.01 †
Warming, sucrose	17	9.6	P < 0.01 §
Warming, HCl	9	11.0	0.05 < P
Warming, quinine	9	6.6	0.05 < P

* See Siegel, 1956.

† Responses to a pair of stimuli are not independent of each other. Units that respond well to NaCl do not respond to sucrose and warming, and *vice versa*.

§ Responses to a pair of stimuli are not independent of each other. Units that respond well to either one of the pair also respond well to the other of the pair.

Expected numbers were calculated from the data shown in Table IV.

on their highest sensitivity to each of the stimuli during the first 5 s, as done by Frank (1973, 1974). The number in each class of fibers and the mean spontaneous discharge rate is shown in Table VI. The number of each class of fibers, determined from the number of impulses during the second 5 s in each fiber, yields a slightly different number of fibers belonging to each class from that determined from the first 5-s data, but the results are essentially

TABLE VI
FIBERS RESPONDING BEST TO ONE OF THE FOUR BASIC STIMULI
AND THEIR MEAN RATE OF SPONTANEOUS DISCHARGE

	No. of fibers	Mean spontaneous discharge rate (\pm SD)
Salt-best fibers	29 (27)	11.8 \pm 10.5
Sucrose-best fibers	16 (20)	8.4 \pm 13.3
HCl-best fibers	10 (8)	10.8 \pm 8.9
Quinine-best fibers	11 (12)	5.6 \pm 4.1

Numerals outside and inside parentheses represent the numbers of fibers, determined from the number of impulses during the first and second 5 s of stimulation, respectively. One fiber responded best to NaCl and quinine during the first 5 s, and therefore this was omitted from the number.

similar for both sets of determinations. In Table VI, the mean rate of spontaneous discharges in quinine-best and sucrose-best fibers is smaller than the one in the other two classes of fibers, but the difference is not statistically significant.

Samples of response profiles of 20 chorda tympani fibers are presented in Fig. 7 in a similar manner to that adopted by Frank (1973): In the figure five fibers most sensitive to NaCl, sucrose, HCl, and quinine are demonstrated. They are some of the more and less sensitive in each of the categories. Other fibers showed similar patterns of response profiles. Many salt-best fibers responded second best to HCl, and many acid-best fibers second best to NaCl. Also some of the sucrose-best fibers responded second best to NaCl, and some quinine-best fibers second best to HCl, but the magnitude of responses of the latter two classes of fibers to NaCl or HCl are small compared with sucrose or quinine response.

Response profiles of the four classes of fibers, represented by mean numbers of impulses for each stimulus, are shown in Fig. 8. The Fig. 8 *a* was obtained from 66 fibers and *b* from 37 fibers whose response to Na saccharin was examined. Sucrose- and quinine-best fibers responded very little to the other three stimuli and showed relatively high selective sensitivity to sucrose and quinine, respectively. On the other hand, salt-best fibers responded second best to HCl with a magnitude of about one-third NaCl response, and acid-best fibers yielded a second-best response to NaCl which is more than one-half HCl response.

Concentration-Response Functions for the Four Basic Stimuli and Saccharin

Responses to NaCl solutions of varying concentrations were examined in six fibers, those for sucrose, HCl, and quinine in two fibers each, and in most of these fibers concentration-response functions for Na saccharin were also studied. The concentration-response relations for sucrose, NaCl, and Na

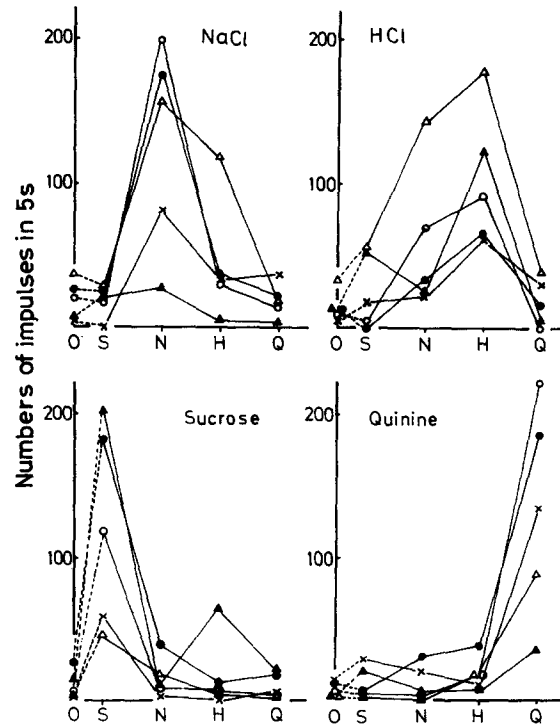


FIGURE 7. Response profiles of 20 monkey chorda tympani fibers across the basic taste stimuli: Five fibers each which responded most to 0.3 M sucrose (S), 0.3 M NaCl (N), 0.01 M HCl (H), and 0.003 M quinine hydrochloride (Q). The response measure is the number of impulses in the first 5 s of stimulation. The number of impulses at point 0 represents the magnitude of spontaneous discharge in each fiber.

saccharin in two fibers are presented in Fig. 9, one unit being best responsive to sucrose among the four basic stimuli (*a*), and the other to NaCl (*b*). In both *a* & *b* the magnitudes of responses to sucrose and NaCl during the first 5 s increased almost linearly with a logarithmic increase in concentration, and reached a saturated value at 0.3 M sucrose and 0.1 M NaCl, respectively. The threshold concentrations for sucrose and NaCl in these units are about 0.03 and 0.001 M, respectively. These are in approximate agreement with those shown in the whole chorda tympani (Ogawa et al., 1972).

In the sucrose-best fiber shown in Fig. 9 *a* the threshold concentration for Na saccharin is about 0.0001 M, which agrees well with the threshold determined in the whole nerve (Ogawa et al., 1972). In this unit the response magnitude increased with increasing concentration up to 0.003 M, and declined with a further increase in the concentration, showing a maximum at 0.003 M. Below the optimum concentration the saccharin concentration eliciting a response magnitude equal to that for sucrose is about 2 log units below the sucrose concentration. On the other hand, in the unit predominantly

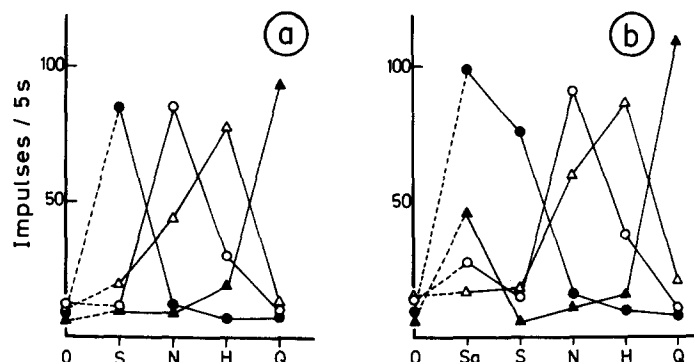


FIGURE 8. (a) Mean response profiles of monkey chorda tympani fibers across the four basic stimuli. The fibers were divided into four groups: those that responded best to 0.3 M sucrose (\bullet , $n = 16$), 0.3 M NaCl (\circ , $n = 29$), 0.01 M HCl (Δ , $n = 10$), and 0.003 M quinine (\blacktriangle , $n = 11$). (b) Mean response profiles of the four classes of monkey chorda tympani fibers across the four basic stimuli and 0.01 M Na saccharin. The number of sucrose-best (\bullet), salt-best (\circ), acid-best (Δ), and quinine-best (\blacktriangle) fibers is 9, 18, 5, and 5, respectively. In both *a* and *b* the number of impulses at point 0 represents the magnitude of mean spontaneous discharge in each class of fibers. S, N, H, Q and Sa denote sucrose, NaCl, HCl, quinine, and Na saccharin, respectively.

responsive to NaCl, the magnitude of response to Na saccharin increased in parallel with that for NaCl, and reached a saturated value at 0.1 M (Fig. 9 *b*).

The concentration-response relations for HCl, quinine, and NaCl in two fibers, one which responded best to HCl and the other to quinine, are demonstrated in Fig. 10. The threshold concentrations for HCl and quinine in the units shown in Fig. 10 are a little less than 0.001 and 0.0002 M, respectively. These are in approximate agreement with the observations in the whole chorda tympani (Ogawa et al., 1972). These two fibers responded also to NaCl, but less than to HCl or quinine, and the threshold for NaCl is high compared with that of the unit shown in Fig. 9 *b*. The response to quinine in the unit shown in Fig. 10 *b* becomes sharply increased in magnitude with an increase in concentration above 0.003 M. This quinine-responsive unit also responded well to Na saccharin, the threshold for which being about 0.003 M.

As shown in Figs. 9 and 10, the spontaneous discharges were reduced by subthreshold stimuli. Such reduction of spontaneous discharges by subthreshold stimuli was also observed in the whole chorda tympani of macaque monkeys (Ogawa et al., 1972).

Responses to Saccharin

In the present experiments responses to 0.01 and 0.3 M Na saccharin were examined in 38 fibers, and those to 0.01 M insoluble saccharin in 41 fibers.

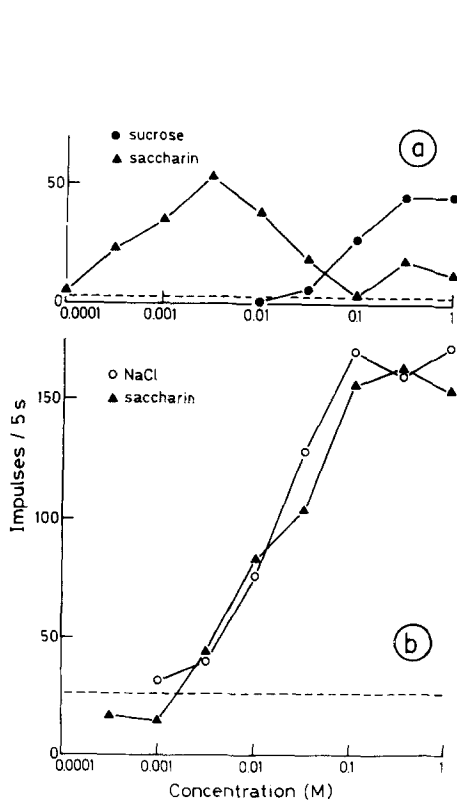


FIGURE 9

FIGURE 9. Concentration-response relations for sucrose and Na saccharin in a monkey chorda tympani fiber (fiber no. 6-2-71) predominantly responsive to sucrose (a), and for NaCl and Na saccharin in a fiber (fiber no. 10-22-69B) predominantly responsive to NaCl (b). The magnitude of response indicated is the number of impulses during the first 5 s. Dashed line in each figure represents the amount of spontaneous discharge.

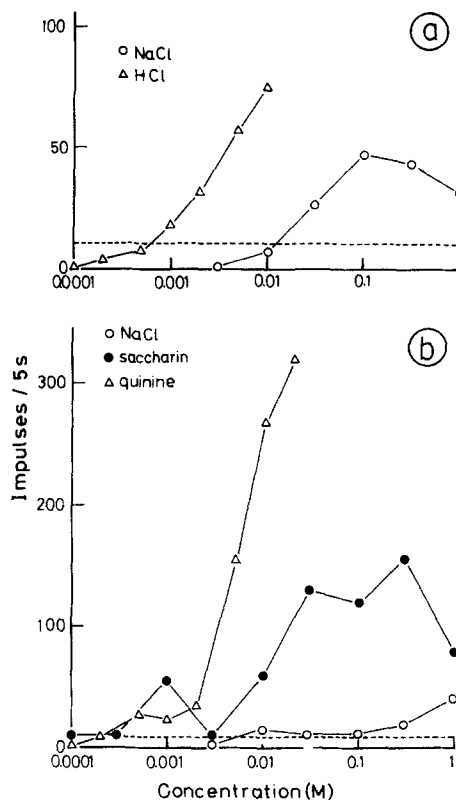


FIGURE 10

FIGURE 10. Concentration-response relations for NaCl and HCl in a monkey chorda tympani fiber responding best to HCl (fiber no. 10-22-69A), and for NaCl, quinine hydrochloride, and Na saccharin in a fiber (fiber no. 10-20-71A). Dashed line in each figure represents the amount of spontaneous discharge.

All the sucrose-best, and quinine-best fibers responded to 0.01 M Na saccharin, and in addition, 16 out of 18 salt-best fibers, and 4 out of 5 acid-best fibers yielded responses to 0.3 M Na saccharin, probably because the latter were also responsive to NaCl. Fig. 11 demonstrates impulse discharges produced by the four basic stimuli, Na saccharin and insoluble saccharin in two units, one (small spike) predominantly responsive to sucrose and the other (large spike) to quinine. The former scarcely responded to NaCl, HCl, and quinine, but responded well to sucrose, Na saccharin, and insoluble saccharin. In this unit response to 0.3 M saccharin is smaller than that to

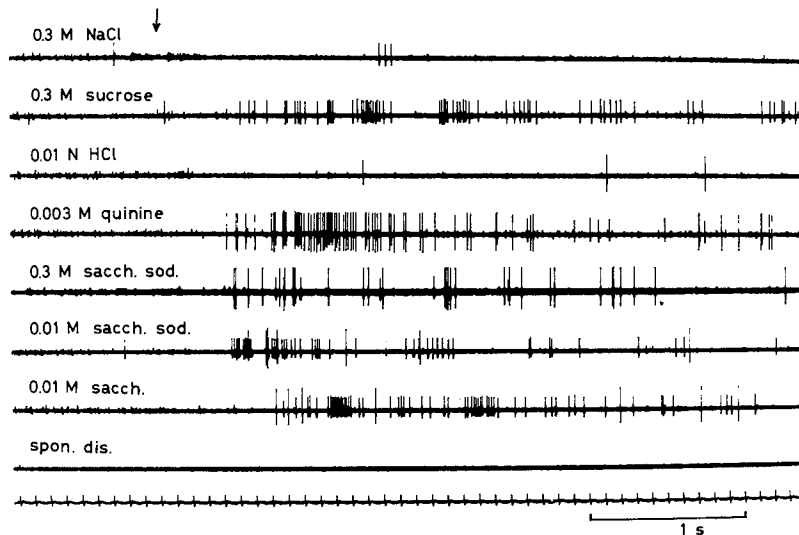


FIGURE 11. Impulse discharges produced by 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, 0.003 M quinine hydrochloride, 0.3 M and 0.01 M Na saccharin, and 0.01 M insoluble saccharin in two monkey chorda tympani fibers, one being a sucrose-best fiber (small spike) and the other a quinine-best (large spike). The arrow represents the moment of application of stimuli.

0.01 M, as can be expected from the concentration-response function shown in Fig. 9 *a*. On the other hand, the quinine-best fiber in Fig. 11 did not respond to the other three basic stimuli, and responded better to 0.3 M than to 0.01 M Na saccharin.

Fig. 8 *b* shows the effect of 0.01 M Na saccharin on the four basic classes of fibers ($N = 37$). As shown in this figure, the sucrose-best fibers yielded the largest response to saccharin among the four classes of fibers, the quinine-best fibers a response which is about one-half of the response in the former, and the salt-best fibers a response which is less than one-third of the response in the first group of fibers.

Correlation coefficients between the responses to saccharin solutions and those for the four basic stimuli across 30–32 fibers are shown in Table VII. Responses to 0.01 M saccharin and insoluble saccharin are significantly and positively correlated with those to 0.3 M sucrose ($r = 0.82$, $P < 0.001$, t test), but no significant correlation was found between saccharin response and response to quinine, HCl, or NaCl, although a slight negative correlation exists between saccharin response and NaCl response.

When saccharin concentration was increased to 0.3 M, the correlation between saccharin response and NaCl response became positive and statistically significant ($r = 0.63$, $P < 0.001$). On the other hand, the correlation between saccharin response and sucrose response became small and

statistically not significant ($r = 0.21$, $P < 0.05$). Changes in the across-fiber correlation coefficients with increase in saccharin concentration may be attributed to the following two facts: (a) decrease in impulse frequency produced by Na saccharin in fibers highly responsive to sucrose, as shown in Fig. 9 *a*, and (b) increase in impulse frequency in fibers highly responsive to NaCl due to high concentration of sodium in 0.3 M Na saccharin.

Correlation coefficients based on the numbers of impulses during the second 5-s period after stimulation are also presented in Table VII. They are mostly

TABLE VII
ACROSS-FIBER CORRELATION COEFFICIENTS BETWEEN RESPONSES
TO THE FOUR BASIC STIMULI AND SWEET-TASTING SUBSTANCES

	Coefficients based on numbers of impulses during initial 5-s period				
	<i>N</i>	0.3 M Sucrose	0.3 M NaCl	0.01 M HCl	0.003 M Quinine
0.01 M Na saccharin	32	0.82*	-0.27	-0.22	-0.02
0.01 M Insoluble saccharin	32	0.72*	-0.24	0.03	0.00
0.3 M Na saccharin	30	0.21	0.63*	0.25	0.00
0.003 M Dulcin	32	0.71*	-0.11	0.07	-0.13
0.1 M Pb acetate	31	0.72*	0.04	0.34	-0.04
0.1 M Na cyclamate	31	0.21	0.74*	0.24	-0.25
	Coefficients based on numbers of impulses during second 5-s period				
0.01 M Na saccharin	32	0.84*	-0.14	-0.09	0.09
0.01 M Insoluble saccharin	32	0.68*	-0.05	0.39‡	0.04
0.3 M Na saccharin	30	-0.02	0.75*	0.36‡	0.19
0.003 M Dulcin	32	0.85*	-0.11	0.25	-0.10
0.1 M Pb acetate	31	0.58*	-0.07	0.60*	0.06
0.1 M Na cyclamate	31	0.19	0.80*	0.42	-0.08

* $P < 0.001$.

‡ $0.01 < P < 0.05$ (*t* test).

N: Number of fibers, on which calculation of coefficients was based.

the same as those obtained from the numbers of impulses during the first 5-s period, but in addition response to 0.3 M saccharin is positively correlated with responses to HCl and quinine during the second 5-s period, although the correlation is not very high.

Responses to Dulcin, Pb Acetate, and Na Cyclamate

Responses to 0.003 M dulcin, 0.1 M Pb acetate, and 0.1 M Na cyclamate were examined in 34, 33, and 32 fibers, respectively, and in one unit, which was exclusively responsive to sucrose among the four basic stimuli, concentration-response relations for dulcin and Na cyclamate were determined. These are shown in Fig. 12, in which the threshold concentration for dulcin is a little above 0.0001 M and that for Na cyclamate 0.001 M. These values are a little lower than those estimated from the whole chorda tympani nerve

responses (Ogawa et al., 1972). The number of impulses in individual fibers produced by 0.003 M dulcin, 0.1 M Pb acetate, 0.1 M Na cyclamate are shown in the scattergrams in Fig. 13 in relation to that produced by 0.3 M sucrose. As shown in this figure, in general, sucrose-best fibers responded better to 0.003 M dulcin and 0.1 M Pb acetate. Therefore, as shown in Table VII, the responses to dulcin and Pb acetate are significantly ($P < 0.001$, t test) and positively correlated with those for sucrose ($r = 0.71$ and 0.72 , respectively), but not significantly with those for the other three basic stimuli. However, in Table VII responses to Na cyclamate are significantly and positively correlated with those to NaCl, but not significantly with sucrose response, though there is a small positive correlation between the two. This situation can be seen more in detail in the scattergram in Fig. 13, where the salt-best fibers responded to 0.1 M Na cyclamate more highly than did the sucrose-best fibers. Therefore, the concentration of Na cyclamate employed in the present experiment is considered to be too high.

Responses to Salts and Acids

Responses of 31 chorda tympani fibers to 0.3 M chloride salts with different cations were recorded, and the number of impulses elicited during the first 5-s period of stimulation in individual units is shown in Fig. 14. As shown in this figure, fibers sensitive to NaCl responded to LiCl to a similar extent, but not to the other five salts. On the other hand, KCl, NH_4Cl , CaCl_2 , MgCl_2 , and SrCl_2 yielded a response pattern similar to each other. The order of effectiveness of the salts, estimated from the mean impulse numbers, is $\text{LiCl} \doteq \text{NaCl} > \text{CaCl}_2 > \text{MgCl}_2 \doteq \text{SrCl}_2 > \text{NH}_4\text{Cl} > \text{KCl}$. This order is in essential agreement with that determined from the whole chorda tympani nerve response (Ogawa et al., 1972). Based on the response profiles to the four basic stimuli, acid-best fibers responded best to KCl and NH_4Cl ; salt-

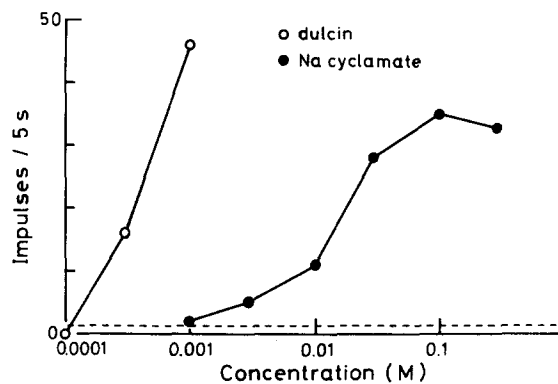


FIGURE 12. Concentration-response relations for dulcin (○) and Na cyclamate (●) in a monkey chorda tympani fiber, predominantly responsive to sucrose (fiber no. 12-15-71).

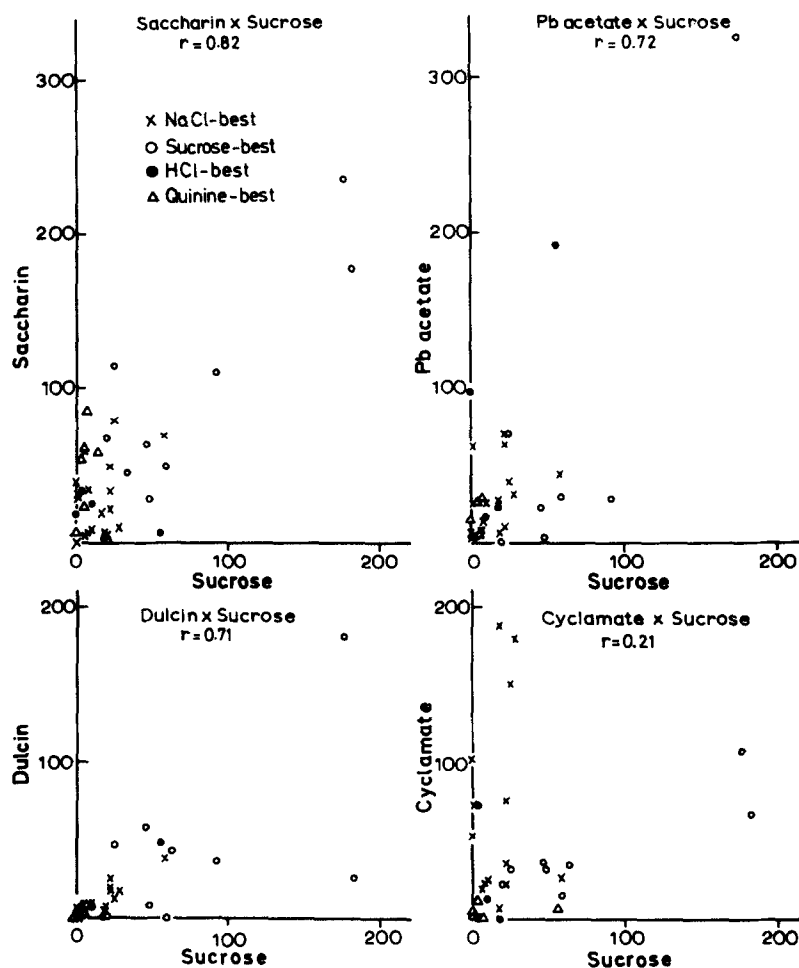


FIGURE 13. Scatterplots for responses (number of impulses in 5 s) of 30–32 monkey chorda tympani fibers to 0.01 M Na saccharin, 0.1 M Pb acetate, 0.003 M dulcin, 0.1 M Na cyclamate, and 0.3 M sucrose. r : Across-fiber correlation coefficients.

best fibers were next, but quinine-best and sucrose-best fibers scarcely responded to these two salts.

Correlation coefficients between responses to the salts and those for the four basic stimuli across 30–31 fibers are shown in Table VIII. Response to LiCl is highly correlated with that to NaCl, and correlations between the latter and responses to SrCl₂ and MgCl₂ are also significant. Responses to salts are all correlated with HCl response but not at all with quinine response. Responses to most of the salts are not correlated with those to sucrose, although a significant positive correlation is seen between NH₄Cl response and sucrose response.

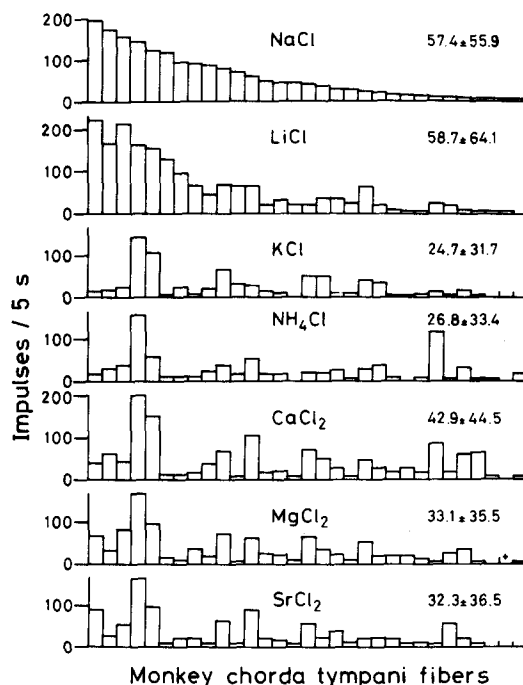


FIGURE 14. Response profiles of 31 monkey chorda tympani fibers for seven kinds of 0.3 M salts. Numerals indicate the mean number (\pm SD) of impulses elicited by each stimulus during the initial 5-s period of stimulation. +: lack of data.

TABLE VIII
ACROSS-FIBER CORRELATION COEFFICIENTS BETWEEN RESPONSES
TO THE FOUR BASIC STIMULI AND VARIOUS SALTS AND ACIDS

	Coefficients based on numbers of impulses during first 5-s period				
	<i>N</i>	0.3 M NaCl	0.3 M Sucrose	0.01 M HCl	0.003 M Quinine
0.3 M LiCl	31	0.95*	-0.02	0.64*	-0.10
0.3 M KCl	31	0.40‡	0.14	0.81*	-0.06
0.3 M NH ₄ Cl	31	0.29	0.56§	0.63*	-0.06
0.3 M CaCl ₂	31	0.37‡	0.28	0.65*	0.02
0.3 M MgCl ₂	30	0.57§	0.04	0.76*	0.00
0.3 M SrCl ₂	31	0.56§	0.05	0.66*	0.12
0.01 M Tartaric acid	26	0.52§	0.21	0.89*	-0.04
0.02 M Acetic acid	29	0.10	0.75*	0.46‡	-0.12
	Coefficients based on numbers of impulses during second 5-s period				
0.01 M Tartaric acid	26	0.33	0.51§	0.84*	-0.05
0.02 M Acetic acid	29	0.29	0.55§	0.84*	-0.15

* $P < 0.001$.

‡ $0.01 < P < 0.05$.

§ $0.001 < P < 0.01$ (*t* test).

Good responses to 0.02 M acetic acid and 0.01 M tartaric acid were obtained in fibers responsive to HCl. The mean magnitudes of responses to these acids are 26.4 ± 32.4 impulses/5 s (26 fibers) and 18.8 ± 19.0 impulses/5 s (29 fibers), respectively, as compared with 36.3 ± 33.9 for 0.01 M HCl (\pm SD). Correlation between the responses to tartaric acid and to HCl across fibers is statistically significant ($r = 0.89$, $P < 0.001$), and that between acetic acid and HCl calculated from the number of impulses during the second 5 s is highly significant ($r = 0.84$), although it is not very high ($r = 0.46$) during the first 5-s period (Table VIII). Responses to tartaric and acetic acids are both correlated with sucrose response ($r = 0.51$ and 0.55 , respectively) during the second 5 s, but neither of them possesses any correlation with quinine response. There is a significant positive correlation between response to tartaric acid and NaCl response, while the correlation between responses to NaCl and to acetic acid is low.

Responses to Thermal Stimulation of the Tongue

As shown in Figs. 4, 5, and 6, many fibers responded to either cooling or warming, or both. The number of fibers responsive to either cooling or warming, determined by the 5% tolerance limit, is about 40 and 30% of the total population, respectively (Table IV). The number of impulses discharged during the initial 5 s of cooling or warming the tongue by 20°C amounted to nearly 100 in a few units, but it is not high in most of the units. The mean thermal sensitivity in 28 units responsive to cooling was -1.4 impulses/5 s°C, while that in 20 units responsive to warming was 2.1 impulses/5 s°C. Such thermosensitive properties of macaque monkey chorda tympani fibers are very similar to those of hamster chorda tympani fibers: The average thermal sensitivities are -2.2 impulses/5 s°C in hamster fibers sensitive to cooling and 3.3 impulses/5 s°C in those sensitive to warming (Ogawa et al., 1968).

The number of impulses discharged is dependent on temperature of water applied to the tongue. Examples of relations between temperature of water applied and the number of impulses during the initial 5 s after thermal change are presented in Fig. 15. In one unit (filled circles) lowering of temperature yielded increase in the number of impulses elicited, while in another unit (open circles) the number of impulses discharged was increased by a rise in temperature. Both units responded to taste stimuli as well; the former was responsive to all the four basic stimuli, while the latter to sucrose only. In these units impulse discharges at temperature either above or below 25°C were reduced below the spontaneous discharge level, respectively. Thermal sensitivities in these units are -3.3 impulses/5 s°C and 4.4 impulses/5 s°C, respectively.

A significant positive correlation ($r = 0.41$, $P < 0.001$, t test) was found

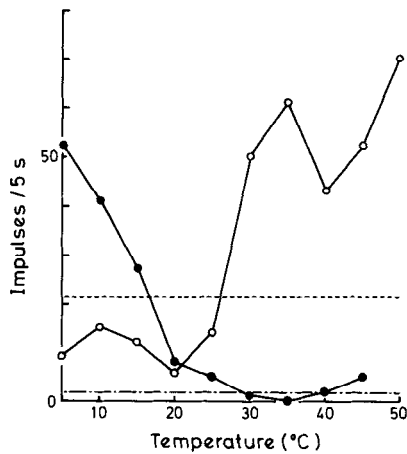


FIGURE 15

FIGURE 15. Relationships between temperature of water applied to the tongue at 25°C and the number of impulses elicited during the initial 5-s period of stimulation. Filled circles indicate responses to cooling in fiber 10-20-71A, while empty circles indicate responses to warming in fiber 10-7-71. The lower broken line represents the mean spontaneous discharge level in the former unit (1.8/5 s), while the upper dashed line the similar level in the latter (22/5 s). Both units responded to taste stimuli: The number of impulses elicited by 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, and 0.003 M quinine during the initial 5-s period were 54, 16, 46, and 19 in the former and 22, 53.5, 19, and 17 in the latter, but the latter is considered to be responsive to sucrose only because of the high rate of spontaneous discharges.

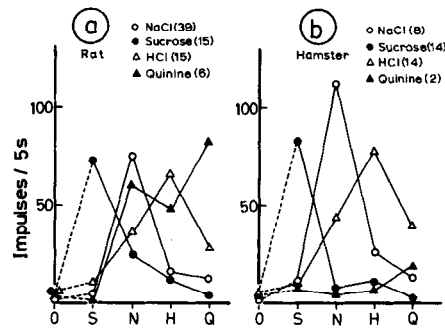


FIGURE 16

FIGURE 16. Mean response profiles of the four categories of chorda tympani fibers of rats (a) and hamsters (b) across the four basic stimuli: 0.5 M sucrose (S), 0.1 M NaCl (N), 0.01 M HCl (H), and 0.02 M quinine hydrochloride (Q). The number of impulses at point 0 represents the magnitude of mean spontaneous discharge in each class of fibers. Data from Ogawa et al. (1968, 1969).

between responses to cooling and spontaneous discharges (Table IX). However, no correlation was obtained between response to warming and spontaneous response magnitude ($r = -0.08$), or between responses to cooling and warming ($r = -0.01$).

As demonstrated in Fig. 6 and Table V, fibers that responded better to sucrose yielded a greater response to warming while those responsive to NaCl do not respond to warming. As indicated in Table IX, there is a highly significant positive correlation between responses to sucrose and warming across fibers ($r = 0.75$, $P < 0.001$, t test), but a significant negative correlation exists between responses to NaCl and warming ($r = -0.38$, $0.001 < P < 0.01$). On the other hand, there is a highly significant positive correlation between responses to cooling and NaCl ($r = 0.47$, $P < 0.001$) and a significant correlation between responses to cooling and HCl ($r = 0.39$, $0.001 < P < 0.01$). Response to quinine is correlated with neither cooling nor warming. Therefore, it can be said that fibers sensitive to sucrose tend

TABLE IX
CORRELATION COEFFICIENTS BETWEEN TASTE AND THERMAL STIMULI
ACROSS 67 FIBERS

	Cooling (−20°C)	Warming (+20°C)
NaCl	0.47*	−0.38‡
Sucrose	0.21	0.75*
HCl	0.39‡	−0.11
Quinine	0.03	−0.13
Spontaneous discharge	0.41‡	−0.08

* $P < 0.001$.

‡ $0.001 < P < 0.01$.

All the coefficients were based on numbers of impulses during the first 5 s of stimulation in 67 fibers.

to respond to warming, while fibers sensitive to NaCl or HCl tend to respond to cooling, but quinine-sensitive fibers scarcely possess sensitivity to thermal stimuli. These are also reflected in the results shown in Table V.

DISCUSSION

The results of the present experiments on afferent impulse discharges in single chorda tympani fibers of crab-eating monkeys confirm in general the earlier report by Ogawa et al. (1972) on the whole chorda tympani response. For example, many monkey chorda tympani fibers respond well not only to the stimuli representing the four basic tastes but also to saccharin, dulcin, and Na cyclamate with the thresholds comparable with those determined in the whole nerve, and the order of the mean magnitude of responses to 0.3 M chloride salts in single fibers, $\text{Li} \doteq \text{Na} > \text{Ca} > \text{Sr} \doteq \text{Mg} > \text{NH}_4 > \text{K}$, is the same as that determined from the whole chorda tympani.

Fiber Types and Response Characteristics of Macaque Monkey Chorda Tympani Fibers

Recently Frank (1973, 1974) and Pfaffmann (1974) classified individual chorda tympani fibers of hamsters and squirrel monkeys into four categories salt-best, sucrose-best, acid-best, and quinine-best fibers, according to their highest responsiveness to NaCl, sucrose, HCl, and quinine. In the present experiment also, each chorda tympani fiber of the macaque monkey was found to respond most to one of the four basic stimuli, and therefore the monkey chorda tympani fibers were classified similarly into the four categories. One of the great differences between our results on macaque monkeys and those by Frank on hamsters and squirrel monkeys is that 17% of all the macaque monkey fibers responded best to quinine, while only a few quinine-best fibers were sampled by Frank (1973, 1974) in squirrel monkeys

and hamsters.² Also, in the macaque monkeys quinine-best and sucrose-best fibers are relatively specifically responsive to quinine and sucrose, respectively.

Since responses to taste and thermal stimuli in 28 chorda tympani fibers of hamsters and 50 fibers of rats had been recorded previously by Ogawa et al. (1968, 1969), classification of 28 hamster chorda tympani fibers and 75 rat fibers³ into four categories according to their best sensitivity to the four basic stimuli was made for comparison. The number of each class of fibers in each animal is shown in Table X. In the rat salt-best fibers are largest in number, while in the hamster sucrose-best fibers are largest, but in both animals a small number of quinine-best fibers is present.

In order to compare the response profiles of chorda tympani fibers in macaque monkeys with those in hamsters and rats, the mean response profiles of the four classes of fibers in the latter animals are presented in Fig. 16. As shown in this figure, quinine-best fibers in rats do not specifically respond to quinine, but do respond equally well to NaCl and HCl; in both rats and hamsters acid-best fibers show a good response to quinine. Sucrose-best fibers in rats respond to NaCl with a magnitude which is about one-third of the size of sucrose response, though those in hamsters possess relatively high specific sensitivity to sucrose. In both animals salt-best and acid-best fibers respond well to HCl and quinine, and to NaCl and quinine, respectively. Therefore, specific sensitivity to each of the four basic stimuli, especially to quinine and sucrose, is less developed in rats and hamsters than in macaque monkeys.

Gordon et al. (1959) reported that some fibers in the rhesus monkey respond very specifically to sucrose as well as to other sweet-tasting substances, and that there exists a fiber which responds to both quinine and saccharin but not to sucrose. The results demonstrated in the present experiments are consistent with the finding by Gordon et al. (1959): In crab-eating monkeys, not only sucrose-best and salt-best fibers but also quinine-best fibers respond well to saccharin (Fig. 8 *b* and Fig. 11). Since sucrose- and quinine-sensitive fibers in the monkey respond rather specifically to sucrose (and other sweet-tasting substances) and to quinine, respectively, the former fibers mediate primarily a taste quality comparable with "sweet" taste in humans while the latter fibers a taste quality comparable with "bitter" taste. If so, responses to saccharin in quinine-best fibers in the monkey may explain the mechanism of bitter aftertaste in saccharin taste in humans (Rader et al., 1967).

² Noma and Sato (1974), in their paper on the difference in responses of single hamster chorda tympani fibers to sugar anomers, presented response characteristics of four sucrose-best, one salt-best, one acid-best, and two quinine-best fibers, indicating the presence of four categories of fibers in the hamster.

³ After publication of the paper by Ogawa et al. (1968), responses in 25 rat chorda tympani fibers were recorded by the same authors, and therefore these were added to the published data.

TABLE X
NUMBER OF CHORDA TYMPANI FIBERS RESPONDING BEST TO ONE OF THE
FOUR BASIC STIMULI IN RATS, HAMSTERS, AND MONKEYS

Fiber class	Rat*	Hamster*	Macaque monkey‡
Salt-best fibers	39 (52%)	8 (29%)	29 (44%)
Sucrose-best fibers	15 (20%)	14 (50%)	16 (24%)
Acid-best fibers	15 (20%)	4 (14%)	10 (15%)
Quinine-best fibers	6 (8%)	2 (7%)	11 (17%)
Total	75	28	66

* The basic stimuli: 0.1 M NaCl, 0.5 M sucrose, 0.01 M HCl, and 0.02 M quinine hydrochloride (Ogawa et al., 1968, 1969).

‡ The basic stimuli: 0.3 M NaCl, 0.3 M sucrose, 0.01 M HCl, 0.003 M quinine hydrochloride.

For the squirrel monkey NH_4Cl and KCl are more effective taste stimuli than NaCl (Snell, 1965; Frank, 1974). However, the present study has revealed that NH_4Cl and KCl are less effective than NaCl and LiCl for the macaque monkey, and that responses to NH_4Cl and KCl are very significantly correlated with those to HCl but not significantly with those to NaCl , indicating that acid-best fibers respond better to KCl and NH_4Cl than do salt-best fibers. Therefore, the macaque monkey chorda tympani fibers are different from the squirrel monkey fibers in the properties of salt-sensitive fibers.

*Distribution of Sensitivities to the Four Basic Taste Stimuli in
Chorda Tympani Fibers*

In rats and hamsters sensitivities to the four basic stimuli (0.1 M NaCl, 0.5 M sucrose, 0.01 M HCl, and 0.02 M quinine) are not randomly distributed among chorda tympani fibers. Sensitivity to HCl tends to occur with that to quinine in the rat and hamster, and responses to NaCl and quinine tend to occur together with each other in the hamster. In both rats and hamsters, higher sensitivity to NaCl is associated with lower sensitivity to sucrose, and vice versa (Ogawa et al., 1968; Sato et al., 1969). Frank (1973) also reported in her study on hamster chorda tympani fibers that sucrose sensitivity is combined little with other sensitivities, and sensitivities to NaCl, HCl, and quinine are correlated significantly with one another. As described in the Results, sensitivities to the four basic taste stimuli in macaque monkey fibers are correlated little with one another, although a significant correlation exists between responses to NaCl and HCl.

Assuming that sensitivity to one stimulus is independent of that to the other, probabilities of occurrences of responses, and therefore the numbers of fibers responsive to pairs of stimuli or combinations of stimuli could be calculated (Frank and Pfaffmann, 1969; Ogawa et al., 1968). The numbers of fibers responding to six pairs of the four basic stimuli expected from such a model

are shown in Table V. As shown in this table, the observed numbers of fibers responsive to NaCl and sucrose are too small, and those of fibers responsive to NaCl and HCl are too many compared with the expected numbers. The difference could not be explained unless there is a dependency between sensitivities to NaCl and sucrose, and between those to NaCl and HCl; that is, fibers responsive to NaCl tend to respond to HCl but not to sucrose.

Discrimination of Taste Quality in Macaque Monkeys

Since most chorda tympani fibers in mammals respond to more than one kind of stimulus, it has been proposed that the stimulus quality is coded by the response pattern across many neurons. Therefore, any pairs of stimuli which show similar response profiles across many neurons produce a similar taste, while those which give different profiles taste different (Erickson et al., 1965; Ganchrow and Erickson, 1970). The similarity or dissimilarity of pairs of response profiles is represented by the correlation coefficient of the number of impulses in unit time across neurons, and discriminability of taste stimuli, determined behaviorally, has been found to be reciprocally related to the correlation coefficient magnitude (Marshall, 1968). In the macaque monkey chorda tympani correlation coefficients across 67 fibers between any pairs of responses to the four basic stimuli are low, even the highest correlation between NaCl and HCl responses is only 0.45. Such low correlation magnitudes indicate that in macaque monkeys each of the four basic stimuli is distinctly different in quality from the remaining three stimuli.

As argued by Frank (1973), if the basic taste stimuli are considered to be prototypes of four basic tastes in macaque monkeys, then correlations between their taste profiles and that of any other stimulus measures the extent to which that stimulus represents the basic qualities. The taste profiles for 14 stimuli are illustrated in Fig. 17. Taste profiles for each of the four basic stimuli are quite different. Taste profiles for 0.01 M Na saccharin, 0.003 M dulcin, and 0.1 M Pb acetate are all alike and similar to that for sucrose, although Pb acetate possesses a small positive correlation with HCl. Taste profiles for 0.3 M Na saccharin and 0.1 M Na cyclamate are different from those for sucrose, but show a high correlation with NaCl and low correlation with sucrose and HCl, suggesting different qualities from those of sucrose or 0.01 M Na saccharin. The reason for such a "salty" quality of 0.3 M Na saccharin and 0.1 M Na cyclamate is, as stated in the Results, mainly due to a dominant activity of NaCl-sensitive fibers resulting from the presence of a high concentration of sodium ions.

Taste profiles for KCl, NH_4Cl , CaCl_2 , MgCl_2 , and SrCl_2 are different from those for LiCl and NaCl. The first five salts show a large "sour" component and a moderate salty component. All the salts possess no bitter component. This is different from the situation in rats (Sato et al., 1969) and

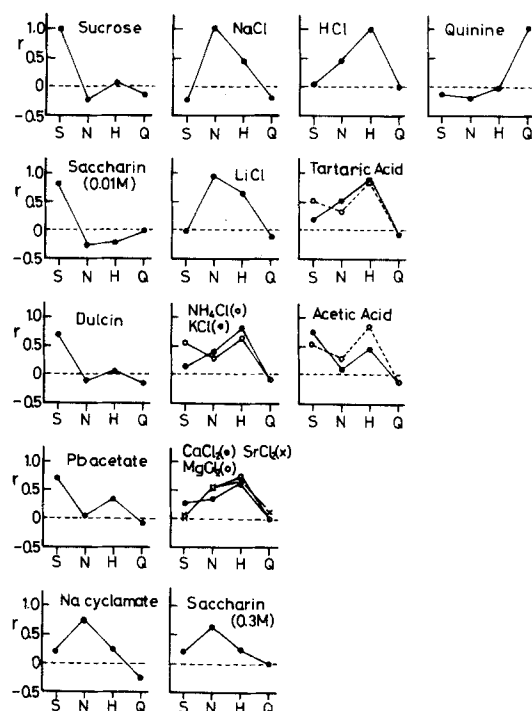


FIGURE 17. Correlation taste profiles of varying taste stimuli across the four basic tastes: 0.3 M sucrose (S), 0.3 M NaCl (N), 0.01 M HCl (H), and 0.003 M quinine hydrochloride (Q). The taste stimuli are 0.3 M sucrose, 0.01 M Na saccharin, 0.003 M dulcin, 0.1 M Pb acetate, 0.1 M Na cyclamate, 0.3 M NaCl, 0.3 M LiCl, 0.3 M NH_4Cl (KCl), 0.3 M CaCl_2 (MgCl_2 , SrCl_2), 0.3 M Na saccharin, 0.01 M HCl, 0.01 M tartaric acid, 0.02 M acetic acid, and 0.003 M quinine hydrochloride. The r 's plotted are across-fiber correlation coefficients between responses to the test stimulus and to one of the four basic stimuli.

hamsters (Frank, 1973), where a high positive correlation was obtained between some salt and quinine responses.

Tartaric acid shows a taste profile similar to that for HCl, while the profile for acetic acid shows a large sweet component and a moderate sour component, as shown in Fig. 17. However, when the across-fiber correlation coefficients during the second 5-s period are examined (Table VIII), both acids show a similar taste profile, in which a sour component is highest, a sweet component is next highest, and there is a small salty component, but no bitter component.

Changes in correlation taste profiles with time can also be noted for 0.01 and 0.3 M Na saccharin: Saccharin begins to show a moderate amount of bitter component during the second 5-s period (Table VII), which probably is reflected in its bitter taste in humans (Rader et al., 1967). Also Pb acetate is more sweet during the first 5 s, but becomes more sour during the second

5-s period (Table VII). These are the only examples indicating changes in taste correlations over time.

Significance of Thermal Response in Gustatory Nerve Fibers

In the macaque monkey chorda tympani fibers, responses to warming are positively and significantly correlated with those to sucrose but negatively with those to NaCl, while responses to cooling are positively and significantly correlated with those to NaCl and HCl (Table IX). As also indicated in Table V, responsiveness to thermal and gustatory stimuli in macaque monkey fibers is not randomly distributed, but the number of fibers responsive to both warming and sucrose is too large and the number of fibers responsive to both warming and NaCl is too small to be accounted for by the assumption that sensitivity to warming is independent of that to sucrose or NaCl. Such properties of macaque monkey taste nerve fibers are rather akin to those of hamster chorda tympani fibers, in which responses to cooling are highly correlated with those to HCl while responses to warming are significantly correlated with those to sucrose (Ogawa et al., 1968). On the other hand, taste nerve fibers of macaque monkeys are different from those of rats in which response to warming is almost absent and that to sucrose is relatively small, though the rat fibers responsive to HCl and quinine are sensitive to cooling. Therefore, it would appear that in mammals whose sensitivity to sucrose is highly developed their chorda tympani fibers are likely to respond to warming of the tongue.

Physiological significance of the role of impulses produced by warming and cooling in macaque monkey chorda tympani fibers cannot definitely be stated here, but they would possibly mediate a taste quality somewhat related to that produced by sucrose and that by NaCl and HCl, respectively. Békésy (1964), based on psychophysical experiments, demonstrated that sensations on the human tongue are separated into two groups, bitter, warm, sweet versus sour, cold, salty, two sensations in each group interacting with one another. In the present study of macaque monkey chorda tympani fiber responses the four basic taste stimuli and thermal stimuli may be grouped, based on across-fiber correlations, into two or three groups; the first group consists of NaCl (salty), HCl (sour), and cooling (cold), the second sucrose (sweet) and warming (warm), and third quinine (bitter). Except for quinine, the grouping of six stimuli is in good agreement with the grouping of six human tongue sensations by Békésy.

The authors are grateful to Dr. A. Noma for kind assistance in experiments and to Professor C. Pfaffmann for reading the manuscript.

This work was supported by research grants from the Ministry of Education in Japan (Grant Nos. 91006, 92491, 811009 and 911109).

Received for publication 20 January 1975.

REFERENCES

- BEIDLER, L. M., I. Y. FISHMAN, and C. W. HARDIMAN. 1955. Species differences in taste responses. *Am. J. Physiol.* **181**:235.
- BÉKÉSY, G. VON. 1964. Duplexity theory of taste. *Science (Wash. D. C.)*. **145**:834.
- BROUWER, J. N., G. HELLEKANT, Y. KASAHARA, H. VAN DEL WEL, and Y. ZOTTERMAN. 1973. Electrophysiological study of the gustatory effects of the sweet proteins Monellin and Thaumatin in monkey, guinea pig and rat. *Acta Physiol. Scand.* **89**:550.
- CARPENTER, J. A. 1956. Species differences in taste preferences. *J. Comp. Physiol. Psychol.* **49**:139.
- ERICKSON, R. P., G. S. DOETSCH, and D. A. MARSHALL. 1965. The gustatory neural response function. *J. Gen. Physiol.* **49**:247.
- FISHER, G. L., C. PFAFFMANN, and E. BROWN. 1965. Dulcin and saccharin taste in squirrel monkeys, rats and men. *Science (Wash. D. C.)*. **150**:506.
- FISHMAN, I. Y. 1959. Gustatory impulses of the white-faced ringtail monkey. *Fed. Proc.* **18**:45.
- FRANK, M. 1973. An analysis of hamster afferent taste nerve response functions. *J. Gen. Physiol.* **61**:588.
- FRANK, M. 1974. The classification of mammalian afferent taste nerve fibers. *Chem. Sens. Flav.* **1**:53.
- FRANK, M., and C. PFAFFMANN. 1969. Taste nerve fibers: A random distribution of sensitivities to four tastes. *Science (Wash. D. C.)*. **164**:1183.
- GANCHROW, J. R., and R. P. ERICKSON. 1970. Neural correlates of gustatory intensity and quality. *J. Neurophysiol.* **33**:768.
- GLASER, D. 1972. Die Reaktionen bei einigen Primaten auf zwei künstliche Süsstoffe und H₂O dest. *Folia Primatol.* **18**:433.
- GORDON, G., R. KITCHELL, L. STRÖM, and Y. ZOTTERMAN. 1959. The response pattern of taste fibers in the chorda tympani of the monkey. *Acta Physiol. Scand.* **46**:119.
- JOHNSON, P. O. 1949. *Statistical Methods in Research*. Prentice-Hall, Inc., Englewood Cliffs, N. J.
- MARSHALL, D. A. 1968. A comparative study of neural coding in gustation. *Physiol. Behav.* **3**:1.
- NAGAKI, J., S. YAMASHITA, and M. SATO. 1964. Neural response of cat to taste stimuli of varying temperatures. *Jap. J. Physiol.* **14**:67.
- NOMA, A., and M. SATO. 1974. Taste effectiveness of anomers of sugars and glycosides as revealed from hamster taste responses. *Comp. Biochem. Physiol.* **48A**:249.
- OGAWA, H., M. SATO, and S. YAMASHITA. 1968. Multiple sensitivity of chorda tympani fibers of the rat and hamster to gustatory and thermal stimuli. *J. Physiol. (Lond.)*. **199**:223.
- OGAWA, H., M. SATO, and S. YAMASHITA. 1969. Gustatory impulse discharges in response to saccharin in rats and hamsters. *J. Physiol. (Lond.)*. **204**:311.
- OGAWA, H., M. SATO, and S. YAMASHITA. 1974. Variation in gustatory nerve fiber discharge pattern with change in stimulus quality and concentration. *J. Neurophysiol.* **37**:443.
- OGAWA, H., S. YAMASHITA, A. NOMA, and M. SATO. 1972. Taste responses in the macaque monkey chorda tympani. *Physiol. Behav.* **9**:325.
- PFAFFMANN, C. 1955. Gustatory nerve impulses in rat, cat and rabbit. *J. Neurophysiol.* **18**:429.
- PFAFFMANN, C. 1974. Specificity of the sweet receptors of the squirrel monkey. *Chem. Sens. Flav.* **1**:61.
- RADER, C. P., S. G. TIHANYI, and F. B. ZIENTY. 1967. A study of the true taste of saccharin. *J. Food Sci.* **32**:357.
- SATO, M., S. YAMASHITA, and H. OGAWA. 1969. Afferent specificity in taste. In *Olfaction and Taste III*. C. Pfaffmann, editor. The Rockefeller University Press, New York.
- SEIGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Book Co., New York.
- SNELL, T. C. 1965. The responses of the squirrel monkey chorda tympani to a variety of taste stimuli. Thesis for degrees of Master of Science. Brown University, Providence, R. I.
- WEISKRANTZ, L. 1960. Effects of medial temporal lesions on taste preference in the monkey. *Nature (Lond.)*. **187**:879.