Sodium Deprivation Alters Neural Responses to Gustatory Stimuli

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ABSTRACT The effects of sodium deprivation for 10 d, a period sufficient to induce sodium appetite, on gustatory nerve discharges in rats were determined. Chorda tympani responses to concentration series of sodium chloride, sucrose, hydrochloric acid, and quinine hydrochloride were recorded and analyzed without the experimenter knowing the animal's deprivation condition. After deprivation, both whole nerve and single nerve fiber responses to sodium chloride were smaller; NaCl-best fibers, those more responsive to sodium chloride than to sucrose, hydrochloric acid, or quinine, were most affected. Thresholds had not changed; however, slopes of the stimulus-response functions for sodium chloride were lowered. Comparable changes in responses to the other stimuli did not occur. These results were discussed with respect to a possible relationship between changes in sodium chloride responsivity and changes in sodium intake, differences between methods of inducing sodium appetite, coding of taste quality and intensity, and mechanisms which might effect the responsivity change.

INTRODUCTION

In mammals, the amount of sodium in the extracellular fluid must be kept within narrow limits despite a continuous exchange of sodium with the external environment. It is generally assumed that there are two primary mechanisms which have evolved to protect an animal against sodium imbalance (Denton, 1965). Sodium regulation depends upon the release of aldosterone from the adrenal cortex and sodium appetite. Sodium deprivation results in an activation of the renin-angiotensin system which induces an increased secretion of sodium-retaining aldosterone (Davis and Freeman, 1976) which reduces sodium levels in urine, perspiration, and saliva (Ganong, 1971). In addition, sodium deprivation, in many terrestial species, stimulates the specific hunger for sodium known as sodium appetite. A failure of one mechanism can often be compensated for by the other mechanism in order that the animal survive. For example, rats without adrenal glands can survive and remain in relatively good health provided they are allowed to consume extra salt.

C. P. Richter, a pioneer in the investigation of self-regulatory behaviors, studied the behavior of the adrenalectomized rat. Using the relative intake method where water and sodium chloride solutions were simultaneously presented to the animal, Richter found that adrenalectomized rats immediately consumed moderate or strong saline usually rejected by normal rats (Richter,

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1936) and would drink sodium chloride solutions at low concentrations to which intact animals were indifferent (Richter, 1939). Gustatory sensibility seemed to be crucial for the expression of salt appetite; after surgical denervation of the taste receptors on the tongue, several adrenalectomized rats lost the ability to increase their intake of salt and consequently died (Richter, 1956). In fact, Richter and others have provided substantial evidence that the gustatory sense is important both for the initiation and satiation of sodium appetite (Denton, 1965; Nachman and Cole, 1971).

To explain the role gustatory sensibility plays in the salt intake of an adrenalectomized rat, Richter proposed that sodium deficiency might make taste receptors more sensitive to sodium chloride stimulation. Pfaffmann and Bare (1950), however, reported that the concentration of sodium chloride necessary to reliably evoke a discharge of the chorda tympani nerve greater than that evoked by water was the same in intact and adrenalectomized rats. This electrophysiological result was supported by psychophysical studies; when rats were forced to discriminate between distilled water and weak salt solutions (Carr, 1952; Harriman and MacLeod, 1953), normal rats displayed lower detection thresholds than preference thresholds for sodium chloride.

These classical experiments on sodium appetite and sodium chloride thresholds were carried out on adrenalectomized rats, but the results of subsequent experiments were based on dietary induced need. The secretions of the adrenal gland (catecholamines, glucocorticoids, sex hormones, mineralocorticoids) are vital to carbohydrate and protein metabolism, reproduction, resistance to stress, as well as to the maintenance of salt balance and extracellular fluid volume (Ganong, 1971). Sodium deprivation of the intact animal produces a sodium appetite comparable to that following adrenalectomy (Nachman, 1962) but deprivation specifically affects sodium balance. Inasmuch as sodium deprivation more closely approximates that which occurs in nature and has more limited physiological consequences, under most circumstances, it is the method of choice for inducing sodium appetite.

Nachman and Pfaffmann (1963) measured the activity of the total chorda tympani nerve to threshold and suprathreshold concentrations of sodium chloride and several other chemicals. They found that responses to these stimuli, measured relative to the activity evoked by 0.01 M sodium chloride, were the same in normal and sodium deprived rats. More than a decade after this classical observation, however, a peripheral effect of sodium deprivation was observed (Contreras, 1975; 1977). Contreras, recording from single fibers, has shown that there is a decrease in the discharge frequency of chorda tympani units in response to 0.1 M sodium chloride (not to 0.01 N hydrochloric acid, 0.5 M sucrose, or 0.02 M quinine hydrochloride) in rats fed a sodium-free diet for 10 d, sufficient time to induce sodium appetite (Contreras and Hatton, 1975).

Sodium deprivation of normal intact rats was associated with urinary sodium losses averaging 0.37 meq in 10 d which compares with 23.0 meq in the same period for sodium replete rats (Contreras and Hatton,1975). The concentrations of sodium in plasma and plasma protein (an indirect measure of blood volume) were not altered, most likely because the adrenal gland and kidney responded

quickly and efficiently to minimize sodium loss. Bone contains appreciable amounts of sodium, almost as much as the body fluids, which can also be mobilized to counteract obligatory losses due to sodium deprivation (Michell, 1976). An increase in plasma potassium was detected, however, when deprivation was extended to 20 d. Adrenalectomized rats, without sodium retaining aldosterone, rapidly lose sodium in urine and have reduced levels of plasma sodium, reduced blood volume, and elevated levels of plasma potassium (Jalowiec and Stricker, 1973).

The present study was undertaken to determine the effects of sodium deprivation on responses of single chorda tympani neurons of the rat to sodium chloride, hydrochloric acid, sucrose, and quinine hydrochloride from threshold to saturation and to determine whether or not recently discovered reductions in single fiber activity to sodium chloride (Contreras, 1975; 1977) can be detected in whole nerve recordings. Both whole nerve and single fiber recordings were obtained and analyzed without knowledge of the animal's deprivation condition, insuring that biases of the experimenter played no role in the outcome.

METHODS

Subjects

Data were obtained from 67 male albino rats (Sprague-Dawley, 90–120 d old), the data from 19 of which have been previously reported (Contreras, 1977). All animals were individually housed, with food and distilled water *ad libitum,* in a colony room on a 14-10 h light-dark cycle. They were fed a powdered, sodium-free diet (Test Diet, ICN Pharmaceuticals, Inc., Cleveland, Ohio) to which 1 g of sodium chloride crystals was added to 99 g of powder. After being adapted to this diet for at least 5 d, 33 animals were assigned to a sodium-deprived (experimental) group and fed a sodium-free diet for a 9–10-d period, sufficient time to induce sodium appetitie (Jalowiec and Stricker, 1973; Contreras and Hatton, 1975), before being used for chorda tympani recording. The other group of rats (n = 34) were assigned to the control, sodium-replete group. 12 animals from each group were used for whole nerve recording; the remainder were used for single fiber recording. On the day of recording, each animal was weighed and a urine specimen was collected and frozen. Because sodium-deprived rats excrete less sodium (Contreras and Hatton, 1975), analysis of urinary sodium concentration by flame photometry was used to verify diet conditions. Every sodium-deprived animal excreted less sodium than any control animal (t = 26.06, df = 53, $P < 0.001$), but there were no differences in urinary potassium or body weight between the two groups.[1] Also, 10 d of sodium deprivation did not noticeably weaken the rats' physical conditions.

Preparation

Each animal was anesthetized with a fresh solution (36%, wt/vol) of urethane (i.p., 1.1 g/kg of body weight) which was prepared on the day of recording. The trachea was cannulated and body temperature was maintained between 36 and 38°C with a body warmer. The animal's head was held stable with a clamp and the chorda tympani branch of the seventh cranial nerve was dissected free using a mandibular approach. The right

[1] Average body weights were 454.2 and 453.8 g, average losses of urinary potassium were 3.49 and 3.56 meq in 24 h, and average losses of urinary sodium were 2.78 and 0.12 meq in 24 h for control and experimental animals, respectively.

chorda tympani nerve was isolated from the point where it joins the lingual nerve to its exit from the bulla, where it was cut. Either the entire nerve with sheath intact (whole nerve recording) or a small strand separated from the desheathed nerve (single fiber recording) was placed over a nichrome recording electrode. Action potentials were differentially amplified with respect to a similar indifferent electrode positioned in the wound near the nerve. The animal was grounded through the head clamp.

For 48 of the preparations, gravity flow from an overhead funnel and stopcock assembly delivered solutions to the anterior portion of the rat's tongue which was enclosed in a flow chamber (Frank, 1973). An alternative method of flowing solutions over the tongue from a glass faucet was used in 19 preparations (Contreras, 1977). Preliminary tests revealed that the magnitudes of the peak whole nerve responses to chemical stimulation of the tongue by these two methods were similar. A test solution, which flowed for 10–15 s (3 ml/s from the funnel, 0.8 ml/s from the faucet), was followed by a distilled water rinse which flowed (at the same flow rates) over the tongue until (faucet method) or until ~ 10 s before (flow chamber method) the next test solution was presented. Solutions were made of reagent grade chemicals in distilled water (singly distilled, resistivity > 2 MΩcm) and were kept at room temperature (23–26°C).

Whole Nerve Recording

In all of the whole nerve experiments the funnel-flow chamber method of stimulation was used. Stimulation of the nerve included three categories of stimuli that were presented in the following order: (*a*) standards—0.5 M sucrose, 0.1 M NaCl, 0.01 M HCl, and 0.02 M quinine hydrochloride (J. T. Baker Chemical Co., Phillipsburg, N.J.); (*b*) concentration series—0.01–1.0 M sucrose, 0.00003–3.0 M NaCl, 0.00001–0.01 M HCl, and 0.0001–0.003 M quinine hydrochloride; and, in some preparations (*c*) other salts—0.1 M LiCl and 0.1 M KCl. The order of presentation of stimuli (or series) within a category was random. Within a concentration series, stimuli were presented at increasing one-half log steps of molarity. Rinse duration between successive stimulations was at least 1 min but was longer after more concentrated solutions. The total sequence of solutions was presented once for each subject. Occasionally, a portion or the entire sequence was repeated due to a change in amplification setting or alteration in nerve sensitivity or position on electrode.

Responses of the whole nerve were monitored with an oscilloscope and audiomonitor and stored on magnetic tape. These responses, comprised of impulses from many neurons, were fed through a resistor-capacitor circuit "integrator" (time constants: 0.6 s, rise; 2.6 s, fall) and a running average of neural activity was displayed on a stripchart recorder (for a sample record, see Fig. 1). Because the preparation deteriorates in time, the magnitude of the integrated response to a particular stimulus (either 0.1 M KCl or 0.1 M NaCl) was used to monitor the stability of a preparation. Mineral oil was placed over the nerve to prolong the duration of stable recording. Two measures of whole nerve activity after stimulation were taken from the strip-chart records: one was the maximum pen deflection (in chart units) above an estimated prestimulation level, and the second was the pen deflection, above the same prestimulation level, at ~ 10 s after the beginning of the response. The first is a measure of the initial peak neural discharge and the second a measure of the later tonic neural discharge.

Altered conditions from one preparation to another, or sometimes while recording from one preparation, required changes in amplifier gain settings.[2] Variation in baseline neural activity during continuous water flow was reflected in small variations in

[2] Of the 24 whole nerve preparations, the four with the smallest peak responses to 0.1 M NaCl were not included in further analyses: two were from experimental and two were from control animals.

recorder pen level. The average range of variation in recorder pen level (maximum minus minimum) during 10-s periods before and after presentation of a category of stimuli was used as a reference. These reference measures did not differ for experimental and control groups: medians for both groups equalled 6.0 chart units. The responses to all other solutions in a category were calculated as ratios to the reference response (see Fig. 1). These ratios might be considered signal-to-noise ratios. This reference was selected over a response to 0.01 M NaCl, or any other test chemical, to prevent obscuring possible differences in the absolute magnitude of the responses of experimental and control nerves. The use of a reference, however, permitted utilization of data from most preparations.

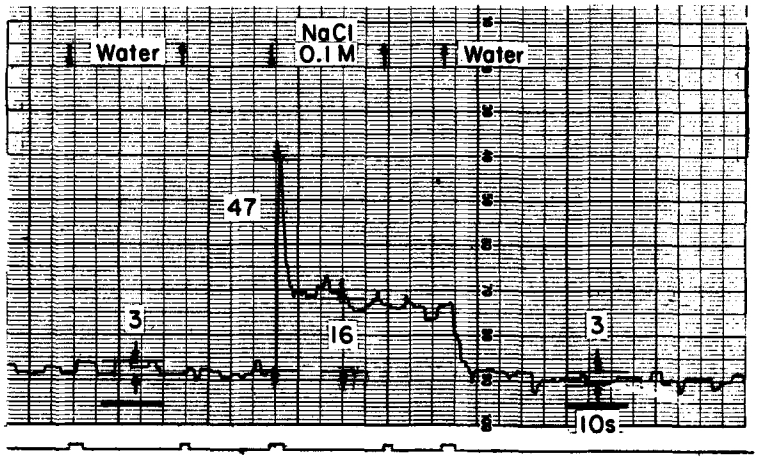

FIGURE 1. Inkwriter record of the summated responses of the whole chorda tympani nerve of the rat to water and 0.1 M NaCl. Above this record, downward directed arrows refer to the onset and upward directed arrows refer to the offset of stimulus flow. Stimulus solutions remained in the flow chamber and continued to bathe the taste receptors even after termination of flow. The tonic response to 0.1 M NaCl disappears only after the tongue is washed with distilled water. The reference level was computed for a 10-s period before and after the presentation of test solutions. In this example, the peak response was computed relative to this reference as 47 chart units/3 chart units or 15.7, while the tonic response was 16 chart units/3 chart units or 5.3.

Single Fiber Recording

Four stimuli (0.5 M sucrose, 0.1 M NaCl, 0.01 N HCl, 0.02 M quinine hydrochloride), the same four as the standard solutions used during whole nerve experiments, tested a fiber's sensitivity to the four traditional taste qualities. Stimuli at these molarities had been chosen previously (Contreras, 1977) because the concentrations of sucrose, HCl, and quinine hydrochloride were reported to elicit about the same number of impulses in fibers sensitive to them as 0.1 M NaCl does in fibers sensitive to NaCl (Sato, 1971). Active fibers were detected either by their spontaneous discharges or their responses to stimulation with a mixture of the four standard solutions.

The responses of a total of 133 units, 60 from sodium-deprived animals and 73 from controls, were studied. 90 of these units (39 experimental and 52 control) were stimulated

via the funnel-flow chamber; 42 units (21 in each group) were stimulated via the faucet (Contreras, 1977). The 60 experimental units were sampled from 31 nerves and the 73 control units from 32 nerves. The proportions (total units/total nerves) for the two groups of data were not different ($z = 0.89, P > 0.10$). The data obtained using the two stimulation methods were combined, although there was yet a second major difference in method: in one case the data were obtained without knowledge of the animal's dietary condition; in the other case (Contreras, 1977), the dietary condition was known. These two differences were judged not to be critical because the distributions of responses to each of the four standard solutions or water in the two sets of data did not differ in either mean (t test, P's > 0.05) or variance (F test, P's > 0.05). This was equally true for data obtained from sodium-deprived animals and for data obtained from control preparations.[3]

The stimulation protocol for single fiber recording was similar but not exactly the same as that used for the whole nerve. Because of the variation of the length of time during which the responses of a fiber were identifiable, the NaCl concentration series always immediately followed the presentation of the standard solutions. This was done to increase the probability that this series was included in the fiber's response profile. The order of presentation of the three remaining concentration series was random. The range of NaCl concentrations tested in the single fiber experiments was the same as tested in the whole nerve experiments; however, smaller ranges were tested for sucrose (0.03–0.3 M), HCl (0.0001–0.001 M), and quinine hydrochloride (0.0003–0.003 M) in the single fiber experiments. Also, for all series, concentration was increased by full log steps in the single fiber work. The standard solutions were repeated both before and after presentation of the other salts if a fiber was still functionally isolated. Too few data were obtained from the other salts to warrant their inclusion in the results. Most fibers responded with approximately the same frequency to repeated presentations of a stimulus; responses reported are means when several measures were taken.

The responses of a single fiber were identified by the size, shape, and sound of its impulses on oscilloscope and audiomonitor displays. Tape recorded responses (Magnecord 1028, Telex Communications, Inc., Minneapolis, Minn.) were, afterwards, played back and photographed from oscilloscope traces, and the number of action potentials in the first 10 s of a response were counted. Because response frequencies for all fibers were tabulated without knowledge of the animal's diet condition, for the part of these data not reported previously by Contreras (1977), the possibility of a bias of the experimenter was minimized both during the data acquisition and data analysis phases. As shown in Fig. 2 (a sample response of a single fiber recorded from a strand of chorda tympani), the point in the photographic record where a response began was usually associated with an abrupt change in ongoing activity. A mean spontaneous rate of activity for each fiber was determined by counting the number of impulses occurring during the 2 s preceding every stimulus presentation and dividing their sum by the total number of seconds. This method yielded a rate which was representative of the entire period of study. This spontaneous rate is a measure of the tonic level of activity to water flow in that water was presented before each stimulus; the reference measure used to normalize the whole nerve records is an indicator of variation in that level. A second measure of a fiber's response to water was obtained by presenting water as a stimulus after the tongue

[3] In an effort to obtain unbiased samples, responses of all possible units were counted. This yielded an unusually large number of units that responded at low frequencies. Of these fibers, 18 sampled from control and 15 from experimental animals showed responses of less than four impulses/s for 10 s to any of the standard stimuli. These low responders, mostly (30/33) from the data not reported previously (Contreras, 1977), were excluded from subsequent analyses.

had been rinsed by water for at least 1 min. This measure would include any transient change in activity accompanying the onset of water flow, whereas the spontaneous rate or whole nerve reference measure would not.

RESULTS

Whole Nerve Recording

The functions in Fig. 3 show that the size of the chorda tympani response, either earlier peak (A) or later tonic (B), increases with concentration to all four compounds. The numbers plotted are medians of ratios between responses to the test stimuli and the reference measure of base-line variation (median value of six chart units for both experimental and control preparations).[4] The peak

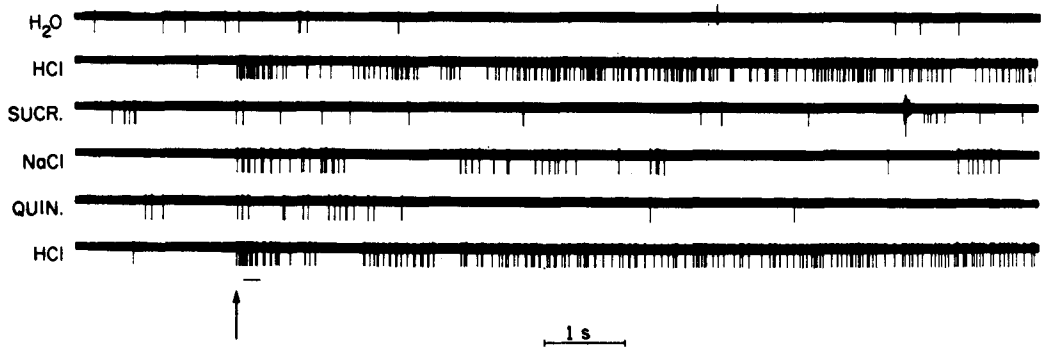

FIGURE 2. Photographs of oscilloscope tracings of one taste fiber's responses to distilled water, 0.01 N HCl, 0.5 M sucrose, 0.1 M NaCl, 0.02 M quinine hydrochloride, and 0.01 N HCl repeated. The arrow indicates the beginning of the response. Activity that appears before response onset was considered part of the fiber's spontaneous response. 12 s of record are shown in each tracing: 2 s before and 10 s of the response. This fiber is an HCl-best fiber because it responds (in terms of number of impulses during 10 s of stimulation) more to HCl than the other stimuli. For this fiber the 10-s responses are (172 + 187)/2 = 179.5 impulses to HCl, 8 impulses to distilled water, 18 impulses to sucrose, 51 impulses to NaCl, and 18 impulses to quinine.

response shows a lower threshold for NaCl, HCl, and quinine than the tonic response. In deprived rats (n = 10) the whole nerve response to NaCl is smaller than in control rats (n = 10). Threshold concentrations of NaCl (0.001 M for peak and 0.01 M for tonic response) do not change but the slopes and maximum responses to NaCl solutions are lower after sodium deprivation. The reduction

[4] A relative response of one indicates that the stimulus evoked a response equal to the reference. Weaker concentrations of some stimuli evoked a response smaller than the reference; this is especially true for the tonic meaure. The peak response was taken as the first upward deflection of the pen (minus estimated prestimulation level) after stimulation whereas the tonic response was taken as the pen level (minus the same prestimulation level) at ~ 10 s after stimulation began. Thus, it was more likely that the peak measure would at least equal the reference inasmuch as a deflection was chosen as the peak; in contrast, the tonic measure was taken at a fixed point in the record.

is statistically reliable over a range of NaCl concentrations (0.03–3.0 M) for both the initial peak and later tonic responses (Chi-square tests, 1-tail P's < 0.05).[5] The response functions for sucrose, HCl, or quinine generated from the sodium-deprived and control animals' nerves do not differ in threshold, slope, or maximum response magnitude. Responses from only four animals in each group were obtained to 0.1 M KCl and 0.1 M LiCl. The median relative responses (peak) to 0.1 M KCl were 9.5 for sodium-deprived rats and 10.5 for controls; whereas the responses to 0.1 M LiCl were 12.5 and 14.3, respectively; differences between experimental and control values are not statistically significant.

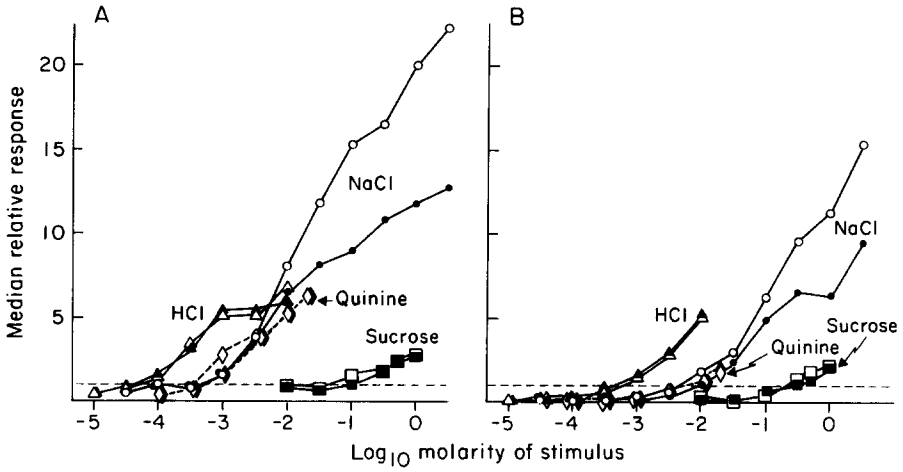

FIGURE 3. The median responses of 10 whole nerves of sodium-deprived (filled symbols) and 10 whole nerves of control (open symbols) rats to a range of concentrations of NaCl, HCl, sucrose, and quinine hydrochloride. Two measures of the summed evoked activity of the nerve were taken: (A) a measure of the peak discharge; (B) a measure of the tonic discharge. The numbers plotted are ratios of evoked responses to a reference level of activity during continuous water flow. A dashed line marks the reference level. Both peak and tonic responses to NaCl (0.03 –3.0 M) are smaller after sodium deprivation.

Single Fiber Recording

In Fig. 4 the responses of 45 single fibers from sodium-deprived and 55 fibers from control rats are rank ordered five different times. They are ordered according to the response frequency (number of impulses elicited in 10 s) to each standard solution (0.5 M sucrose, 0.1 M NaCl, 0.01 N HCl, 0.02 M quinine

[5] Inasmuch as the direction of the effect of sodium deprivation on responses to NaCl was determined previously (Contreras, 1975; 1977) a one-tailed probability is appropriate. Incidentally, the experimenters tried to guess the unknown deprivation state of seven preparations on the basis of the magnitude of the chorda tympani response to NaCl solutions while recording; they were correct six times out of seven. The probability of that occurring by chance is 0.016.

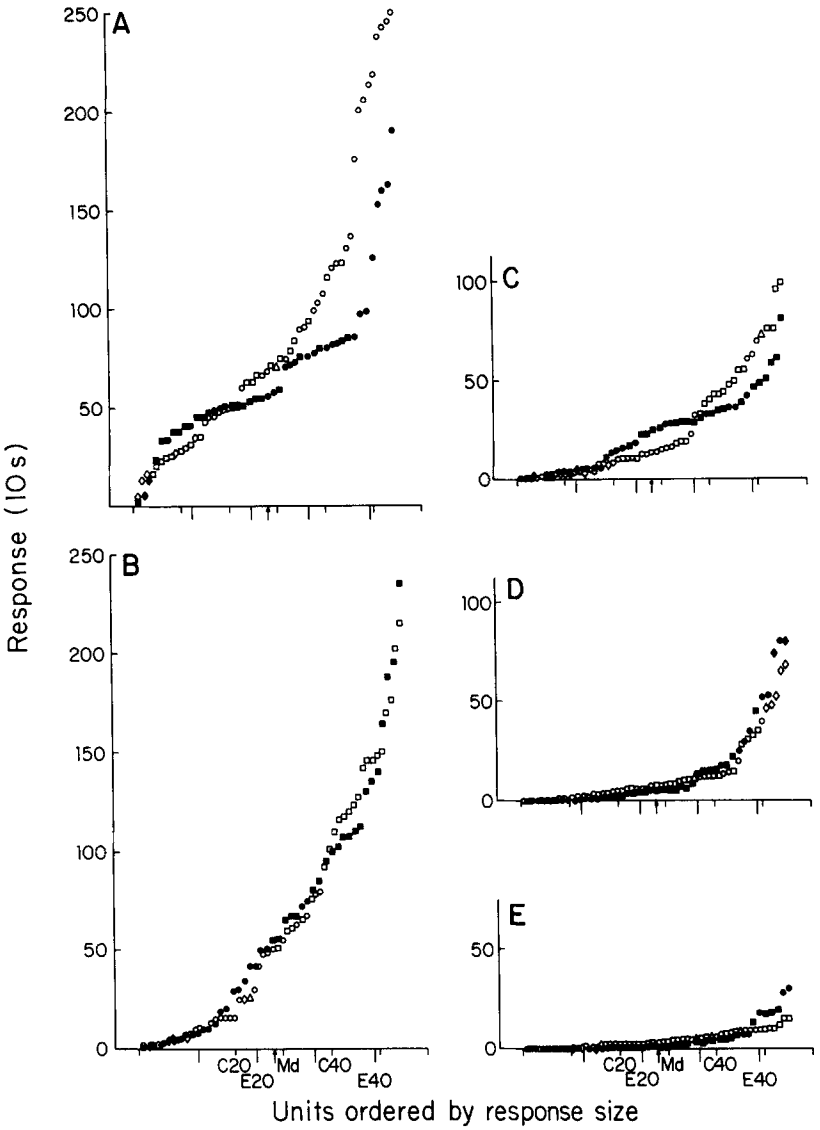

FIGURE 4. Responses of 45 chorda tympani units (*E*'s) from experimental (sodium-deprived—solid symbols) and 55 units (*C*'s) from control (open symbols) rats rank-ordered according to their response frequencies (number of impulses elicited in 10 s) to each standard solution: (A) 0.1 M NaCl; (B) 0.01 N HCl; (C) 0.02 M quinine hydrochloride, (D) 0.5 M sucrose; and (E) water. Position of medians along abscissa is marked *Md*. Unit symbols: (circles) NaCl-best; (squares) HCl-best; (trangles) quinine-best; (diamonds) sucrose-best. The major difference between the fibers sampled from experimental and control rats is in their responses to NaCl, with NaCl-best units from sodium-deprived animals showing lower response frequencies to NaCl as corresponding fibers from controls.

hydrochloride) and water. Overall, Fig. 4 indicates that each stimulus differs in its effectiveness in eliciting responses from chorda tympani fibers of both experimental and control groups. The most effective stimuli are 0.1 M NaCl and 0.01 N HCl because they stimulate a greater number of fibers to a greater degree than the sucrose or quinine solution. For example, response frequencies range from 0 to approximately 80 impulses in 10 s for sucrose stimulation, but the range for HCl is roughly from 0 to 200. The range for quinine is similar to that for sucrose and the range for NaCl is similar to that for HCl. In general, testing with a single concentration of each compound, the effective order across single fibers is NaCl > HCl > quinine > sucrose. This parallels the effective order in whole nerve sensitivity to a wide range of stimulus concentrations (see Fig. 3).

Fibers from sodium-deprived rats differ from fibers from sodium-replete rats in their responses to 0.1 M NaCl; the average response ($t = 1.83$, $df = 98$, $P <$

TABLE I

STATISTICS OF DISTRIBUTIONS OF RESPONSES (10 s) OF SINGLE FIBERS TO STANDARD TASTE STIMULI AND WATER OF CONTROL AND EXPERIMENTAL GROUPS

	Sucrose (0.5 M)	NaCl (0.1 M)	HCl (0.01 N)	Quinine-HCl (0.02 M)	Water
Control ($n = 55$)					
Mean	12.9	88.2*	63.6	24.6	4.1
Variance	281.3	4,627.1*	3,534.5	708.4‡	16.0‡
Experimental ($n = 45$)					
Mean	14.6	67.2*	65.0	23.1	4.9
Variance	476.1	1,577.8*	3,480.1	351.7‡	56.8‡

* Mean or variance difference between experimental and control units is statistically significant ($P < 0.05$, 1-tail; direction established previously [Contreras, 1977]).

‡ Variance difference between experimental and control units is statistically significant ($P < 0.05$, 2-tail).

0.05) and response variance ($F = 2.93$, $df = 44/54$, $P < 0.001$) are smaller in deprived animals' nerves (see Table I). This difference between NaCl response distributions derives from the more responsive fibers, the responses of which occur at the top half of each distribution. Frank (1973) has divided chorda tympani units into four groups according to which of the four standards elicits the largest response, naming them sucrose-best, NaCl-best, HCl-best and quinine-best units. Units in a group tend to have a similar response profile across the four standards as well as across a number of other stimuli. Because mostly NaCl-best fibers produce the responses (circles in Fig. 4) that occur in the top half of the distribution for both groups, it was determined that just the NaCl-best fibers from sodium-deprived animals also generate a smaller response mean ($t = 2.26$, $df = 47$, $P < 0.05$) and a smaller response variance ($F = 3.03$, $df = 21/26$, $P < 0.02$) to 0.1 M NaCl than the corresponding fibers from control

animals (see Table II). The means and variances of responses of HCl-best units to 0.1 M NaCl in the two groups did not differ.

The distribution of responses to 0.5 M sucrose or 0.01 N HCl from the two groups of fibers do not differ in central tendency or variance (Table I). The experimental and control distributions of responses to 0.02 M quinine hydrochloride do not differ in central tendency but there is a larger response variance

TABLE II

STATISTICS FOR RESPONSES (10 s) OF NACl-BEST, HCl-BEST, AND SUCROSE-BEST FIBERS TO THE STANDARD TASTE STIMULI AND WATER

	Sucrose (0.5 M)	NaCl (0.1 M)	HCl (0.01 N)	Quinine-HCl (0.02 M)	Water
NaCl-best units					
Control (n = 27)					
Mean	5.9	129.1*	26.9	15.0	3.5
Variance	71.2‡	5,178.3*	631.4	362.7	12.6‡
Experimental (n = 22)					
Mean	13.9	90.1*	24.0	13.9	4.8
Variance	503.5‡	1,706.3*	505.1	179.2	82.0‡
HCl-best units					
Control (n = 22)					
Mean	11.7	54.6	123.1	39.1	5.1
Variance	101.6	960.3	2,047.4	818.1	21.2
Experimental (n = 21)					
Mean	9.3	48.8	113.9	34.8	5.4
Variance	98.8	402.3	2,389.9	303.8	38.1
Sucrose-best units					
Control (n = 5)					
Mean	56.4‡	18.6	8.0	3.2	2.0
Variance	99.3	142.8	82.0	4.7	5.5
Experimental (n = 2)					
Mean	77.0‡	8.5	3.0	2.0	0.5
Variance	18.0	24.5	2.0	8.0	0.5

* Mean or variance difference between experimental and control units is statistically significant ($P < 0.05$, 1-tail; direction established previously [Contreras, 1977]).

‡ Mean or variance difference between experimental and control units is statistically significant ($P < 0.05$, 2-tail).

in the control group's units ($F = 2.01$, $df = 44/54$, $P < 0.02$). It is of particular importance that there are no differences in either central tendency or variance in the distributions of responses to 0.01 N HCl because this HCl solution and 0.1 M NaCl have more similar response distributions.

Spontaneous firing rate, the rate of tonic activity to water flow during the 2 s before each stimulus presentation, was compared with the rate of response to

water presented as a stimulus. There was no statistically significant difference in the two average response rates in units from either the control or experimental group. Moreover, these two measures were correlated across units: rank-difference correlation coefficients equalled +0.66 for control and +0.70 for experimental units. Thus, spontaneous firing rate and rate of activity to water after water were related measures. The average spontaneous firing rates were 0.41 impulses/s for control and 0.49 impulses/s for experimental fibers; this is not a statistically significant difference. Although the responses to water of the two groups of fibers did not differ in central tendency, response variance was larger for experimental units ($F = 3.55$, $df = 54/44$, $P < 0.02$) as reported in Table I. A greater variance in responses to water of fibers from sodium-deprived rats is also observed when just the NaCl-best units are considered ($F = 6.51$, $df = 26/21$, $P < 0.02$); there are no differences between groups in the responses to water of HCl-best units (see Table II).

Response profiles for 20 different fibers are presented in Fig. 5. These include those that gave the five largest responses to NaCl and those that gave the five largest responses to HCl for both control and experimental groups. The degree to which a rat chorda tympani fiber is specific to HCl or NaCl, at test concentrations, varies from fiber to fiber. Those that respond best to HCl (Fig. 5 II) also respond moderately to NaCl and quinine, but give very weak responses to sucrose. The responses of HCl-best fibers to NaCl, quinine, sucrose, or water of experimental (D) and control (C) groups do not differ in either mean or variance (Table II). Besides the lowered mean response to NaCl in the NaCl-best units, some of these fibers sampled from deprived animals' nerves (Fig. 5 IB) are less specific in that they respond more to sucrose (Fig. 5 IA) or water than comparable fibers from controls. The response variances to sucrose ($F = 7.07$, $df = 26/21$, $P < 0.02$) as well as to water are greater in the experimental group of NaCl-best fibers although the means do not differ from control group means (see Table II).

A general description of the response profiles from all sampled fibers is shown in Fig. 6. Of the 45 fibers in the sodium-deprived group, 22 responded best to NaCl, 21 best to HCl, 2 best to sucrose, and 0 best to quinine. Of the 55 fibers in the control group, the numbers are 27, 22, 5, and 1, respectively. The average profiles (means across all units in a group are plotted) for NaCl-best fibers (Fig. 6 A) show a large difference between groups in response to NaCl; average profiles for HCl-best units (B) are similar for sodium-deprived and control groups; but the profiles for sucrose-best units (C) differ (see Table II), experimental fibers showing a larger response to sucrose ($t = 2.70$, $df = 5$, $P < 0.05$); however, there are very few sucrose-best fibers in the sample. When the response profiles from all sampled fibers from each group are combined (D), only average NaCl responses differ; average responses to the other stimuli overlap.

Fig. 7 is divided into separate graphs showing the average response functions for (A) NaCl-best fibers, (B) HCl-best fibers, and (C) all fibers, regardless of classification, which includes only the NaCl-best and HCl-best because no complete response functions were obtained from sucrose-best units. A response

function for all four chemicals was not necessarily obtained for each fiber; a minimum of 23 and a maximum of 28 different control fibers, or a minimum of 16 and a maximum of 21 different experimental fibers contributed responses toward these average functions for all units. This included 10–15 control and 7–

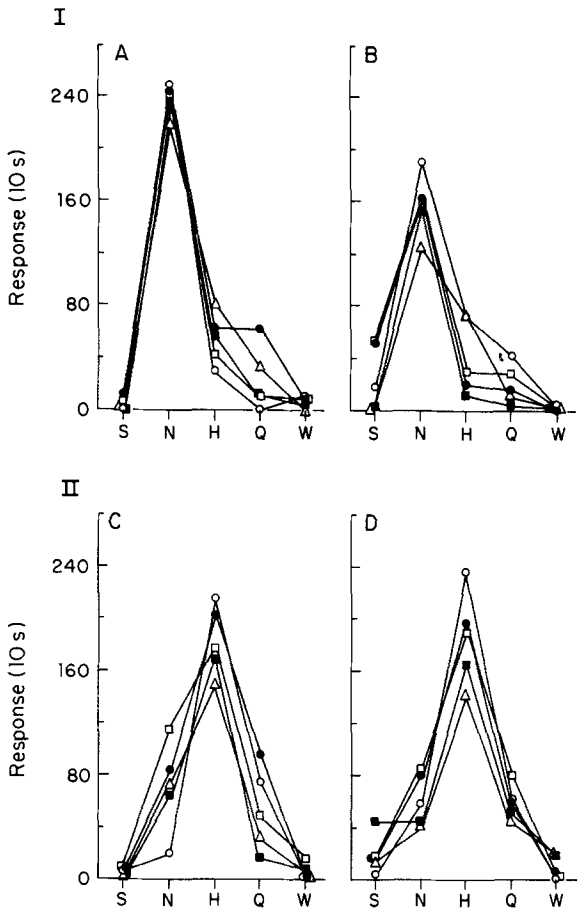

FIGURE 5. Response profiles for 20 different rat chorda tympani units. These units include those that gave the five largest responses to (I) 0.1 M NaCl and those that gave the five largest responses to (II) 0.01 N HCl sampled from control (A, C) or experimental (sodium-deprived—B, D) animals. The points representing the responses of a unit are connected for identification of individual profiles. Along the abscissa, *S* represents 0.5 M sucrose; *N*, 0.1 M NaCl; *H*, 0.01 N HCl; *Q*, 0.02 M quinine hydrochloride; and *W*, distilled water. The response plotted is the number of impulses elicited in 10 s of stimulation.

8 experimental NaCl-best fibers, as well as 13 control and 9–13 experimental HCl-best fibers. There appear to be two prominent groups of fibers in the rat chorda tympani. One group of fibers, the NaCl-best, responds strongly to NaCl and very little, if at all, to the other stimuli. A second group, the HCl-best fibers,

responds strongly to both HCl and NaCl. After sodium deprivation, the NaCl-best units show, on the average, a decreased reactivity to NaCl solutions. Sodium chloride thresholds do not differ (varying between 0.01 M and 0.03 M), but the average responses to a range of suprathreshold NaCl solutions (0.1–3.0 M) are smaller in the experimental NaCl-best fibers than in control NaCl-best

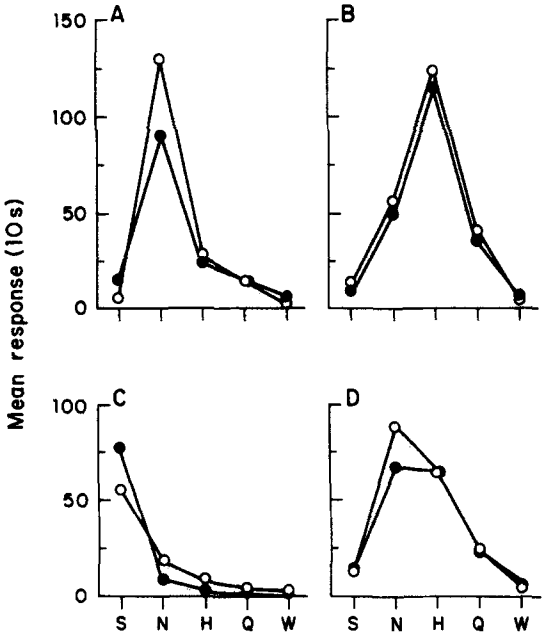

FIGURE 6. Average response profiles for (A) NaCl-best, (B) HCl-best, (C) sucrose-best, and (D) all fibers sampled from the rat chorda tympani. Solid symbols refer to profiles from sodium-deprived animals and open symbols refer to profiles from controls. Along the abscissa, *S* represents 0.5 M sucrose; *N*, 0.1 M NaCl; *H*, 0.01 N HCl; *Q*, 0.02 M quinine hydrochloride; and *W*, distilled water. The numbers plotted are means of responses (the number of impulses elicited in 10 s of stimulation) of 45 fibers in the sodium-deprived group (22 responding best to NaCl, 21 best to HCl, 2 best to sucrose, and 0 best to quinine) and of 55 fibers in the control group (27 responding best to NaCl, 22 best to HCl, 5 best to sucrose, and 1 best to quinine). Units from sodium-deprived rats responded to NaCl with a lower mean impulse frequency than units from controls (considering just NaCl-best (A) or all units (D)), whereas responses to sucrose (C) had a higher mean impulse frequency in sodium-deprived preparations.

fibers (Chi-square = 6.01, $df = 1$, $P < 0.05$). However, HCl-best fibers from sodium-deprived rats responded more to 3.0 M NaCl than comparable fibers from control rats (Mann-Whitney $U = 29.5$, n's = 10 and 13, $P < 0.05$). Incidentally, if responses to 0.3 M or 3.0 M NaCl, rather than 0.1 M, had been used to classify experimental fibers, 10 of the 12 fibers classified as being HCl-best would have been NaCl-best. In contrast, only 2 of the 13 control units

would have been classified differently had responses to the stronger NaCl solutions been used for classification.

Only NaCl-best and HCl-best fibers contributed responses to the average response functions for all units (Fig. 7 C). However, because of the preponderance of these two types typically sampled from the chorda tympani of the rat

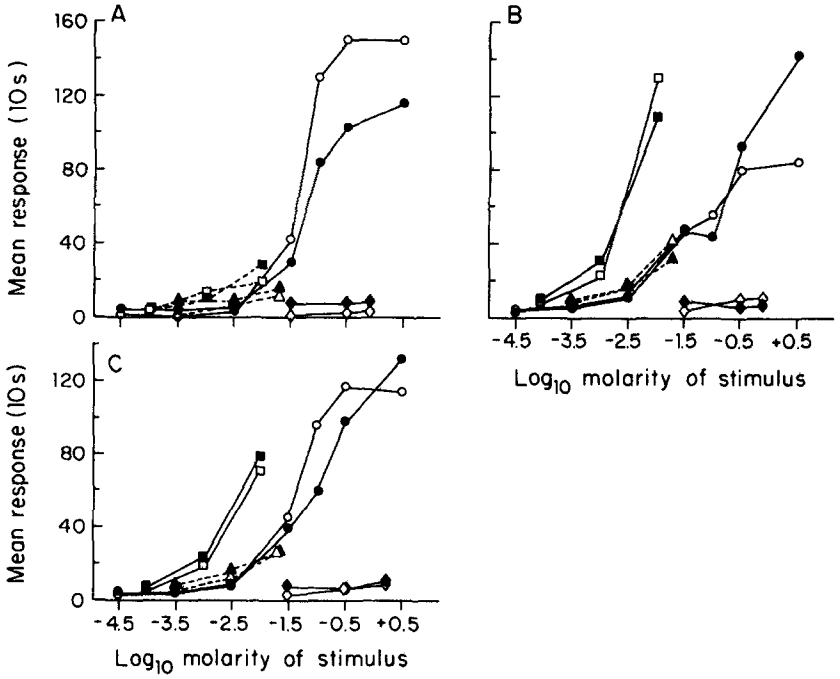

FIGURE 7. Average responses of single fibers of the chorda tympani nerve of experimental (sodium-deprived—solid symbols) or control (open symbols) rats as a function of the logarithm of stimulus molarity. Response (number of impulses elicited in 10 s of stimulation) functions for (A) NaCl-best, (B) HCl-best, and (C) all fibers, regardless of classification,were averaged separately. Unit symbols: (circles) NaCl-best; (squares) HCl-best; (triangles) quinine-best; (diamonds) sucrose-best. The points plotted are means of responses of 10–15 control, or 7–8 experimental NaCl-best units; from 13 control, or 9–13 experimental HCl-best units; or from a total of 23–28 control or 16–21 experimental units. The mean response to water, presented as a stimulus, was similar for all the control (4.8 impulses/10 s) and all the experimental (6.0 impulses/10 s) units. Smaller responses to NaCl (0.03–3.0 M) in the NaCl-best fibers but a larger response to 3.0 M NaCl in the HCl-best fibers resulted from sodium deprivation.

(92% in these data), the combined effects of the single fibers approximates the response of the whole nerve (see Fig. 3). The measure of peak whole nerve activity, however, exaggerates the relative effect of NaCl in comparison to HCl more than does the measure of tonic whole nerve activity. Of course, the measure used for the responses of single fibers (number of impulses elicited in

10 s of stimulation) is a more integral measure over the entire stimulation period than either of the two measures of whole nerve activity.

DISCUSSION

The chorda tympani nerves of sodium-deprived rats respond differently from those of control (sodium-replete) rats. Impulse frequency in response to sodium chloride (0.03–3.0 M) tends to be lower for units in the chorda of deprived rats. An analysis of single fiber responses shows that the NaCl-best units are most affected. Whether or not these changes in nerve sensitivity after sodium deprivation are related to the sensory control of a concomitant increased sodium chloride intake displayed by these animals is not known. It is also not known if the same decrease in responsivity would occur in adrenalectomized rats which also show increased salt appetite and salt intake. In sodium-deprived rats, interest is focused on the behavior of an intact organism responding to a nutritional deficiency; in adrenalectomized rats, interest is focused on an organism with a major component of its reactive system, the salt-retaining component, missing. Mechanisms underlying salt appetite in these two preparations may be different.

Taste Acuity in Animals Showing Salt Appetite

Richter (1956) concluded that the taste receptors of the adrenalectomized rat should be more sensitive to solutions of sodium chloride inasmuch as the animal's preference threshold for sodium chloride (determined in a two-bottle, 48-h test) is reduced. It is not possible, however, to make strong inferences regarding gustatory sensitivity using this method alone. Measures of relative consumption from two bottles, one containing water and the other a solute dissolved in water, have been used to infer the relative hedonic value (pleasantness or unpleasantness) of two solutions, not their sensory quality or intensity. It is possible, for example, that the lowest concentrations of sodium chloride are tasted by both intact and adrenalectomized rats but preferred only by the animals which need to compensate for their lack of adrenals and the consequent loss of sodium from their tissues (Pfaffmann and Bare, 1950).

Furthermore, using the two-bottle test makes it difficult to establish adequate control over adaptation of the taste receptors which is crucial for determination of thresholds. To humans, a solution of sodium chloride at a concentration equal to an adapting sodium chloride solution applied to the tongue preceding the stimulus is tasteless; both lower and higher concentrations have a taste but the former is bitter-sour and the latter is salty. The intensity of the taste increases as the test concentration either increases or decreases from the adapting concentration (McBurney and Pfaffmann, 1963; Bartoshuk et al., 1964; Bartoshuk, 1974).

In rats, taste intensity discrimination is affected by adaptation also (McCutcheon, 1971; Bealer, 1978). For example, Bealer has recently shown that adaptation, effected with solutions applied to the tongue through an implanted fistula, reduces the intensity of a sodium chloride stimulus, measured by generalizations of conditioned taste aversions. Because the two-bottle paradigm provides the animal with saline and water *ad libitum*, the tongue may, from

moment to moment, be adapted to the sodium concentration of saliva, the sodium concentration of the test stimulus, water, or any concentration within these limits, depending upon which bottle was just sampled (Bartoshuk, 1974). One possibility is that adrenalectomized rats prefer weak concentrations of saline because they avoid the greater bitter-sour taste of water which may result from their elevated salivary sodium levels (see below).

The two-bottle method, then, does not necessarily measure either a detection threshold (the weakest concentration of sodium chloride which can be distinguished from water whatever its quality) or a recognition threshold (the weakest concentration of sodium chloride recognized as salty); the effects of oral stimulation, ingestion, and postingestional feedback affect the relative consumption of the two stimuli: water and a particular sodium chloride solution. In fact, psychophysical (Carr, 1952; Harriman and MacLeod, 1953) and neurophysiological (Pfaffmann and Bare, 1950) studies have shown that the detection threshold for NaCl solutions was not affected by adrenalectomy in rats. Thus, the elevated drinking of weaker solutions of sodium chloride with adrenalectomy does not appear to have as its basis receptors which are more sensitive to sodium chloride.

Adrenalectomized or sodium-deprived rats, however, also drink more of suprathreshold concentrations of sodium chloride than their sodium-replete counterparts. This increased consumption of stronger concentrations of sodium chloride cannot be accounted for by a simple increase in receptor sensitivity. It has been suggested that there must also be a change in the acceptability of the sensory stimulus (Nachman and Pfaffmann, 1963). Barnes (1969) and Barnes and Morrison[6] developed a method which allowed rats to scale the perceived intensity of sucrose (0.009–0.3 M) and sodium chloride (0.0017–0.5 M). The resulting psychophysical functions for sucrose solutions were similar for intact and adrenalectomized rats, but suprathreshold concentrations of sodium chloride elicited less intense sensations in adrenalectomized rats. Sodium chloride thresholds did not differ but sensitivity differences between the two groups of rats increased as intensity increased. It was suggested that this decrease in perceived intensity accounts for the consumption of greater amounts of suprathreshold sodium chloride solutions by sodium-deficient rats (Morrison, 1974).

Salivary Sodium Levels and Sodium Chloride Preference

It is possible that variation in salivary sodium levels could influence the ingestion of sodium chloride solutions by varying the adaptation of the receptors (see above). In the normal rat, the sodium concentration of whole saliva (collected in animals anesthetized with sodium pentobarbital and injected with pilocarpine) is ~ 0.04 M (Hiji, 1969), but the two-bottle preference for sodium chloride starts at 0.01 M (Richter, 1939; Bare, 1949; Pfaffmann, 1957). This sodium concentration in stimulated saliva is probably somewhat above resting levels because the percentage of sodium ions in saliva is influenced by flow rate (Schneyer et al., 1972). Measurement of electrolyte levels from whole saliva (collected in the same way) in adrenalectomized rats shows the average concentration has increased

[6] Barnes, D. S., and G. R. Morrison. Personal communication.

(Catalanotto and Sweeney, 1978), yet the animals' preference threshold for sodium chloride is reduced to about 0.001 M. On the other hand, rats deprived of sodium for 10 d show a decrease in salivary sodium concentration (to about 0.02 M, also measured after stimulation).[7] These changes in salivary sodium presumably reflect the outpouring of sodium in the adrenalectomized preparation and the operation of an efficient salt-retaining mechanism in the intact deprived organism.

If, through adaptation, differences in salivary sodium concentration are related to differences in sodium chloride ingestion, they may mostly affect the consumption of weaker solutions inasmuch as the effect of gustatory adaptation in man is primarily on the intensities of solutions near the adapting concentration (McBurney, 1966). Also, the effect of adrenalectomy, with its accompanying increase in sodium in saliva, could not reduce the recognition threshold for sodium chloride; it could only increase it. The increased sodium concentration adapting the receptors, however, might make weaker solutions of sodium chloride (0.001–0.03 M) more noticeably different from water due to a contingent response to water after sodium chloride adaptation (Bartoshuk, 1974), allowing the animals to make the discrimination which will alleviate their need. The fact that sodium-deprived animals have lower salivary sodium levels would predict, if salivary sodium has anything to do with salt preferences, differences in the behavior of adrenalectomized and sodium-deprived animals with respect to the lower concentrations of sodium chloride; this possibility has not yet been tested experimentally.

Effects of Sodium Deprivation on the Response of the Whole Chorda Tympani Nerve

Nachman and Pfaffmann (1963) found that 20 d of sodium deprivation did not alter responses of the whole chorda tympani nerve to sodium chloride solutions (0.0003–0.3 M). They calculate responses, however, as ratios to responses to 0.01 M sodium chloride, a procedure which would considerably mask any absolute change in responsivity to sodium chloride brought on by deprivation. In the present experiments, 0.01 M sodium chloride elicited a response which was about half as large as the response to 0.1 M sodium chloride and which was about four-fifths as large in deprived preparations as in replete. When responses are calculated relative to the response to 0.1 M sodium chloride with the present data, differences between deprived and replete animals' responses to sodium chloride are eliminated. When the reference changes with experimental treatment as do the responses to all suprathreshold concentrations of sodium chloride, absolute differences between treatments diminish. In the present study, the reference, a measure of variation in nerve activity during 10 s of a steady flow of water did not differ for the two conditions; therefore, absolute differences in sensitivities to sodium chloride were not lost.

Variation in absolute responses recorded from whole nerves often requires that the response be standardized with respect to some aspect of the response of that particular nerve at that point in time. An unfortunate choice of standard is

[7] Contreras, R. J., and F. A. Catalanotto. Unpublished data.

possibly the major reason the earlier workers did not discover a difference in response to sodium chloride between deprived and replete rats' nerves. Nachman and Pfaffmann (1963) also report, however, no differences when responses are calculated as ratios to responses to 0.1 M potassium chloride. Responsivity to 0.3 M potassium chloride is not correlated with responsivity to 0.1 M sodium chloride in the fibers of the rat chorda tympani (Erickson et al., 1965). There were not enough data collected in the present study to decide if sodium deprivation affected the responsivity to 0.1 M potassium chloride. There are several other differences between the experimental procedures of the present and earlier studies. First, in the earlier study the rats were deprived of sodium for 19–20 d; in the present study they were deprived for 9–10 d. Second, in the present study, recordings were made without knowledge of the animal's dietary condition; in the earlier study, it was known. Third, the tongue was adapted to distilled water in the present work, but to dilute saliva in the earlier work. Finally, in the present study, urethane was used; in the earlier study, sodium pentobarbital was used as the anesthetic. Any of these other differences may have conceivably contributed to the end result.

Sodium Deprivation and Sensory Coding

Although it is generally assumed that the intensity of a taste stimulus is coded in the number of nerve impulses it evokes, less intense stimuli evoking fewer impulses than more intense stimuli, there are two opposing views on how information about taste quality is coded in the nervous system. The major controversy involves disagreement about whether gustatory quality consists of only four different sensations: sweet, salty, sour, and bitter; or a continuum of qualitatively different sensations. One view predicts four different taste receptor systems, each sensitive to stimuli of one quality, and four fiber types, also specific to a quality, which relay information about a single taste quality to the central nervous system. It has been proposed (Pfaffmann, 1974; Bernard, 1975; Pfaffmann et al., 1976; Nowlis and Frank, 1977) that a successful division of afferent fibers into four types, by using the stimulus to which each unit is most sensitive (e.g., NaCl-best) as a label (Frank, 1973), provides neural evidence for a labelled-line system. Others maintain (Erickson, 1977; Scott, 1977; Travers and Smith, 1976), however, that the variability in the sensitivity profiles of units at all levels of the taste system defy the grouping of units into four categories and that the broad tuning of these units necessitates a "population" or "across-neuron pattern" code for taste quality.

A large and consistent difference in taste neurons sampled from rats deprived of sodium is found in fibers highly sensitive to sodium chloride, many of which are NaCl-best units which, according to labelled-line notions, code "saltness." The effect of sodium deprivation is a decrease in the responsivity to sodium chloride, a change in the number of impulses evoked by a given concentration of sodium chloride, or, according to labelled-line, a change in the intensity of the evoked saltiness. For example, if the deprived animal has 0.3 M sodium chloride on his tongue, it evokes a signal in NaCl-best units which approximates the size of the signal evoked by 0.07 M (cf. Fig. 7) in replete animals. The

reductions in responses to sodium chloride are greatest at the highest concentrations. The range of concentrations which evoke threshold (0.001 M) to greater than saturation responses (3.0 M) in control animals evoke responses in deprived animals which would be interpreted as a much reduced concentration range by control animals (0.001–0.1 M). If there is no change in the central neural interpretation of the intensity signal (i.e., x impulses/unit time always represents one intensity value), the deprived animals would sense very strong sodium chloride solutions as relatively weak.

There is also an increase in the effect of 3.0 M sodium chloride on HCl-best units in deprived animals. This would imply to a labelled-line theorist that the intensity of the "sourness" coded by HCl-best units, evoked by this concentration of sodium chloride, is increased with deprivation. Very little 1.0 M sodium

TABLE III

RANK-DIFFERENCE CORRELATIONS BETWEEN RESPONSES TO ALL PAIRS OF THE FOUR STANDARD TASTE STIMULI AND WATER*

Stimulus pair	Control (n = 55)	Sodium-deprived (n = 45)
NaCl - water	+0.26	−0.04
NaCl - sucrose	−0.23	+0.05
NaCl - HCl	+0.04	−0.08
NaCl - quinine	+0.22	+0.10
Sucrose - water	+0.19	+0.58‡
Sucrose - HCl	+0.17	+0.30
Sucrose - quinine	+0.30	+0.57‡
HCl - water	+0.32	+0.53‡
HCl - quinine	+0.76‡	+0.82‡
Quinine - water	+0.36	+0.69‡

* The stimuli were 0.1 M NaCl, 0.5 M sucrose, 0.01 N HCl, 0.02 M quinine hydrochloride, and distilled water. Spearman rank-difference correlation coefficients, measures of how similarly different pairs of stimuli order the fibers responses, are listed.

‡ Statistically significant correlations (t tests, P's < 0.01).

chloride is ingested by either intact or adrenalectomized rats, still less 3.0 M. The activity evoked by 3.0 M sodium chloride in HCl-best units of replete animals approximates that evoked by 0.003 M hydrochloric acid, whereas 3.0 M sodium chloride evokes a response in deprived rats which is even greater than that evoked by 0.01 M hydrochloric acid in replete animals. Neither 0.003 M nor 0.01 M hydrochloric acid is preferred by rats.

Those who invoke an "across-neuron pattern" as the code for taste quality often use correlation coefficients to describe similarities in the neural patterns evoked by two stimuli in a population of taste units and to predict similarity in their taste quality. Correlation coefficients indicate the degree to which two stimuli tend to evoke activity in the same neurons in the population. In Table III coefficients of correlation between responses to each possible pair of the five stimuli (the four standards and water) are presented. Correlations coefficients,

as determined by the Spearman rank-order method, for all 55 control fibers and for all 45 fibers from sodium-deprived rats are tabulated. The evoked pattern of activity is similar for quinine and hydrochloric acid in control fibers ($r_s = +0.76$; $t = 8.51$, $df = 53$, $P < 0.01$) although the responses to hydrochloric acid are larger than responses to quinine. Also, the low coefficients of correlation with each of the other four stimuli are similar for hydrochloric acid and quinine (e.g., r_s for HCl and water is +0.32; r_s for quinine and water is +0.36). Hydrochloric acid and quinine also have highly correlated effects ($r_s = +0.82$; $t = 9.39$, $df = 43$, $P < 0.01$) and similar correlations with the effects of the other stimuli in fibers from sodium-deprived animals. It should be noted that HCl-best fibers are more sensitive to quinine than the other two fiber types.

The correlation between hydrochloric acid and quinine is the only statistically significant correlation in control fibers, a result similar to that obtained by Ogawa et al. (1968). In experimental fibers, however, in addition to the hydrochloric acid-quinine correlation, the units' responsiveness to three of the four standard stimuli is significantly correlated with activity to water, and responsiveness to sucrose is correlated with responsiveness to quinine. These correlations are not very strong, varying from +0.53 to +0.69, but are considerably larger than in control fibers and are statistically significant (t tests, P's < 0.01). The one responsivity not correlated with activity to water in deprived preparations is that to sodium chloride. This might be taken to mean that the stimuli, with the exception of sodium chloride, taste more similar to water to deprived rats. It could also indicate that the salience of the sodium chloride stimulus is retained, whereas the salience of the other stimuli is decreased after sodium deprivation.

Although rats can recognize the quality of a taste solution in < 200 ms (Halpern and Tapper, 1971), and the early part of the nerve response contains information about both taste quality (Halpern and Marowitz, 1973) and intensity (Bealer, 1978), a long-term response measure for single fiber activity (response frequency for a 10-s period) is adequate to uncover differences due to sodium deprivation. In fact, early peak response measures and later tonic response measures of whole nerve activity both show the effect of deprivation; as the 10-s response, the first 5-s response, the second 5-s response, or the first 1-s response of single fibers all show the effect of sodium deprivation (Contreras, 1975). Therefore, it appears as if any reliable measure of response, long-term or short, can be used effectively in analyzing effects of sodium deprivation on peripheral taste afferents even though it may not mimic responses which result from stimulation during licking behavior (Marowitz and Halpern, 1977).

Possible Relationships between Reduced Neural Responsivity and Increased Sodium Chloride Intake

Although the motivation to seek and ingest sodium chloride after sodium deprivation is presumably triggered through some innate, centrally organized processes, the sensory signal from the taste receptors plays a role both in the initial detection of the appropriate stimulus, a sodium salt, and in determining, to some degree, the amount ingested. Ingestion accompanied by stimulation of

taste receptors by sodium chloride leads to a rapid (Denton, 1965), short-term satiation (Nachman and Valentino, 1966; DiCara and Wilson, 1974) which does not occur without taste receptor stimulation (e.g., when solutions are introduced into the stomach via an esophageal fistula). If cessation of salt intake were simply under control of postingestional effects, peripheral stimulation would not have this effect (Morrison and Young, 1972).

Stimulation of taste receptors might play a role in short-term control of amount of salt consumption if cessation of intake requires a critical number of sodium chloride-driven impulses that are relayed by taste afferents (perhaps only NaCl-best units) to the central nervous system (Contreras, 1975, 1977). Because impulse frequency generally increases as concentration is increased (Sato, 1971; Frank, 1973; our Fig. 7), this notion requires an inverse relationship between the amount of time an animal keeps his receptors bathed with a sodium chloride solution (or continues to drink) and the concentration of that solution. Therefore, the animal should consume more and lick for longer periods the weaker the salt solution. It also requires an identification of the sodium chloride stimulus; otherwise, an animal would drink water (or any nonsalty solution) forever, never accumulating a critical number of salt-driven impulses. The salt signal must be clearly distinguishable from background to trigger this mechanism. Accordingly, a sodium salt stimulus would probably be recognizable only if it were more intense than the sodium concentration of saliva (0.03–0.04 M).

Because the chorda tympani of the sodium-deprived rat is less responsive (producing fewer impulses) to suprathreshold concentrations of sodium chloride, more consumption by deprived than by normal rats at each concentration would be predicted by this notion of a critical number of impulses. The idea runs into difficulty if the preference curve for different concentrations of sodium chloride generated by two-bottle 48-h tests (Bare, 1949; Young and Chaplin, 1949; Pfaffmann, 1957) or one-bottle 10-min tests (Weiner and Stellar, 1951) is considered. In such tests, neither normal nor adrenalectomized rats drink more of near-threshold concentrations (< 0.03 M) than higher concentrations (0.03–0.1 M) of sodium chloride and they both show a peak preference at $\sim$ 0.1 M (Pfaffmann, 1957). These results seem to indicate that solutions of sodium chloride are the most palatable or acceptable at intermediate concentrations. A number of studies have shown, however, with very brief exposure to sodium chloride (Smith et al., 1969; Morrison, 1972) or sham drinking (Mook, 1963), that ingestion rate in water-deprived rats is an inverse function of sodium chloride concentration. These results suggest that acceptability is inversely proportional to sodium chloride concentration; however, such an interpretation requires data derived from similar tests using rats not deprived of water; thirst can influence sodium chloride acceptability (Weiner and Stellar, 1951; Young and Falk, 1956).

Possible Mechanisms for Reduction in Responsiveness of Taste Neurons

There are several possiblities for mechanisms effecting the sensory change after sodium deprivation (Beidler, 1961; Halpern, 1967). First, the change may be effected through the circulatory system, either changing the immediate environment of the taste receptors themselves (Bradley, 1973), their development, or

the transmission of activity to (or by) the afferent nerves innervating them (Henkin, 1969). Second, the change could be mediated by the autonomic nervous system via efferent fibers in the chorda tympani (Hellekant, 1971; Farbman and Hellekant, 1976) and (or) the superior cervical ganglion (Kimura, 1961). Efferents in the chorda tympani are secretomotor fibers which innervate salivary glands and vasodilators that innervate blood vessels of the tongue, not taste buds (Farbman and Hellekant, 1978); efferent activity could affect the receptors indirectly via salivary outflow or blood vessel size (Graziadei and Graziadei, 1978). Third, the change may be related to the animal not having tasted sodium chloride for a long period of time; the receptor system might undergo some internal change simply through disuse. There is not yet a clue as to how the reduction in responsivity is effected.

However it is effected, physiological changes due to deprivation alter the information that is sent from the gustatory receptors to the brain. This process may help determine the relative detectability and desirability of sodium chloride by increasing its relative salience and reducing its intensity signal. The latter may account, in part, for the dramatic change from rejection to acceptance of strong sodium chloride solutions after sodium deprivation.

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