NaCl concentration alters temporal patterns of drinking and eating by rats

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Abstract. To obtain an understanding of the role of taste in NaCl preference—aversion under standard laboratory feeding conditions, we characterized the eating and drinking patterns of rats maintained on powdered food, water, and NaCl solution. The concentration of NaCl was varied systematically from 0.01 to 0.4 M with a single concentration present for four consecutive days. In addition to daily intake, the number and duration of ingestion bouts, and the number of switches between food and fluid and between water and saline were recorded throughout the day/night cycle. The availability of NaCl solution did not alter the typical pattern of night-time feeding and prandial (drinking after a meal) drinking. As shown previously, NaCl intake was highest for 0.15 M NaCl and declined at both stronger and weaker concentrations. Variations in drinking bout number and duration determined amount consumed. Drinking bout duration was highest for 0.2 M NaCl then declining progressively at both stronger and weaker concentrations. The number of drinking bouts was highest for 0.04 M NaCl, a concentration slightly above the adapting salivary sodium concentration, declining linearly thereafter with stronger NaCl concentrations. The availability of NaCl solution influenced the amount of food consumed, as well as the number and duration of food bouts. Food bout number was highest in the presence of the weakest 0.01 M NaCl solution, while food bout duration was highest in the presence of hypertonic NaCl concentrations. Most switching behavior occurred between meal consumption and drinking and little between drinking fluids. When 0.01–0.08 NaCl solutions were available, the rats drank saline after a meal; when hypertonic 0.3–0.4 M NaCl solutions were available, they drank water after a meal. In the presence of intermediate NaCl concentrations (0.15–0.20), the choice of fluid consumed after a meal was more equivocal to the extent that there was increased switching between water and saline and vice versa. The significance of these differences in the micromolar features of eating and drinking are discussed in relationship to taste and post-ingestional control mechanisms of ingestion.

Introduction

When given a two-bottle intake test between water and various molar concentrations of NaCl solution, the NaCl solution intake of rats, maintained on laboratory chow containing adequate NaCl, typically peaks at a concentration near isotonicity. At both higher and lower concentrations, NaCl solution intake declines, particularly at the high end for stronger concentrations. This classic bell-shaped function of NaCl intake is also known as the preference—aversion function for NaCl (Young and Chaplin, 1949; Bare, 1949; Epstein and Stellar, 1955; Richter, 1956). Water intake has the converse U-shaped function; water intake is lowest when isotonic NaCl is available, and increases in the presence of weaker and stronger NaCl concentrations. Thus, total intake (NaCl + water intake) remains fairly constant across NaCl concentration, although being somewhat elevated when preferred NaCl concentrations are available.

Under the conditions imposed in the two-bottle drinking test, NaCl intake is assumed to be governed mainly by the taste (intensity, quality, affect) properties of the solution (Pfaffmann, 1957, 1961): the animal consumes the NaCl solution because it tastes pleasant or unpleasant at certain intensities. The affective property (pleasantness/
unpleasantness) of the NaCl solution is inferred by amount drunk relative to total intake. A preference is indicated and operationally defined as a high proportional intake of NaCl solution relative to total intake, and an aversion as a low proportional intake. This makes intuitive sense because the animal obtains more than adequate NaCl from food consumption and has a separate source of water apart from the NaCl solution. In effect, there is an absence of a specific internal signal of sodium need to activate the central control of NaCl intake other than through exteroceptive stimulation by taste.

While it is generally recognized that the NaCl preference—aversion function is determined mainly by preabsorptive taste signals, postabsorptive signals must also influence intake. By measuring intake over 24-h periods, measures for which much of the experimental literature is based, postabsorptive signals from excess NaCl and water intake can influence subsequent intake (Blake and Lin, 1978; Gibbs et al., 1986; Tordoff et al., 1986). Thus, in the two-bottle test situation, postabsorptive signals may have a limited role in initiating ingestion; on the other hand, they may have a major role in satiation and limiting ingestion (Davis and Levine, 1977). Taste is also known to play a role in the satiation of NaCl intake (Nachman and Valentino, 1966; DiCaro and Wilson, 1974; Contreras and Hatton, 1975; Contreras and Frank, 1979).

Little is known about how preabsorptive taste signals, apart from postabsorptive factors, contribute to the NaCl preference—aversion function. The contribution of taste, relatively independent of postigestational signals, has been studied in short-term intake tests (Nachman and Pfaffmann, 1963; Smith et al., 1969; Wagman, 1963), in rats with an esophageal fistula (Stellar et al., 1954; Mook, 1963) or a gastric fistula (Contreras, 1987, 1989), when little of the ingested NaCl can be absorbed and, therefore, influence intake. In these circumstances, there is usually no other ingestible substance available other than NaCl solution to complicate the testing conditions. This restricted single component examination of the role of taste in NaCl intake lacks, on the one hand, the richness of the background normally present in a free-feeding situation and therefore the information obtained may have limited general applicability. On the other hand, the difficulty in assignment of causal factors to NaCl intake is abetted by the availability of food and water in the test feeding situation. Ingestion must also be influenced by the temporal relationship between food, water, and NaCl intake, and the concentration of NaCl, all of which may interact with changes in the light/dark cycle. As shown previously, the consumption patterns of rats presented with food, water, and sucrose solution differ considerably with changes in sucrose concentration and light/dark cycle (Spector and Smith, 1984). As best we know, the temporal pattern of food and fluid ingestion when NaCl solution is available has never been reported.

We therefore characterized the eating and drinking patterns of rats maintained on powdered food, water, and one of several different NaCl concentrations that span the range of the bell-shaped function of NaCl intake. To accomplish this, a computerized system, capable of simultaneously recording in real time the feeding activity of rats over a 23-h period, was used. This type of analysis has been applied successfully to show that although the two sweeteners, sucrose and saccharin, are consumed in equal quantities, they nevertheless elicit distinct sweet taste sensations as evident from markedly different consumption patterns (Smith et al., 1987). The goal of the present study is to obtain a clearer understanding of the contribution of taste to the NaCl preference—aversion function under standard laboratory feeding conditions.
Materials and methods

Subjects

Eight male Sprague-Dawley rats (Charles River Breeding Laboratories), 64 days of age and weighing an average of 302 g at the start of the experiment, were housed in modified Hoeltge 11B cages in a temperature-regulated colony room on a 12:12 day-night cycle with lights on at 0700 h. They had continuous access to water and powdered Purina Chow (containing 1% NaCl) throughout the experiment.

Apparatus

Eight Hoeltge 11B stainless steel rat cages were modified by attaching two stainless steel drinking tubes on the back wall of the cage and a feeding station on the cage front. An infrared emitter and receptor were aligned at each of these ingestion stations, so that licking on a drinking tube or entry into the feeding jar interrupted the infrared beam. These beam interruptions were transmitted through an interface board to a PIO-12 parallel I/O card (Metrabyte), that was installed in an expansion slot of a ZFA-161-52 portable Zenith Computer. Each day’s data were kept in RAM and written to a floppy disk at the end of each 24-h period.

The data collection software was written in C, permitting the simultaneous input from the eight cages over a 23-h daily testing period. Each beam break was recorded in sequential 6-s bins over 23-h, yielding 13,800 data points daily for each ingestion port. Changes in room illumination were transmitted to the computer via a photocell-activated detector. Between 0900–1000 h each day, after the data were written to the disk, the cages were cleaned and the food and water containers were weighed, washed, and replenished.

Procedure

The rats were allowed to live in the specially constructed cages for two weeks to become accustomed to the location of the food and liquid ingestion stations. During this time only one drinking bottle containing water was available. To establish a baseline condition, detailed patterns of food and water ingestion were recorded only for the last four days of this period. Thereafter, NaCl solution was also given to the rats from a second drinking bottle for the daily 23-h measurement period. The animals were presented with an ascending concentration series consisting of 0.01, 0.02, 0.04, 0.08, 0.15, 0.18, 0.2, 0.3 and 0.4 M NaCl. Each concentration was presented for four consecutive days to minimize the influence of possible sequence effects among NaCl test concentrations; despite this precaution, absolute levels of NaCl preference can differ between sequences presented in an ascending versus a descending NaCl concentration series (Rowland and Fregly, in press). The position of the water and NaCl drinking bottles was reversed daily to prevent the formation of a position preference.

Data reduction and analysis

The data analysis program, also written in C, allowed a daily graph of each rat’s activity, showing the temporal pattern of food and liquid ingestion throughout the day and night.
periods, to be plotted. Each graph was accompanied by a numeric table of the same information. For each rat and each ingestion port, the table listed the starting and stopping time of each feeding bout, the number of licks per drinking bout, number of seconds spent over the food jar, and all inter-bout intervals. To initiate a feeding bout, the rat had to spend at least 3 s over the food jar and then remain there at least a total of 30 s for it to be counted as one feeding bout. Water and NaCl solution drinking bouts were defined similarly. Three licks initiated a bout but at least 30 licks were required to define one drinking bout. The end of a feeding or drinking bout was defined by the absence of a beam break for 50 consecutive bins (5 min). With these criteria, 98% of all feeding and drinking activity was incorporated in the analysis of the baseline condition with just food and water available. With the addition of NaCl at all concentrations, these percentages did not change.

Results

Three ingestion scores were calculated for each rat by averaging the 4-day intakes of NaCl solution, water, and food during the presentation of each NaCl concentration. The average ingestion scores for the eight rats are plotted as a function of NaCl concentration and illustrated in the upper panel of Figure 1. In addition, the total average fluid intake is shown. To compare the present functions with results representative of the experimental literature, the NaCl and water intake scores were also calculated relative to the animal's body weight. As can be seen from the lower panel of Figure 1, the present results compare favorably with the typical intake functions reported by Fregly and Rowland (1986).

To analyze the data presented in the upper panel of Figure 1, a two-factor analysis of variance with repeated measures across concentration was performed to compare water and NaCl solution intake. The overall difference between water and NaCl solution intake was significant \( F = 36.42, \text{df} = 1/7, P < 0.001 \). Subsequent comparisons using the method described by Keppel (1973) indicated that water and NaCl solution intake were different at each concentration except at 0.2 M (all \( F \)-values were significant beyond the 0.001 level). More NaCl solution than water was ingested at all concentrations below 0.2 M, and more water than NaCl solution was ingested at the two highest concentrations.

NaCl solution drinking

There were significant differences in absolute NaCl solution intake among the nine NaCl concentrations \( F = 19.86, \text{df} = 8/56, P < 0.001 \). Further comparisons of NaCl drinking by Tukey's method (from Keppel, 1973) showed that the rats drank significantly less of 0.3 and 0.4 M solutions in comparison to all other NaCl concentrations. Furthermore, additional comparisons showed that 0.08 and 0.15 M concentrations were ingested in larger quantities than the two weakest concentrations.

Water drinking

The differences in absolute water intake across the nine NaCl concentrations were also significant \( F = 46.10, \text{df} = 8/56, P < 0.001 \). The Tukey post hoc test showed that
the water intake was significantly greater than 0.3 and 0.4 M NaCl intake. In addition, water intake was significantly greater when 0.01 NaCl was available than when 0.04–0.18 M NaCl solutions were available.

Food ingestion

Food intake scores were analyzed by a one-factor analysis of variance with repeated measure across NaCl concentration. Absolute food intake varied significantly across NaCl concentration ($F = 3.40$, df = 8/56, $P < 0.01$). Post hoc comparisons showed that the slight elevation in food intake when 0.02 and 0.04 M NaCl solutions were available, accounted for the source of the overall main effect. The within-subject variation in food intake was so low that the mean food intake during 0.02 and 0.04 M NaCl presentations was less than 2 g above that during presentations of other NaCl concentrations.

Total fluid ingestion

Total fluid intake was also analyzed by a one-factor analysis of variance with repeated measures across NaCl concentration. Total fluid intake varied significantly across NaCl concentration ($F = 4.27$, df = 8/56, $P < 0.001$). Post hoc comparisons by the Tukey
method showed that total fluid intake was significantly greater when 0.08, 0.15 and 0.2 M NaCl were available in comparison to all other measurement points.

Figure 2 is an example of a typical daily record of the pattern of food and liquid ingestion occurring during the day and night periods. This record is from Rat 1 on the fourth day of 0.2 M NaCl availability. The number of licks on the fluid tubes and the time spent over the food jar was recorded every 6 s throughout the 23 h period. As can be seen from this figure, most of the drinking activity occurred during the dark period, indicated by the dark horizontal bar in each panel. This rat had a total of 19 feeding bouts, five of which occurred during the daylight hours. The feeding bouts averaged 10.64 min in duration. The daytime bouts, however, averaged only 3.84 min while night-time bouts averaged 13.06 min. This animal had 20 NaCl drinking bouts which lasted an average of 4.88 min. One of these bouts occurred just before the lights went off. There were 20 water drinking bouts which lasted an average of 2.55 min. None of these water drinking bouts occurred during the daylight hours. It is also obvious from Figure 2 that most of the night-time feeding bouts were accompanied by drinking from one of the two fluid bottles.

Figure 3 is a record of the typical pattern of water and NaCl drinking when NaCl concentration is varied. This record is from Rat 1 on the second day for all NaCl concentrations. Since little drinking occurred during the day for any concentration, only nighttime drinking is shown. As can be seen from this record, the number of drinking bouts are many and fairly constant between 0.01 and 0.18 M NaCl. At higher NaCl concentrations, drinking bout number declines progressively. Water drinking bouts are few in number and fairly constant when 0.01 – 0.04 M NaCl solutions are available. Water drinking bouts are absent completely when 0.08 and 0.15 M NaCl solutions are available.

![Diagram of fluid intake patterns](image)

**Fig. 2.** Ingestive data for one rat are plotted for a 23-h period when water, 0.2 M NaCl, and powdered chow were available. The dark horizontal bars in each panel indicate the period when the room lights were off. Discrete drinking and eating bouts can be seen occurring most often during the dark period.
For stronger NaCl solutions (0.18–0.4 M), the number of water drinking bouts increases progressively. Thus, the drinking record of this rat is marked by three transition points: (i) between 0.18 and 0.2 M NaCl, when the number of NaCl drinking bouts begins to decline; (ii) between 0.04 and 0.08 M NaCl, when water drinking stops; and (iii) between 0.15 and 0.18 M NaCl, when water drinking bouts begin to increase.

The records from all of the rats were averaged and the number and duration of drinking bouts are presented in the upper and lower panels of Figure 4, respectively. As can

![Diagram of water and NaCl bouts](image)

**Fig. 3.** Night-time drinking bouts of NaCl and water are shown for a single rat on the individual days when the various concentrations of NaCl were presented. The maximum height of the vertical lines corresponding to drinking bouts represents about 40 licks.
be seen in the upper panel, the number of NaCl drinking bouts is relatively constant for the five weakest NaCl concentrations; however, the number of NaCl drinking bouts decreases linearly between 0.04 and 0.4 M NaCl. A two-factor analysis of variance with repeated measures was performed on the number of drinking bouts. The overall difference between the number of NaCl and water drinking bouts was significant ($F = 31.17, \text{df} = 1/7, P < 0.001$). Further comparisons showed that the number of water and NaCl drinking bouts was significantly different at each concentration except 0.2 M NaCl. The number of water drinking bouts bottomed to a small number (except for a small increment at 0.15 M) between 0.04 and 0.18 M NaCl. At both weaker and stronger NaCl concentrations, the number of water drinking bouts increased precipitously, particularly between 0.18 and 0.2 M NaCl.

A similar analysis was performed on the mean number of licks per drinking bout (see lower panel of Figure 4). As we have repeatedly observed, the rats’ local rate of licking is constant at 6 ± 0.5 licks per second; local drinking rate was not influenced by changes in NaCl concentration. Thus, ‘licks per bout’, is an excellent measure of drinking bout duration. The difference between NaCl solution and water ‘licks per bout’ was significant ($F = 23.22, \text{df} = 1/7, P < 0.001$). Post hoc tests showed that this difference was significant for all NaCl concentrations except 0.02 M NaCl. A comparison of the functions for drinking bout number (upper panel) with those for drinking bout duration (lower panel) reveals some differences. Overall, the NaCl drinking functions differ between the two measures, while the water drinking functions are more similar. Drinking bout number peaks at 0.04 M NaCl while bout duration peaks at the stronger 0.2 M NaCl; thus, between 0.04 and 0.2 M NaCl, the progressive decline in drinking bout number is compensated to a degree by a progressive increase in drinking bout duration. With regard to the water drinking functions, when drinking bouts are few in number, they are also short in duration, particularly when 0.04—0.15 M NaCl solutions are available. When hypertonic NaCl solutions (0.2—0.4 M NaCl) are available, water drinking bouts are large in number and long in duration.

The upper panel of Figure 5 presents the number of food bouts as a function of NaCl concentration. A one-factor analysis of variance with repeated measures was performed on these data. As can be seen, the number of feeding bouts decreased significantly as NaCl concentration increased ($F = 11.97, \text{df} = 8/56, P < 0.001$). An orthogonal test for linear trend was significant ($F = 90.10, \text{df} = 1/56, P < 0.001$) and accounted for all of the variance. Illustrated in the lower panel of Figure 5 is food bout duration as a function of NaCl concentration. A one-factor analysis of variance with repeated measures yielded a significant difference across NaCl concentration ($F = 2.58, \text{df} = 8/56, P < 0.025$). An orthogonal test showed that all of the variance could be accounted for by contrasting the three highest concentrations against the six weakest concentrations.

In similar unpublished studies, we typically find that about 80% of all feeding bouts are followed by a water bout. This percentage would be higher if observations are limited only to night-time bouts. In the present study, 80—85% of all feeding bouts were followed by drinking, either of water or NaCl solution. ‘Switches’ from food to water or food to NaCl solution were measured on the last day of testing for each NaCl concentration. Changes from food to one of the test fluids was designated a ‘switch’ if the time from the end of the feeding bout and the beginning of the drinking bout did not exceed 50 of the 6 s time bins (a total of 5 min). These data are illustrated in Figure 6.
A two-factor analysis of variance with repeated measures was performed on these data; this analysis yielded a significant difference between switches from food to NaCl solution and switches from food to water ($F = 28.15$, df = 1/7, $P < 0.001$). It can be seen that as the concentration of NaCl solution increases, the number of switches from food to NaCl solution decreases and the number of switches from food to water increases. The difference between the two kinds of switches was significant at all NaCl concentrations except 0.2 M. If these two kinds of switches were added at each NaCl concentration, then the resultant function would approximate the food bout function shown in Figure 5. At least 80% of the food bouts would correspond to the number of switches from food to water or food to NaCl solution.

There were occasional switches from water to NaCl solution or from NaCl solution to water (see Figure 7), but these were not significantly different from each other. There was no significant trend in NaCl-to-water or water-to-NaCl switches across NaCl concentration. The number of switches was very low at 0.04 and 0.08 M NaCl because
Fig. 5. Upper panel: mean number of feeding bouts plotted as a function of NaCl concentration. Lower panel: mean feeding bout duration plotted as function of NaCl concentration.

so little water was consumed. A similar lack of switches was apparent at the highest concentrations because little of the NaCl solution was consumed.

Discussion

In the present study, with the addition of different concentrations of NaCl solution available in the test situation, we have been able to reproduce documented characteristics of eating and drinking in rats. First, most eating and drinking occurred during the hours of darkness, as has been reported in numerous prior studies. Second, the rats’ fluid consumption was prandial, such that the rats consumed most of their fluid soon after the end of a food bout. Thus, the availability of NaCl solution had little bearing on these typical patterns of feeding. Third, we have reproduced the typical bell-shaped NaCl preference—aversion function that is well described in the experimental literature.

With this as a backdrop, there were three general findings in the present research. First, the two parameters that determine the amount of NaCl solution consumed, drinking bout number and duration, varied systematically across concentration although in
NaCl alters temporal patterns of consumption

Fig. 6. The mean number of 'switches' from a feeding bout to an NaCl or a water drinking bout as a function of the available NaCl concentration. If the rat initiated a drinking bout within 5-min following the termination of a feeding bout, then this was considered a 'switch'.

Fig. 7. The mean number of switches from an NaCl drinking bout to a water drinking bout and vice versa as a function of the available NaCl concentration.

different ways. Drinking bout number was the greatest for 0.04 M NaCl, and then declined with increasing NaCl concentration. Drinking bout duration was the longest for 0.20 M NaCl, and then declined progressively at both stronger and weaker concentrations. Second, the availability of NaCl solution and ultimately its consumption in the test situation influenced the amount of food consumed, as well as the number and duration of food bouts. Food bout number was the greatest in the presence of the weakest
test solution (0.01 M NaCl), decreasing progressively thereafter with increasing NaCl concentration. Food bout duration was less systematic; nevertheless it was the lowest in the presence of the weakest concentrations (0.01–0.18 M NaCl) and increased in the presence of the three hypertonic NaCl (0.20–0.40 M) solutions. Third, the choice of fluid consumed for prandial drinking depended upon the NaCl concentration available to the animal when dilute NaCl solution (0.01–0.08 M) was available, it was the unequivocal choice over water; when hypertonic NaCl solution (0.30–0.40 M) was available, water was the unequivocal choice. The choice was more equivocal when intermediate NaCl concentrations (0.15–0.20 M) were available. We interpret these changes in the micromolar features of eating and drinking mainly to the sensory properties of the NaCl solution.

Taste-mediated changes in NaCl intake must depend upon the intensity of the stimulus and the concentration of sodium in saliva. To humans, a NaCl solution, at a concentration equal to the adapting NaCl concentration preceding the stimulus, is tasteless; both weaker and stronger NaCl concentrations have a taste but the former is bitter-sour and the latter is salty. Taste intensity increases as the difference between the test concentration and the adapting concentration increases both above and below the adaptation level (McBurney and Pfaffmann, 1963; Bartoshuk, et al., 1964; Bartoshuk, 1974). Similarly, rats respond in a discrimination task to concentrations of 0.05 M NaCl and above as similar in taste to 1.0 M NaCl, and to concentrations below 0.05 M as similar in taste to water (Morrison, 1969). Furthermore, elevating the adapting NaCl concentration bathing the receptors by infusion through an implanted oral fistula, reduces rats’ perceived intensity of NaCl as inferred by changes in generalizations of conditioned taste aversion (Bealer, 1978). Thus, as in humans, the behavioral evidence indicates that the adapting NaCl concentration also determines the NaCl intensity of rats.

Because the two-bottle test situation provides the animal with water and saline ad libitum, the taste receptors may, from moment to moment, be adapted to the sodium concentration of saliva, the sodium concentration of the test solution, water, or any concentration within these limits, depending upon which solution was just consumed (Bartoshuk, 1974). However, in the present study we found that the rats make few switches between water and NaCl solution and vice versa. They consume either water or NaCl solution; they do not alternate much between the two. In addition, most of their drinking comes after a meal or food bout. Therefore, it is likely that the consumption of 1% NaCl (0.15 M) chow, if anything, would increase the resting salivary sodium concentration normally found between 0.01–0.03 M NaCl (Hiji, 1969; Contreras and Catalanotto, 1980). The sodium concentration of food coupled with the increased salivary sodium concentration stimulated by chewing (Schneyer et al., 1972) together should elevate the adapting sodium concentration bathing the taste receptors and thereby influence the quality and intensity of the NaCl test solution. If the psychophysical evidence in humans apply to rats, than NaCl test concentrations below the adapting concentration should be discriminated by taste, but only those test concentrations above the adapting concentration should be recognized as tasting ‘salty’ (Bartoshuk, 1974).

In this context, we interpret the changes in the patterns of consumption with NaCl test concentration to mean that the NaCl recognition threshold occurs somewhere between 0.04 and 0.08 M NaCl. This is exemplified in the patterns of drinking of Rat 1, shown in Figure 3. The 0.04–0.08 M transition point is marked by a slight upsurge in the
number of NaCl drinking bouts and a total absence of water drinking bouts. It is also marked by the obvious perturbations in the average water and NaCl curves of Figures 6 and 7 and the subtle perturbations in Figure 4. Test concentrations of \(\leq 0.04\) M are presumably discriminated by taste as evident by significant differences between water and NaCl solution in drinking bout number, duration, and volume consumed. The fact that all three of these variables are higher for NaCl drinking compared to water drinking would suggest that these weak NaCl solutions taste better to rats than water. This preference for dilute saline could not be a reflection of a salty taste, but perhaps a reflection of the greater bitter-sour taste of water or the sweet taste of dilute saline.

The perceived intensity of NaCl solutions in humans (Bartoshuk, 1974) and the neural response of the whole chorda tympani as well as salt-sensitive N-neurons in rats (Contreras and Frank, 1979; Frank et al., 1983) increases as the test concentration increases above the adapting NaCl concentration. If taste plays a critical role in determining NaCl drinking in a two-bottle test situation, then there should be a behavioral measure obtained from the micromolar analysis of rat drinking that would be analogous to the psychophysical NaCl intensity function of humans and the neural response function of rats. The amount consumed over 24 h is probably not a good measure insofar as once the test stimulus is above the adapting salivary sodium level (0.04–0.08 NaCl), NaCl solution intake increases slightly then decreases (top of Figure 1). Similarly, the function for drinking bout duration (bottom of Figure 4) also does not change linearly with NaCl concentration above the putative adapting concentration. The peak of the function occurs at 0.2 M NaCl, a concentration well above the adapting concentration. The absence of linearity in the amount consumed and drinking bout duration above 0.04–0.08 M NaCl may reflect the variability of the adapting concentration (see discussion above); the NaCl test solution must be one ‘jnd’ above the adapting concentration to be recognized as tasting salty. In fact, the animals alternated between their elective consumption of water and NaCl solution when 0.15–0.2 M NaCl solution were available (Figure 6) and also more switches occurred between these two solutions (Figure 7).

The absence of linearity above 0.04 M NaCl probably also reflects the influence of post-ingestional consequences of drinking and eating (Mook, 1963; Mook and Kozub, 1968; Stricker and Verbalis, 1988). Water drinking is needed to reduce the osmotic effects of drinking palatable saline, particularly when it is also associated with the consumption of 1% NaCl chow (NaCl to water switch). By removal of an inhibitory hyperosmotic signal, water drinking consequently permits hedonically-driven saline ingestion (water-to-NaCl switch). Indeed, the total amount of sodium consumed from chow and solution (see Table I) is highest when 0.15, 0.18, and 0.2 M NaCl solutions are available; as shown in Figure 7, this is also when there is increased switching between NaCl and water and vice versa. The induced increase in total sodium consumption by palatable saline intake (see Table I), is likely also responsible for the decline in food bout number (top of Figure 5). Sodium consumption apparently inhibits food intake by decreasing feeding bouts. This is counteracted by an increase in food bout duration to preserve caloric intake (bottom of Figure 5).

The single micromolar feature of NaCl drinking that seems to be consistent with a taste-mediated explanation is drinking bout number (top of Figure 4). The peak of the function for drinking bout number occurs at 0.04 M NaCl, a concentration near but
Table I. Average total amount of sodium consumed from chow plus saline in rats given a two-bottle preference test between water and various molar concentrations of NaCl.

<table>
<thead>
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<th>NaCl concentration (M)</th>
<th>Sodium consumed (g)</th>
<th>(mEq)</th>
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<td>0.01</td>
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<td>5.21</td>
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<td>0.40</td>
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Values were computed by adding the number of grams of sodium consumed from 1% NaCl-containing chow with that from the specific NaCl solution. mEq, milliequivalent.

likely above the adapting concentration. With stronger NaCl concentrations, drinking bout numbers decrease linearly paralleling the decrease in food bout number (top of Figure 5). Such a function corresponds to the psychophysical function of perceived stimulus intensity in humans (Bartoshuk, 1974), the neural response function to NaCl stimulation in rats (Contreras and Frank, 1979; Frank et al., 1983), as well as the sham drinking function of rats implanted with a gastric fistula preventing NaCl absorption and postintestinal feedback from influencing intake (Contreras, 1989). Why drinking bout number is more systematically associated with NaCl intensity that the other variables is because of its relationship to food intake and prandial drinking. Rats unequivocally elect to consume saline after a meal when the NaCl test concentration is between 0.04 and 0.08 M. Thereafter, the number of food-to-saline switches decline with increasing NaCl intensity and the number of food-to-water switches increase (Figure 6). Rats unequivocally elect to consume water after a meal when the NaCl test concentration is between 0.3 and 0.4 M. When intermediate NaCl concentrations are available (0.15—0.20 M), the switching patterns not only include food-to-fluid, but also saline-to-water and vice versa. This additional switching modifies the volume consumed and drinking bout duration. Furthermore, the number of food bouts decline with increasing NaCl intensity (Figure 5), suggesting a bidirectional influence between the patterns of food intake and NaCl drinking.

Taken together, the present results bear testimony to the value of recording the micromolar features of eating and drinking in a standard laboratory feeding situation. By such analysis, we were able to measure aspects of behavior critical to an understanding of the sensory control of ingestion. Such analysis was done without physiological intervention with the animals being tested in their home cage environment throughout the day—night cycle. The animals were able to express their natural tendencies of nocturnal feeding and prandial drinking while we were able to make assessments of taste-mediated changes in NaCl ingestion. By doing so, the results may be viewed as having power and significance beyond that provided in studies that do not take into account the animals’ native feeding habits.
Table 1. Average total amount of sodium consumed from chow plus saline in rats given a two-bottle preference test between water and various molar concentrations of NaCl.

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<td>0.31</td>
<td>13.47</td>
</tr>
<tr>
<td>0.18</td>
<td>0.33</td>
<td>14.34</td>
</tr>
<tr>
<td>0.20</td>
<td>0.31</td>
<td>13.47</td>
</tr>
<tr>
<td>0.30</td>
<td>0.18</td>
<td>7.82</td>
</tr>
<tr>
<td>0.40</td>
<td>0.15</td>
<td>6.52</td>
</tr>
</tbody>
</table>

Values were computed by adding the number of grams of sodium consumed from 1% NaCl-containing chow with that from the specific NaCl solution. mEq, milliequivalent.

likely above the adapting concentration. With stronger NaCl concentrations, drinking bout number decreases linearly paralleling the decrease in food bout number (top of Figure 5). Such a function corresponds to the psychophysical function of perceived stimulus intensity in humans (Bartoshuk, 1974), the neural response function to NaCl stimulation in rats (Contreras and Frank, 1979; Frank et al., 1983), as well as the sham drinking function of rats implanted with a gastric fistula preventing NaCl absorption and postingestional feedback from influencing intake (Contreras, 1989). Why drinking bout number is more systematically associated with NaCl intensity that the other variables is because of its relationship to food intake and prandial drinking. Rats unequivocally elect to consume saline after a meal when the NaCl test concentration is between 0.04 and 0.08 M. Thereafter, the number of food-to-saline switches decline with increasing NaCl intensity and the number of food-to-water switches increase (Figure 6). Rats unequivocally elect to consume water after a meal when the NaCl test concentration is between 0.3 and 0.4 M. When intermediate NaCl concentrations are available (0.15–0.20 M), the switching patterns not only include food-to-fluid, but also saline-to-water and vice versa. This additional switching modifies the volume consumed and drinking bout duration. Furthermore, the number of food bouts decline with increasing NaCl intensity (Figure 5), suggesting a bidirectional influence between the patterns of food intake and NaCl drinking.

Taken together, the present results bear testimony to the value of recording the micromolar features of eating and drinking in a standard laboratory feeding situation. By such analysis, we were able to measure aspects of behavior critical to an understanding of the sensory control of ingestion. Such analysis was done without physiological intervention with the animals being tested in their home cage environment throughout the day–night cycle. The animals were able to express their natural tendencies of nocturnal feeding and prandial drinking while we were able to make assessments of taste-mediated changes in NaCl ingestion. By doing so, the results may be viewed as having power and significance beyond that provided in studies that do not take into account the animals’ native feeding habits.
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References


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