Loss of sensitivity to low concentrations of NaCl following bilateral chorda tympani nerve sections in rats

Gwen B. O’Keefe¹, Juliann Schumm² and James C. Smith³

Department of Psychology, The Florida State University, Tallahassee, Florida 32306-1051, USA

¹Present address: State University of New York, Health Science Center at Brooklyn, New York, USA
²Present address: University of Central Florida
³To whom correspondence should be addressed

Abstract. A reliable short-term NaCl taste test was developed for rats which resulted in differential responding to a variety of concentrations. The rats were required to exist on a low sodium diet for 8–10 days prior to the initiation of testing. The peak response in this test was to isotonic NaCl with lesser responding to hyper- and hypotonic solutions. After stable responding was obtained, bilateral sections were made of the chorda tympani nerves. This surgery resulted in a loss of sensitivity to the lowest hypotonic solutions (0.03 and 0.06 M NaCl). Little, if any, effect was noted in the perception of sucrose following these nerve sections.

Introduction

Although electrophysiological data from the rat suggest that specific regions of the oral cavity are preferentially responsive to sodium salts and to sucrose (e.g. Boudreau et al., 1983, 1985, 1987; Frank, 1991; Frank et al., 1983; Nejad, 1986; Travers et al., 1986) early behavioral taste experiments in which taste nerves were severed in rats revealed little, if any, specific behavioral deficits (Richter, 1939; Pfaffmann, 1952; Akaike et al., 1965; Vance, 1967). The lack of demonstration of even general changes in ingestive behavior to these stimuli following sectioning of the chorda tympani (CT) or glossopharyngeal nerves most likely stemmed from the behavioral techniques used (intake measures) and too much focus on lingual receptor fields. More recently, using rats as subjects, it has been shown that sweet solutions appear to be most effective on palatal receptors innervated by the greater superficial petrosal nerve (GSP) (Travers et al., 1986; Nejad, 1986).

Behavioral measures of taste based on intake can be influenced by post-ingestive events (e.g. Grill et al., 1987; Rabe and Corbit, 1973; Weingarten and Watson, 1982), making inferences about taste processes questionable. By using short-term measures of taste that minimize the effects of post-ingestive consequences, Spector and his co-workers (Spector et al., 1990a,b; Spector and Grill, 1992; Breslin et al., 1993b) have shown that following bilateral sectioning of the CT, detection thresholds to NaCl are raised by as much as two orders of magnitude, while threshold values for sucrose remained essentially unchanged. They also reported that rats with sectioned CT’s have difficulty discriminating NaCl from KCl and that following furosemide injections the rats showed increased appetite for NaCl, KCl and NH₄Cl, as compared to sham-operated rats which show an appetite for only NaCl, suggesting that the CT contributes to sodium identification.

The effects of bilateral sectioning of CT in a short-term taste test to sucrose solutions

© Oxford University Press 169
was conducted by Krimm et al. (1987). In these experiments the rats were given five
daily 30-s exposures to a specific concentration of sucrose. Over a 5-day period the
sucrose concentration was increased from 0.01 to 1.0 M. These non-deprived male
rats showed an increase in mean licks-per-exposure as the sucrose concentration was
increased. Bilateral sections of CT had little, if any, effect on the response to sucrose,
but rats with GSP sections markedly reduced their response to sucrose at the higher
concentrations. Similar tests of the effects of CT sections on supra-threshold NaCl
solutions were not possible with this procedure because the rats would not reliably lick
the salt solutions in 30-s tests when there was no prior fluid deprivation. Rats can be
induced to drink supra-threshold NaCl solutions in short-term taste tests by acute sodium
depletion with furosemide injections (Sollars and Bernstein, 1991; Breslin et al., 1993b).
In fact, Breslin et al. (1993a) have shown a preference/aversion function over NaCl
concentrations ranging from 0.05 to 0.5 M following such depletions, yielding a curve
not unlike the function seen with long-term NaCl preference tests (Contreras and Smith,
1990). Although Breslin et al. (1993a) reported a preference/aversion NaCl curve for
sodium replete rats where the behavioral response was significantly greater to a 0.15 M
solution than to 0.05 or 0.5 M solutions, these rats failed to initiate nearly as many
trials to the salt solutions as the depleted rats.

Stricker et al. (1991) showed that a very strong sodium appetite could be induced
in male rats to a 0.5 M NaCl solution after 8 days on a sodium-free diet. In a 7-h
preference test these rats consumed an average of 11.2 ml of 0.5 M NaCl solution in
the first 30 min. Although water was available to these animals, they drank little of
it during this first 30 min. They report that this 'procedurally simple physiological
manipulation elicits much greater NaCl consumption than is seen after systemic injection
of a diuretic drug'.

The first purpose of the present study was to see if a more reliable differential response
to various concentrations of NaCl solutions could be elicited in short-term taste tests
by subjecting the rats to a prolonged NaCl deprivation such as that described by Stricker
et al. (1991). Thereby, neither water deprivation nor drug injections would be necessary
to briefly present a daily series NaCl concentrations which because of the short-duration
test, would minimize post-ingestional factors, allowing for the development of response
functions from which the inference of taste could be made (Experiment 1). Subsequently,
the second purpose would be to test the effects of bilateral CT nerve sections on the
behavior of the rats toward these suprathreshold values of NaCl (Experiment 2).

A modification of the short-term taste testing procedure described earlier by Krimm
et al. (1987) was developed by Smith et al. (1992) to study the rat's immediate response
to sucrose solutions. With this procedure, a non-deprived rat was placed in a special
testing chamber and given access to a particular concentration of sucrose for 30 s. Thirty
seconds later another concentration was presented for the 30-s period. This was repeated
until five to eight concentrations were presented for these brief periods in one testing
session lasting little more than 5 min. Responses similar to those obtained by Krimm
et al. (1987) were observed, i.e. an orderly increase in licks per 30 s as a function of
increase in sucrose concentration whether the various concentrations of sucrose were
presented in ascending, descending or random order. This reliable relationship between
rate of licking and concentration which was shown for sucrose, held for tests with
glucose, maltose, fructose and polyose (Smith et al., 1992). In addition, because licking
behavior in these observations could be measured with 1.0 ms resolution, the micro-
structural features of the licking behavior such as number of licking bursts, burst duration
and inter-burst-intervals could be analysed.

In the following first experiment, it was found that a reliable and orderly response
to a variety of concentrations of NaCl could be obtained with this procedure if the rats
were maintained on a salt-restricted diet for 10 days prior to the start of testing.

Experiment 1

Subject

Eight male Sprague-Dawley albino rats (Charles River) with an average weight of
388 g at the beginning of training were kept in a temperature controlled environment
on a 12 h−12 h light−dark cycle (lights on at 07.00 hours). The animals were housed
in special cages described below. They were allowed ad-libitum access to Purina Chow
(5012) and water except where described in the procedure. The NaCl content of Purina
Chow is approximately 1.0%.

Apparatus

The home cages have been described in detail elsewhere (Spector and Smith, 1984;
Smith, 1988a,b; Smith et al., 1988; Smith and Gannon, 1991; Stricker et al., 1992).
Basically, these cages were Hoeltge 11B stainless steel rat cages that were modified
by installing two drinking ports on the back and a feeding station on the front. In front
of each of the two drinking ports and the feeding station an infra-red emitter and receptor
were aligned so that licking on a drinking tube or entry into the feeding jar interrupted
the infra-red beam. When the rat put its head into the food jar the number of seconds
of beam-break was recorded. This information along with the beam-breaks from licks
was transmitted through an interface board to a PIO-10 card (Metabyte), which was
placed in a micro computer. The data collection software allowed for the input from
the eight rat cages simultaneously over a 23 h daily testing period. Beam-breaks were
recorded in sequential 6-s bins. Data were collected daily for 23 h allowing a 1-h period
for cleaning and replenishing the food and water containers. The analysis program
allowed for collection of the data into eating and drinking bouts. The criterion for end-
ing a bout was 50 consecutive bins, i.e. 5 min with no beam-breaks. The typical
variables analysed for both day and night periods were bout number, bout length, number
of licks-per-bout and the inter-bout intervals. For brief periods on selected days, the
rats were removed from these cages and given a brief test in the taste testing chamber.
The taste testing chamber has been described in detail by Smith et al. (1992). Basically,
it was a stainless steel box, 11.5 cm wide, 29.5 cm long and 25.5 cm tall. The floor
was made of 1/4" rods, 1.3 cm apart and the ceiling was Plexiglas. The opening for
a drinking tube was located on the front wall of the chamber and could be covered
by a motor driven shutter. The stainless steel drinking tube was recessed behind the
wall so that in order to drink the rat had to lick through a vertical slot 2.6 cm wide
to make contact with the orifice of the tube. Between the slot and the tip of the tube,
an infra-red (IR) emitter and a photoreceptor were aligned so that each lick on the tube
broke the IR beam allowing for a convenient method for counting licks. Eight such
drinking tubes were securely mounted in a row on a metal plate so that any one of

171
them could be positioned in front of this drinking slot. The plate was mounted on linear bearings, and was moved back and forth by a reversible motor. A helipot monitored the position of the plate and allowed for precise positioning of any of the tubes in front of the drinking slot. A microcomputer controlled the shutter and the positioning of the drinking tube. During each trial, IR beam-breaks, i.e. licks, were collected in consecutive millisecond time bins, transmitted to the microcomputer and saved on floppy disk for subsequent detailed analysis of licking behavior.

Procedure

The regimen for feeding the rats was divided into three phases. During Phase 1 the rats received for 23 h each day *ad lib* food (powdered Purina Chow) and water for 21 consecutive days. In Phase 2 the food was changed to Teklad Sodium Sufficient Control Diet (#170955) for 28 days. During Phase 3 the food was changed to Teklad Sodium Deficient Test Diet (#170950) for 38 days.

During the latter part of Phase 1 the rats were placed in the taste testing chamber for 30 min daily to accustom them to lick readily from the recessed drinking spout. This training occurred over a period of 2 weeks overlapping Phase 2 when the rats had been switched to the sodium-sufficient control diet. During this training period the rats had access to a tube containing 0.25 M sucrose each day. The tube was initially pushed forward into the testing cage and the shutter remained open. Each day that the animal drank more than 3 ml of the sucrose solution within 30 s, the training tube was withdrawn 2–3 mm on the subsequent day. Once the animal readily drank from the spout in the testing position, computer control of training was begun. Three 10-min presentations of the sucrose separated by 10-s inter-trial-intervals (ITI) were given for 4 days with the shutter opening and closing under computer control. On subsequent days the number of trials were increased, the trials length shortened and the ITI lengthened. The final testing procedure was the presentation of at least five or six trials of 30 s each with an ITI of 30 s. At no time during testing were the animals allowed to remain in the testing chamber for more than 15 min without drinking from the spout. If the animal did not initiate a trial within 15 min of being placed in the chamber or of completing a trial, the shutter was closed and the animal was removed from the chamber for that day.

In order to show that the rats’ behavior in these short-term tests was consistent with previous data from such short-term tests (Smith *et al.*, 1992) where rats were maintained on Purina Chow, baseline taste tests were run with sucrose while they were being maintained on both of the Teklad diets. Twenty-one days after switching the rats to the sodium-sufficient control diet, an ascending series of sucrose concentrations was presented on each of three days separated by three days. The concentrations of sucrose used were 0.01, 0.02, 0.1, 0.3 and 1 M. Twelve days after the rats were switched to the Teklad Sodium Free Diet they were given three additional daily sucrose tests as described above.

Finally, while they were on the sodium-free diet they were given 4 days of training in the test apparatus with an ascending series of NaCl on concentrations of 0.03, 0.06, 0.125, 0.25 and 0.5 M. For the sodium chloride sessions they were only tested every fourth day to avoid replenishing their sodium levels. The data are reported for the last 3 days of NaCl testing.
Fig. 1. Mean licks per 30 s are plotted as a function of sucrose concentration. The solid line represents data collected while the rats were maintained on Teklad Sodium Sufficient Control Diet (#170955) and the dotted line represents data collected after the rats had been on the Teklad Sodium Deficient Test Diet (#170950) for 2 weeks. The differences between the two groups were not statistically significant.

Fig. 2. Mean licks per 30 s (and standard errors) are plotted as a function of NaCl concentration. The eight rats had been maintained on the Sodium Deficient Diet for 20 days.
Fig. 3. Mean cumulative licks are plotted over the 30 s exposure to each of the five NaCl concentrations.

Results

There was little variation in food and water intake in the home cages during Phase 1. On the last day of this phase the rats ate an average of 27.4 g of Purina chow in 17.8 bouts of 7.1 m duration. They drank an average of 44 ml of water in 32.8 drinking bouts of 2.4 m long. On the last day of Phase 2 (the sodium sufficient diet) the average powdered food intake was 25.7 g (in 12.3 bouts of 6.6 m duration) which was not a significant decrease from that of Phase 1 ($t = 1.14$, df = 7, $P > 0.05$). The mean water consumption was significantly lower in Phase 2 than in Phase 1 by 15.6 ml ($t = 3.15$, df = 7, $P < 0.05$). This reduction in water intake from Phase 1 was due to the significant decrease in number of water bouts which averaged 16.8 in Phase 2 ($t = 5.05$, df = 7, $P < 0.01$). Food intake during Phase 3 (sodium-free diet) was 24.6 g (in 8.6 bouts averaging 9.5 m in duration), water intake was 27.7 ml (in 16 bouts of 2.6 m duration). These consumptions and ingestion patterns were comparable to those during Phase 2. The reduction in water intake during periods when the Teklad diets were available had no effect on the performance of the rats in the short-term taste tests with sucrose.

As can be seen in Figure 1, mean licks per 30 s in the sucrose baseline tests increase with increases in sucrose concentration. A $2 \times 6$ repeated sampling of the same subjects ANOVA across these data indicate that the sucrose curves attained during the control diet (Phase 2) and the sodium-free diet (Phase 3) are not different ($F = 2.91$, df = 1.7; $P > 0.05$). Both of these curves are comparable to those from previous studies (Krimm et al., 1987; Smith et al., 1992).

The mean number of licks for each 30-s presentation of the NaCl concentrations can be seen in Figure 2. These data have been averaged over the 3 days of testing. The
Loss of sensitivity to NaCl

Fig. 4. Mean licks per second are plotted over the 30 s exposure. For clarity only three concentrations are shown here, i.e. isotonic saline, a high concentration (0.5 M) and a low concentration (0.03 M).

Fig. 5. Mean pause duration is plotted as a function of concentration of the NaCl. These are pauses between bursts of licking where the criterion for separating bursts is a 300 ms pause.
inverted U-function has a maximum response to the 0.125 M concentration. In Figure 3 the mean cumulative licks over the 30-s testing period are plotted. The rate of licking for each second of testing can be seen in more detail in Figure 4. For clarity, only the middle, high and low concentrations are plotted. Here, it can be seen that the rate during the first second of the test is nearly 6 per second. The initial drop for the high and low concentrations is sharp, followed by a more gradual decline for the remainder for the 30-s testing period. The decline in rate for 0.125 M is more gradual, only dropping to about 4 licks/s by the end of the 30-s test.

A detailed analysis of the NaCl solution drinking during the 30-s test indicated that the ‘local rate’ of licking stayed high, but the length of the pauses between the bursts of licks determined the overall number of licks described in Figure 2. Using a ‘burst criterion’ of 300 ms, i.e. a pause of 300 ms ends the burst, the number of bursts increased with an increase in NaCl concentration and the duration of the bursts decreased with increasing NaCl concentration. The mean pause duration between the bursts resulted in a U-shape function as can be seen in Figure 5. This figure was the inverse of Figure 2.

Discussion

While maintained on the sodium-deficient diets the rats had a lower water intake than was seen when they were maintained on powdered Purina Chow. When rats were eating powdered Purina Chow they interrupted an average of three of their meals to drink. Not any interruptions for drinking were observed when the rats were eating the sodium-free diet. However, this reduction in water intake did not seem to have any effect on the sucrose preference curve as compared to those obtained when the rats were on chow.

From the above results it is quite clear that if the rats are maintained for a few days on a salt-deficient diet a reliable response to NaCl solutions can be obtained in this short-term test, which is preceded by no water deprivation. The function is not unlike the NaCl intake from a two-bottle preference curve from long-term tests for NaCl (e.g. Contreras and Smith, 1990). This ultra-short-term taste test has the advantage of minimizing the post-ingestional influences of NaCl on the ingestive behavior. It is also clear that the overall rate of licking NaCl solutions in a 30-s test is the result of the duration of the pauses between bursts of licks. During the first second or two the rat equally samples the various concentrations of NaCl. The overall rate of licking on the higher and lower concentrations rapidly declines as the pauses between licks increase. In this testing apparatus it takes about 200 licks for the rat to ingest 1 ml of solution. Therefore, in a typical NaCl test session the rat would have ingested about 0.025 g of NaCl. This would be about 10% of normal daily NaCl intake if the rat were maintained on Purina Chow. In this experiment, testing every 3 days was a conservative way to inhibit salt repulsion, while the rats were on a sodium-free diet. The reliability of the NaCl curves obtained here warranted the subsequent experiment to observe the effects of bilateral chorda tympani nerve cuts on this measure of the taste of supra-threshold NaCl solutions.

Experiment 2

Subjects

Twelve male Sprague-Dawley albino rats (Harlan), 320–375 g at the beginning of the experiment, were used. Seven of these rats were housed in the special home cages
Fig. 6. Mean licks per 30 s are plotted as a function of sucrose concentration. The white bars represent data collected prior to the CT sectioning (PRECT) and the shaded bars represent the behavior following CT cuts (POSTCT). Standard errors are shown for each group at each concentration. The differences between the two groups were not statistically significant.

described in Experiment 1. The other five were housed in similar cages but without the capability to monitor the patterns of food and water intake. Water was always available to the rats throughout the experiment. The schedule for the powdered food is indicated below.

**Procedure**

The schedule for the home cage diet was similar to that used in Experiment 1. The rats were initially maintained on Purina Chow and then fed the salt-sufficient control diet for 20 days. During this period they were trained to lick in the short-term testing apparatus as described in Experiment 1. After training was completed the rats were tested for 7 days on a series of sucrose concentrations (0.01, 0.03, 0.10, 0.30 and 1.0 M). The rats were then placed on the sodium-free diet for the next 57 days. Fourteen days after the start of the sodium-free diet the rats were given 5 days of testing in the short-term apparatus with the above series of sucrose concentrations. This was followed by four days of testing with the NaCl series (0.03, 0.06, 0.125, 0.25 and 0.5 M). These four salt taste test days were separated by 3 days of no testing. Three days after the completion of the NaCl taste tests, the rats were divided into two groups of eight and four. Eight rats had bilateral sections made of their chorda tympani nerves and four were sham-operated using the surgical procedures described below. Seven days following surgery the rats were given 1 day of testing with the sucrose and three additional testing days with NaCl. The NaCl tests were scheduled four days apart. Following the last NaCl test the rats were perfused and their tongues were removed for examination of the presence of taste pores.

**Surgery**

Animals were deeply anesthetized with ketamine (80.6 mg/kg) and xylazine (9.9 mg/kg). They were placed in a head holder and the head was rotated approximately 80° away
Fig. 7. Upper panel: mean licks per 30 s as a function of NaCl concentration before (solid line) and after (dashed line) sections were made of the chorda tympani nerves. The error bars represent the standard errors. The differences are statistically significant only for the 0.03 and the 0.06 M concentrations. Lower panel: mean licks per 30 s as a function of NaCl concentration before (solid line) and after (dashed line) sham operations. The differences are not statistically significant at any concentration.

from the surgeon. The external auditory meatus was enlarged using blunted hypodermic needles as retractors until the tympanic membrane and the malleus were easily visualized through the operating microscope. The membrane was removed using curved no. 5 forceps, and a small caudal portion of the bony meatus was removed as well to visualize the chorda tympani. The malleus was then removed. The chorda tympani was then cut unless it had already been cut in the process of removing the malleus. Eight animals had their chorda tympani nerves cut bilaterally and four animals were anesthetized and subjected to a sham operation.

 Procedures for verification of the nerve cuts. After the completion of behavioral testing the animals were deeply anesthetized with intraperitoneal sodium pentobarbital and transcardially perfused with 0.9% saline followed by 10% formalin. The anterior tongue surface was coated with methylene blue. With the aid of a dissecting microscope, two
Loss of sensitivity to NaCl

Fig. 8. In the upper panel mean cumulative licking is plotted over the 30 s exposure to 0.03 M NaCl before (closed triangles) and after (open squares) sectioning of the chorda tympani nerves. Similar data for the 0.06 M NaCl solution is seen in the lower panel.

observers examined the tongues for the presence of taste pores. The observers were blind to the surgical status of the rats.

For a second method of verification of CT transections, Smith et al. (1988) have shown that increases in eating bout duration following the surgery can serve as a reliable behavioral assay. Therefore, in the present experiment, eating bout duration was measured before and after the CT sections were made in the seven rats that lived in the special home cages.

Results

Bilateral sections of the CT had no effect on the response of the rats in the short-term testing apparatus to sucrose. The apparent reduction in lick rate to all of the sucrose concentrations seen in Figure 6 was not statistically significant as was shown by a repeated sampling of the same subjects ANOVA ($F = 3.62$, df 1,7; $P > 0.05$; Keppel, 1973). In contrast, as can be seen in the upper panel of Figure 7, the CT nerve cuts caused a sharp decrement in the mean licks per 30 s for the lower concentrations of NaCl ($F = 6.11$, df 1,7; $P < 0.05$). Matched $t$-tests between pre- and post-CT sections for the 0.03 M and the 0.06 M concentrations were 2.62 ($P < 0.01$) and 4.65 ($P < 0.01$), respectively. The ANOVA on the pre- and post-sham-operated rats (lower panel of Figure 7) was not significant ($F = 0.81$, df 1,7; $P > 0.05$). From Figure 8 it can be seen that the mean decrement in licking both the 0.03 M and the 0.06M CaCl solutions by the eight rats with CT sections was apparent within 2 or 3 s into the testing period.
The rats treated these two low concentration solutions as if the solutions were water in a similar manner to rats run in this apparatus in other studies where water was the only solution present. This rapid discrimination is characteristic of the data shown in Figure 4 of this paper and the results from Spector et al. (1990a) for NaCl solutions, and the data from Smith et al. (1992) for a variety of sugars.

An analysis of the drinking bursts during the pre- and post-CT sectioning periods for the 0.03 and 0.06 M concentrations revealed that the number of bursts remained constant (t values of 0 and 0.10, respectively; $P > 0.05$). Burst duration and licks-per-burst were significantly reduced and the inter-burst-interval was significantly increased after the nerves were cut (all $P$ values were less than 0.01). These data are seen in Figures 9 and 10, respectively, from 0.03 and 0.06 M NaCl solutions.

Both morphological and behavioral evidence was available to verify that the CT nerves were indeed sectioned. Examination of the tongues stained with methylene blue revealed that there was a complete lack of taste pores in the majority of taste buds of the CT-
sectioned rats. The presence of taste pores in the four sham-operated rats was unequivocal. An analysis was also made of the 24-h feeding patterns in the seven rats that were housed in the special cages. The total amount eaten and the number of meals were the same for the pre- and post-CT periods. In contrast, the meal duration for the operated rats went from an average of 5-12 min. This difference was statistically significant ($t = 4.13, P < 0.01$) and is similar to the results reported by Smith et al. (1988).

**Discussion**

All eight rats with bilateral CT sections showed a profound decrement in licking at the 0.03 and 0.06 M concentrations of NaCl. As was seen in Figure 9, this decrement is the result of a marked decrease in the number of licks-per-burst which directly affects the burst duration and inversely affects the inter-burst-interval. There was no decrease
in the number of licking bursts. Spector et al. (1990a,b) reported an increase in threshold of about two orders of magnitude following CT sections. If such a loss in sensitivity occurred in the present experiment, the 0.03 M solution would be equivalent to the rat as 0.001 – 0.0002 M, and the 0.06 M solution would be between 0.002 and 0.0004. This would imply a linear shift across all concentrations in the perceived taste of NaCl which is not evident in the higher concentrations of the present data. The range of thresholds in normal rats to NaCl have been reported to fall between 0.00034 and 0.00084 (Thaw and Smith, 1992). The two lower concentrations of NaCl could have been significantly reduced in perceived intensity to the rats or it is possible that they could not taste them at all and they treated them as they would water. It is also possible that these low concentrations no longer tasted like NaCl to the rats, resulting in a decrease in motivation to continue licking. Spector and Grill (1992) observed a significant decrement in the rat’s ability to discriminate NaCl from KCl at 0.05, 0.1 and 0.2 M concentrations. The CT sections in their study could have resulted in the two lower concentrations ‘tasting’ like water, but in the most extreme case (a 2.33 log unit increase in threshold) 0.2 M solutions would not be reduced in taste to a value less than the rat’s normal threshold (0.0012 M, which is considerably above threshold). It is not clear in this study what effect the salt deprived diet had on the motivation of the rats to consume the higher concentrations of NaCl. It is possible that rats can be taught to lick salt solutions by placing the rats on a mild daily water deprivation and the salt deficient diet would be unnecessary. Further work is in progress to test this hypothesis.

Although the average responses to sucrose in the present and other studies (Krimm et al., 1987; Spector et al., 1990a,b; Slotnick et al., 1991; Spector and Grill, 1992) appear to diminish after CT sections, the statistical analyses indicate that CT sections do not significantly impair the responses to either threshold or suprathreshold sucrose stimulation of the rat. The present experiment adds to that body of knowledge that the CT plays an important role in salty as compared to sweet detection and discrimination.

The CT innervates the submaxillary and sublingual salivary glands and it is known that these glands are markedly affected by CT nerve sections (Stricker and Hainsworth, 1970; Smith et al., 1988). As Spector and Grill (1992) point out, it is unlikely that the loss of function in these glands compromises the ability of the rat to detect and discriminate salt solutions. This possibility is currently being explored in this laboratory because it has been reported that preference for 0.1 M salt solutions is decreased after removal of the submaxillary and sublingual salivary glands (Brosvic and Hoey, 1990). However, these same authors report that taste detection for NaCl is unaffected by the removal of these glands.

Acknowledgements

The research was supported in part by grants from the National Institute on Aging, AG04932 and AG06841. The authors would like to thank Rachel Kelley and Jodi Rhinehart-Doty for data analysis; Dr Alan Spector and Dr Robert Contreras for critical review of the manuscript; Dr Inglis J. Miller for the methylene blue technique for verification of CT sections; and Dr Edward M. Stricker for the suggestion of using the sodium-free diet to motivate spontaneous NaCl solution drinking in the short-term tests.
References


Received on August 9, 1993; accepted on November 16, 1993