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Chorda Tympani Nerve Transection Disrupts Taste Aversion Learning to Potassium Chloride, but Not Sodium Chloride

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In Experiment 1, rats with chorda tympani nerve transection (CTX) acquired a LiCl-conditioned taste aversion to 0.1 M NaCl at the same rate as controls. After 3 conditioning trials, the aversion generalized to 0.03 and 0.3 M NaCl, but did not generalize to KCl (0.03, 0.1, and 0.3 M), in either the sham or CTX group. In Experiment 2, the sham group, but not the CTX group, formed an aversion to 0.1 M KCl after 1 trial. The CTX rats did form a moderate aversion after 2 conditioning trials. Following the 3rd trial, the CTX group did not suppress licking to 0.03 or 0.3 M KCl or any concentration of NaCl in relation to controls. Although there is strong evidence that CTX affects NaCl taste perception, these findings indicate that, under certain conditions, rats can nonetheless distinguish NaCl from KCl after such neurotomy. Moreover, CTX appears to have a substantial effect on the perceived intensity of KCl.

A variety of behavioral studies have indicated a unique role for the chorda tympani nerve (CT) in taste-guided responses to NaCl in rats (Breslin, Spector, & Grill, 1993, 1995; Grill, Schwartz, & Travers, 1992; Markison, St. John, & Spector, 1995; O'Keefe, Schumm, & Smith, 1994; Slotnick, Sheelar, & Rentmeister-Bryant, 1991; Sollars & Bernstein, 1992, 1994; Sollars, Sollars, & Bernstein, 1991; Spector & Grill, 1992, 1994; Spector, Schwartz, & Grill, 1990; St. John, Markison, Guagliardo, Hackenberg, & Spector, in press; St. John, Markison, & Spector, 1995). Two conflicting studies have appeared concerning the role of the CT in establishing taste aversions to 0.1 M NaCl. Specifically, Yamamoto, Shimura, Sako, Yasoshima, and Sakai (1994) found that rats with CT transection could not acquire a taste aversion to 0.1 M NaCl, whereas Raskin, Akey, and Travers (1992) failed to find an effect of CT neurotomy.

The strength of a taste aversion varies in relation to a number of procedural variables, such as the strength of the conditioned stimulus, the strength of the unconditioned stimulus, the delay between conditioned and unconditioned stimuli, and the number of conditioning trials (Domjan, 1980; Nachman & Ashe, 1973; Nowlis, 1974; Shaw, 1983; see also Riley & Clarke, 1977). Regardless of these procedural issues, if rats with CT transection were unable to form a conditioned taste aversion to 0.1 M NaCl under any circumstances, it would imply that gustatory deafferentation of the anterior tongue renders this stimulus behaviorally irrelevant. The present experiments were conducted to test this under conditions that would favor acquisition; the design incorporated a strong dose of the unconditioned stimulus (LiCl) and three conditioning trials rather than one.

Because CT transection impairs performance in a NaCl versus KCl operant taste discrimination task and reduces the sodium specificity of depletion-induced salt appetite, it is possible that the two salts become perceptually similar after CT transection (Breslin et al., 1993; 1995; Markison et al., 1995; Spector & Grill, 1992; St. John et al., 1995). Further circumstantial evidence for this possibility comes from the work of Hill, Formaker, and White (1990). These investigators added amiloride to a 0.5-M NaCl conditioned stimulus and found that aversions to NaCl generalized to KCl. In rats and hamsters, amiloride blocks narrowly tuned sodium-responsive afferents in the CT while having no effect on the broadly tuned sodium-responsive afferents that also respond to KCl (Hettinger & Frank, 1990; Ninomiya & Funakoshi, 1988). On the basis of the neurophysiological profile of the gustatory nerves, as well as amiloride's effects in behavioral studies (Hill et al., 1990; Spector, Guagliardo, & St. John, in press), amiloride application may alter the perceived quality of NaCl. Because transection of the CT eliminates a large population of these amiloride-suppressible sodium afferents, such neurotomy might be expected to cause effects similar to amiloride adulteration of NaCl. Therefore, we examined the possibility that NaCl aversions might generalize to KCl in rats with CT transection.

Finally, it is important to consider that taste aversion generalizations can occur within either the qualitative or intensity domains (Nowlis, 1974; Scott & Giza, 1987; Spector & Grill, 1988; Tapper & Halpern, 1968). Thus, a failure for a NaCl aversion to generalize to KCl could mean that the perceived qualities of the two salts are dissimilar in rats with CT transection, or it could mean that KCl is weaker than NaCl at isomolar concentrations. Therefore, the test stimulus array included a range of concentrations (0.03 to

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0.3 M), and a second experiment was conducted using 0.1 M KCl as the conditioned stimulus. Consequently, the interchemical generalization gradient could be examined in relation to the intrachemical generalization gradient when each salt served as the conditioned stimulus (see Spector & Grill, 1988; Tapper & Halpern, 1968).

Experiment 1

Method

Subjects. Twenty-four naive, adult, male Sprague-Dawley rats (Charles River Laboratories, Wilmington, MA) were housed individually in hanging wire-mesh cages in a room where temperature, lighting (12:12-hr light–dark cycle), and humidity were automatically controlled. The rats weighed 321–421 g at the start of the experiment. Food (Purina Chow 5001) and distilled water were always available except where noted. All manipulations were performed during the lights-on phase of the light–dark cycle.

Gustometer familiarization. Rats were deprived of water approximately 24 hr before gustometer familiarization. The gustometer (Spector, Andrews-Labenski, & Letterio, 1990) is a computer-controlled testing apparatus that monitors licking behavior through a contact circuit that delivers less than 50 nA through the rat. Taste stimuli can be delivered either continuously or in brief access trials. On the first 2 days of training, rats had constant access to distilled water for 30 min (each lick delivered 5 μl of fluid). On the following 3 days, rats had 40-min sessions during which distilled water was delivered in 5-s trials. This phase served to familiarize the rats with the trial structure of stimulus presentation.

Surgery. Surgery followed at least 3 nights of free access to distilled water on the home cage. Twelve rats each received either bilateral CT transection in the middle ear (CTX) or sham surgery (CON). All rats were injected intraperitoneally with a mixture of ketamine hydrochloride (86 mg/kg) and xylazine hydrochloride (13 mg/kg) anesthesia. They were placed in a headholder while resting on an isothermal heating pad. The auditory meatus was retracted with five blunted and curved hypodermic needles and the tympanic membrane was punctured. For the rats in the CTX group, the ossicles were then removed to expose the CT, which was avulsed with microforceps. All procedures were performed bilaterally. Following surgery, the rats had 7–9 nights of free access to distilled water and food on the home cage.

Conditioned taste aversion. After the surgical recovery period, the water bottles were removed from the home cage, and a restricted fluid schedule was begun on the following day that was maintained for 12 days. During this time, fluid was always delivered on the home cage through sipper tubes attached to 100 ml graduated cylinders. The morning fluid access period, which was 15 min in duration, started at 9 a.m. for the first rat, 9:05 a.m. for the second, 9:10 a.m. for the third, and so on until all of the rats received their presentations. Food was removed at 8:45 a.m. for all rats and replaced after the last rat completed its access period. Five hr (± 10 min) after the morning fluid period, rats had distilled water available for 1 hr. On Days 6, 9, and 12 (conditioning trials), rats received 0.1 M NaCl during their morning fluid period. Immediately after this 15-min intake fluid presentation, half of the rats in each surgical group received intraperitoneal injections of 0.15 M LiCl, and the remainder received intraperitoneal injections of 0.15 M NaCl. If any rat failed to drink at least 1 ml on the conditioning trial, then 1 ml of 0.1 M NaCl was infused directly into the mouth by way of a 1-cc syringe before injection. Both injectants were given at a dose of 2 mEq/kg. This dose of LiCl has been shown to produce a robust conditioned taste aversion in rats after a single conditioning trial (Nachman & Ashe, 1973). On all other days, the morning fluid was distilled water, and no injections were administered. Immediately following the injections on Day 12, the rats were given free access to distilled water for 4 days. All chemical solutions were mixed daily from distilled water and reagent grade chemicals (Fisher Scientific, Orlando, FL).

Gustometer test. The water bottles were again removed from the home cage. On the following day, the rats were placed individually in the gustometer for 40 min. During this session, the rat licked the drinking spout to obtain 5-s taste trials of distilled water (water control trials) and three concentrations each of KCl and NaCl (0.03, 0.1, and 0.3 M). These taste trials were always preceded by a distilled water trial (water rinse trials). Taste stimuli were delivered randomly, with the restriction that each block of nine taste trials included one trial at each salt concentration and three water control trials.

Data analysis. A one-way analysis of variance (ANOVA) was conducted at each conditioning trial to determine differences in the amount of 0.1 M NaCl consumed (in milliliters) among the four groups. Post hoc tests were conducted using Tukey's honestly significant difference (HSD) test. For the gustometer test, lick rate to each stimulus during the 5-s trials was standardized by dividing by the mean licks during water control trials for each rat. A one-way ANOVA was conducted for each stimulus to determine differences among groups; differences were analyzed using Tukey's HSD post hoc test. To determine whether an intensity generalization gradient existed, we conducted a within-subjects ANOVA for each group on the lick rate (standardized to water) to the three NaCl concentrations along with paired contrasts comparing the response to the conditioned stimulus with that to the higher and lower concentration. The conventional $p = .05$ value was used as the statistical rejection criterion.

Histology. The rats were perfused intracardially with isotonic saline followed by 10% buffered formalin. The tongue was removed and stored in 10% buffered formalin. The anterior two thirds of the tongue was immersed in water for at least 30 min, then dipped briefly in 0.5% methylene blue and rinsed in distilled water. The epithelium was carefully removed, pressed between two glass slides, and examined under a light microscope. Taste pores appeared as dark blue dots on the pale-stained fungiform papillae. The number of taste pores in relation to the total number of fungiform papillae was used to assess the efficacy of the nerve section and to confirm the absence of CT regeneration (St. John et al., 1995).

Results

Histology. All rats in the CTX groups had fewer than 13% of the fungiform papillae containing a taste pore. In contrast, all rats in the CON groups had at least 87% of the fungiform papillae containing a pore.

Intake tests. Rats drank 19.5 ± 0.76 ml of 0.1 M NaCl on the first presentation (see Figure 1). Intake remained high across the conditioning trials in both CON and CTX rats that received control saline injections, whereas the intake of both CON and CTX rats receiving LiCl injections dropped to 0.33 ± 0.33 ml and 1.42 ± 0.70 ml, respectively, by the third conditioning trial (see Figure 1). There were no significant differences between groups on Trial 1, but there was on Trial 2, $F(3, 20) = 18.33$, $p < .00001$, and Trial 3, $F(3, 20) = 191.92$, $p < .00001$. On both Trials 2 and 3, Tukey's HSD test revealed that LiCl-injected groups did not differ significantly from one another ($p > .65$) but that both CON and

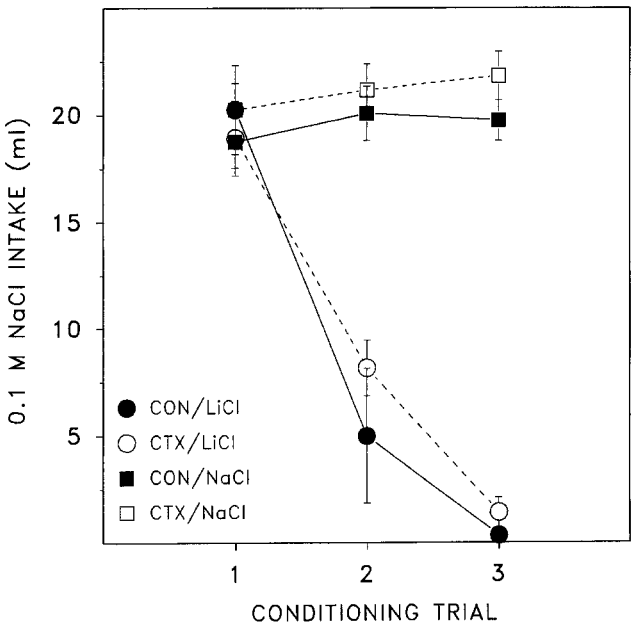

Figure 1. Mean intake (in milliliters) of 0.1 M NaCl (± standard error) on the three conditioning trials for control rats injected intraperitoneally with LiCl (CON/LiCl, solid circles) or NaCl (CON/NaCl, solid squares) and for rats with bilateral chorda tympani transection injected intraperitoneally with LiCl (CTX/LiCl, open circles) or NaCl (CTX/NaCl, open squares).

CTX LiCl-injected groups differed from their respective NaCl-injected controls (all $ps < .001$).

Brief access taste trials. The conditioned taste aversion to 0.1 M NaCl generalized to 0.03 and 0.3 M NaCl in both CON and CTX rats (see Figure 2, left). There were differences among the four groups at each concentration, all $Fs(3, 20) > 28.12$, all $ps < .00001$. Post hoc analysis using the Tukey HSD test demonstrated that, at every concentration, the LiCl-injected groups differed from their saline-injected controls. In no case did the saline-injected CON group differ from the saline-injected CTX group. Likewise, the LiCl-injected groups did not differ from one another.

In the LiCl-injected groups, the strength of the aversion varied with the intensity of the test stimulus in the CTX group, $F(2, 10) = 10.66$, $p < .005$, but did not vary significantly in the CON group, $F(2, 10) = 3.74$, $p > .06$. Specifically, in the CTX group, rats suppressed licking significantly more to 0.1 M NaCl than 0.03 M ($p < .03$). There was no evidence to conclude that the saline-injected groups responded differentially to the three concentrations of NaCl ($ps > .35$). Finally, there was no statistical evidence to conclude that the conditioned taste aversion to NaCl in the LiCl-injected groups generalized to KCl at the concentrations tested (see Figure 2, right).

Experiment 2

Method

In this experiment, naive adult male rats (which weighed 378–484 g at the beginning of the experiment) were conditioned to avoid 0.1 M KCl rather than 0.1 M NaCl after sham surgery (CON,

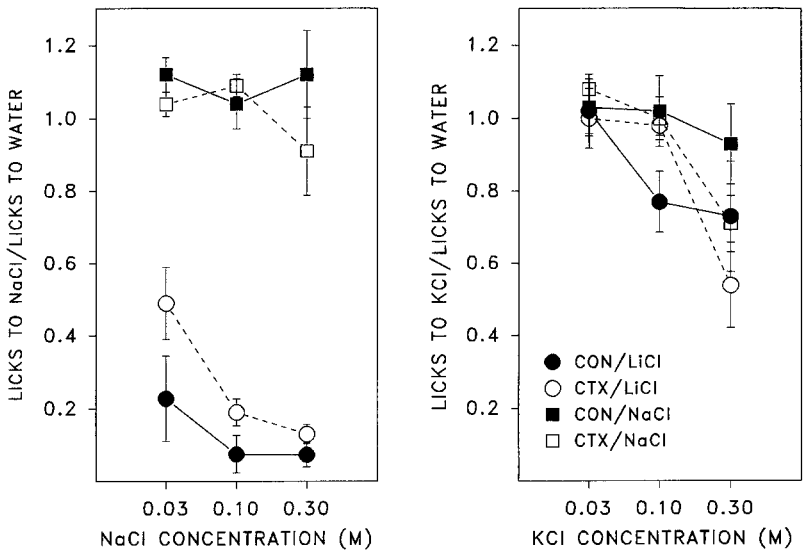

Figure 2. Mean of the ratio of the number of licks to a taste stimulus over the number of licks to distilled water (± standard error) during 5-s trials in the gustometer for control rats (CON/LiCl, solid circles) or rats with bilateral chorda tympani transection (CTX/LiCl, open circles) conditioned to avoid 0.1 M NaCl. Also shown are data for control rats (CON/NaCl, solid squares) or chorda tympani-transected rats (CTX/NaCl, open squares) given control saline injections on the conditioning trials. Rats were tested after the third conditioning trial with NaCl (0.03, 0.1, and 0.3 M), KCl (0.03, 0.1, and 0.3 M), and distilled water presented in randomized blocks throughout the session.

n = 12) or CTX (n = 12). Four rats died following surgery, leaving a sample size of CON (LiCl-injected: n = 5; saline-injected: n = 4) and CTX (LiCl-injected: n = 6; saline-injected, n = 5). The procedure of this experiment was similar to that of Experiment 1, with minor exceptions.[1]

Results

Histology. All rats in the CTX groups had fewer than 11% of fungiform papillae containing a taste pore. In contrast, greater than 90% of the fungiform papillae contained a pore in every control rat.

Intake tests. All rats drank a substantial amount of 0.1 M KCl on the first presentation (see Figure 3). Saline-injected controls that received either CON or CTX surgery maintained a high level of KCl intake across the three conditioning trials. Rats in the LiCl-injected CON group showed evidence of a moderate taste aversion on the second trial, and intake of the conditioned stimulus was reduced to zero by the third trial. In contrast, rats in the LiCl-injected CTX group failed to exhibit a taste aversion on Trial 2 and demonstrated only a moderate taste aversion by Trial 3. There were no differences in intake on Trial 1 between groups, but there was on Trial 2, $F(3, 16) = 22.36$, $p < .00001$, and Trial 3, $F(3, 16) = 378.77$, $p < .00001$. On Trial 2, all groups differed from the LiCl-injected CON group (Tukey HSD $ps < .0004$). The LiCl-injected CTX group did not differ from its saline-injected control, indicating the lack of a taste aversion. On Trial 3, there was no difference between the saline-injected groups, but the LiCl-injected groups differed from the saline-injected groups as well as from each other ($ps < .002$). Thus, the CTX group demonstrated a significant aversion by the third trial, but this aversion was not as pronounced as in the CON group.

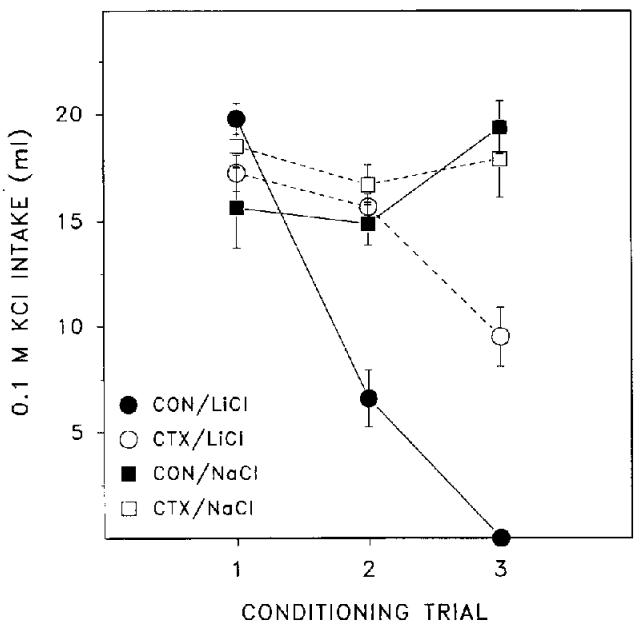

Figure 3. Mean intake (in milliliters) of 0.1 M KCl (± standard error) on the three conditioning trials for control rats injected intraperitoneally with LiCl (CON/LiCl, solid circles) or NaCl (CON/NaCl, solid squares) and for rats with bilateral chorda tympani transection injected intraperitoneally with LiCl (CTX/LiCl, open circles) or NaCl (CTX/NaCl, open squares).

Brief access taste trials. There were significant differences among the four groups in lick rate to 0.03 M KCl, $F(3, 16) = 10.31$, $p = .0005$; 0.1 M KCl, $F(3, 16) = 52.36$, $p < .00001$; and 0.3 M KCl, $F(3, 16) = 7.23$, $p = .0028$. At the lowest concentration, the LiCl-injected CON group did not significantly differ from its saline-injected control (Tukey HSD, $p = .09$), whereas this group did lick significantly less at both 0.1 and 0.3 M ($ps < .005$). In addition, the LiCl-injected CON group responded differentially to the three KCl concentrations, $F(2, 8) = 33.64$, $p < .001$. This group suppressed licking to 0.1 M KCl more than to 0.03 M KCl ($p < .01$). Taken together, these results suggest that the KCl aversion in the LiCl-injected CON group generalized to 0.3 M KCl, but did not generalize to 0.03 M KCl, when tested in the gustometer following a third conditioning trial (see Figure 4, left).

In the gustometer, there was evidence that the LiCl-injected CTX group formed an aversion to 0.1 M KCl, as this group licked significantly less to 0.1 M KCl compared with its saline-injected counterpart ($p < .005$). Nonetheless, this aversion was not as strong as that seen in the LiCl-injected CON group at 0.1 M KCl ($p < .0005$). Furthermore, the licking behavior of the LiCl-injected CTX group differed from that of the saline-injected CTX group only at the 0.1 M concentration of KCl. The LiCl-injected CTX group did show a concentration-dependent decrease in KCl licking (see Figure 4, left); $F(2, 10) = 17.32$, $p < .001$, licking less to 0.1 M than 0.03 M ($p < .01$) and less to 0.3 M than 0.1 M ($p < .05$). In one sense, this could be considered evidence of an intensity generalization gradient. However, the saline-injected CTX group significantly decreased its licking of 0.3 M KCl in relation to the lower concentrations ($p < .02$), thus obscuring evidence of a conditioned aversion in the LiCl-injected CTX group. The mean data thus suggest that CT transection may produce an increased unconditioned aversion to 0.3 M KCl (a trend also evident in the first experiment, see Figure 2, right). Finally, the groups did not differ with respect to lick rate at any NaCl concentration, indicating that the taste aversion to KCl did not generalize to NaCl in the LiCl-injected groups.

General Discussion

Transection of the CT did not affect the rate at which a conditioned aversion to 0.1 M NaCl was acquired. These results are in agreement with Raskin et al. (1992), who also found that CT transection did not affect the conditioning of a NaCl taste aversion. However, these findings conflict with a

[1] Following the gustometer familiarization phase and before surgery, the rats had access to distilled water on the home cage for at least 2 nights rather than at least 3, and following the third taste aversion trial to 0.1 M KCl and before the gustometer test, the rats had access to distilled water on the home cage for 1 day rather than 4.

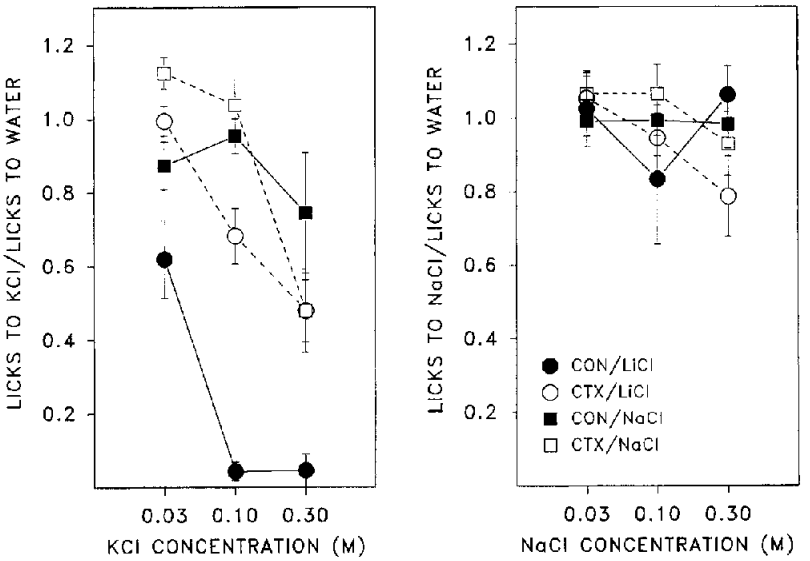

Figure 4. Mean of the ratio of the number of licks to a taste stimulus over the number of licks to distilled water (± standard error) during 5-s trials in the gustometer for control rats (CON/LiCl, solid circles) or rats with bilateral chorda tympani transection (CTX/LiCl, open circles) conditioned to avoid 0.1 M KCl. Also shown are data for control rats (CON/NaCl, solid squares) or chorda tympani-transected rats (CTX/NaCl, open squares) given control saline injections on the conditioning trials. Rats were tested after the third conditioning trial with KCl (0.03, 0.1, and 0.3 M), NaCl (0.03, 0.1, and 0.3 M), and distilled water presented in randomized blocks throughout the session.

study by Yamamoto et al. (1994), who found that CT transection substantially impaired the acquisition (and/or expression) of a conditioned taste aversion to NaCl.

A variety of factors may play a role in the strength of a conditioned taste aversion, and thus it is important to consider procedural differences when interpreting disparate results across studies. In this case, however, it is difficult to speculate on the cause of the differential effects. Compared with Yamamoto et al. (1994), the same concentration of the conditioned stimulus (0.1 M NaCl), a weaker dose of the unconditioned stimulus (LiCl), and a similar interstimulus interval (onset of NaCl intake test to LiCl administration), were used in the present study. Although our design involved three conditioning trials rather than one, there was an unequivocal taste aversion expressed after the first trial in the CTX group; in fact, the behavior of this group was indistinguishable from controls. One possible explanation is strain differences; in the present study, we used Sprague-Dawley rats, whereas Yamamoto et al. used Wistar rats. Whatever the origin of the incongruent results of the two studies, it is clear that in at least some circumstances (this study; Raskin et al., 1992), a pronounced taste aversion to 0.1 M NaCl can be shown in rats with CT transection. Presumably, the information conveyed by the remaining gustatory nerves is sufficient to support the formation of a taste aversion to 0.1 M NaCl.

It is perhaps a little surprising that the 0.1 M NaCl aversion in the CTX group generalized to the lower 0.03 M concentration, given that this concentration is likely close to the detection threshold for rats with CT transection (Slotnick et al., 1991; Spector, Schwartz, & Grill, 1990). A closer examination of the detection threshold study of Spector, Schwartz, and Grill (1990), however, reveals no inconsistency with the present data. In that study, rats were trained to maintain licking to water and suppress licking to NaCl during the avoidance period of a 5-s taste trial. The detection threshold was defined as the concentration of NaCl that produced a "detectability score" of 0.5. The detectability score was defined as $(W - T)/W$, where W was the mean duration of spout contact during the avoidance period of water trials and T was the mean duration of spout contact during the avoidance period of NaCl trials. Thus, a score of 1.0 indicated complete detection (no licks to NaCl), and a score of 0.5 (threshold) indicated the rat spent half as much time licking NaCl as water (on average). The average detection threshold for rats with CT transection was found to be about 0.03 M. This result is in good agreement with the present study (see Figure 2, left); rats with CT transection had about half as many licks to 0.03 M NaCl as water. Given the marked procedural differences in the present study and the Spector et al. study (e.g., the use of LiCl vs. shock to motivate lick suppression, lack of presurgical experience with NaCl in the present study, and the use of classical vs. operant conditioning procedures), the similarity in the response across NaCl concentrations is quite remarkable.

Unlike when NaCl was the conditioned stimulus (Experiment 1), LiCl-injected rats with CT transection did not acquire a robust aversion to 0.1 M KCl (Experiment 2). These rats did reduce their intake of 0.1 M KCl, but only after two conditioning trials. After the third conditioning trial, the suppression of licking to the KCl in the brief access test, while significantly different from the saline-injected

CTX group, was nowhere as pronounced as in the surgical control rats injected with LiCl. The most likely explanation for the relatively weak aversions formed in the CTX group is that transection of the CT reduced the perceived intensity of KCl. It is well established that the strength of a taste aversion depends, among other factors, on the concentration of the conditioned stimulus (Nowlis, 1974; Shaw, 1983; see also Riley & Clarke, 1977). It is clear, nonetheless, that 0.1 M KCl is detectable to rats with CT transection, albeit weaker in intensity. It would be instructive for future work to focus on the effects of CT transection on both KCl detection thresholds and responsiveness to suprathreshold KCl concentrations. On the basis of our results, it seems likely that CT transection affects the perception of nonsodium salts in addition to its influence on sodium sensibility.

In accord with previous findings in hamsters and rats, there was no evidence that the aversion to NaCl generalized to KCl in LiCl-injected surgical control rats (Barry, Larson, & Frank, 1993; Frank & Nowlis, 1989; Hill et al., 1990; Nowlis, Frank, & Pfaffmann, 1980). In and of itself, this result indicates that either the two salts are qualitatively discriminable or that the three KCl concentrations tested were all less intense than the lowest NaCl concentration. The results of Experiment 2 demonstrated, however, that KCl aversions did not generalize to NaCl, supporting the conclusion that these two stimuli can be qualitatively distinguished by the rat (Erickson, 1963; Hill et al., 1990; Morrison, 1967; Spector & Grill, 1992; St. John et al., 1995).

The failure for conditioned NaCl aversions to generalize to KCl (and vice versa) in rats with CT transection was somewhat unexpected. There is evidence suggesting that the perceived quality of these two salts may become more similar after gustatory deafferentation of the anterior tongue. For example, when sodium-depleted rats are tested for their responsiveness to an array of chloride salts in brief access taste trials, rats with CT transection show an attenuated licking response to NaCl (0.05 and 0.3 M) and increase their licking of 0.05 M (but not 0.3 M) KCl compared with surgical controls (Breslin et al., 1993; 1995; Markison et al., 1995). Moreover, transection of the CT unequivocally impairs performance in a presurgically learned NaCl versus KCl discrimination task (Spector & Grill, 1992; St. John et al., 1995). It is important to note that there is some concentration dependency associated with these effects.

One possible explanation for the disparity between the present and previous findings is that CT transection alters, to some extent, the perceptual quality of both NaCl and KCl but does not render them indiscriminable. At low, but detectable, concentrations, it is possible that the two salts become less discriminable as well. Accordingly, performance should be disrupted in tasks that rely on perceiving an innate or presurgically conditioned taste image. It should be stressed that in the present study, the aversions were conditioned postsurgically. When aversions to 0.1 M NaCl are conditioned presurgically, rats and hamsters fail to express this learning after CT transection (Barry et al., 1993; Yamamoto et al., 1994). Given that rats can detect 0.1 M NaCl following CT transection (Slotnick et al., 1991; Spector, Schwartz, & Grill, 1990), the findings from presurgical conditioning studies suggest that the neurotomy changed the qualitative signature of NaCl so that it was not recognized during postsurgical testing. On the other hand, it is possible that the intensity of NaCl was so weakened by CT transection in these other studies that it caused a postsurgical intensity generalization decrement. The latter interpretation is not supported by the present results, however. If the nerve section lowered the intensity of the conditioned stimulus sufficiently to cause a generalization decrement in these other studies, then our rats should have showed impaired acquisition of the NaCl aversion, which they did not (Experiment 1).

This is not to say that the perceived taste intensity of NaCl is unaffected by CT transection in the rat. There is clear evidence that sensitivity to NaCl is compromised, but only at low concentrations. For example, O'Keefe et al. (1994) found that rats with CT transection, maintained on a sodium-deficient diet, reduced licking behavior to 0.03 and 0.06 M NaCl but did not differ from controls with respect licking to 0.125, 0.25, and 0.5 M NaCl. Although transection of the CT raises the NaCl detection threshold by one to two orders of magnitude (Slotnick et al., 1991; Spector, Schwartz, & Grill, 1990), at hypertonic concentrations, water-deprived rats decrease their licking in a concentration-dependent manner just as much as intact rats in brief access taste trials (Cauthon, Garcea, & Spector, 1994).

In conclusion, these findings demonstrate that CT transection compromises the acquisition of a KCl, but not a NaCl, aversion. Moreover, the conditioned aversions to these two salts, contrary to expectations, did not cross-generalize in rats with CT transection. Taken together with numerous behavioral studies demonstrating that transection of the CT has critical effects on the taste perception of NaCl in rats (Breslin et al., 1993, 1995; Markison et al., 1995; O'Keefe et al., 1994; Slotnick et al., 1991; Sollars & Bernstein, 1992; 1994; Sollars et al., 1991; Spector & Grill, 1992, 1994; Spector, Schwartz, & Grill, 1990; St. John et al., 1995), the findings of the present study suggest that rats with CT transection can nonetheless perceptually distinguish NaCl from KCl, at least at midrange concentrations, even if the respective perceived taste qualities of these salts have been altered by the neurotomy.

Endnote: During the review of this article, Sollars, Tracy, and Bernstein (1996) recently reported that bilateral transection of the CT impaired the expression of a presurgically conditioned NaCl aversion only at concentrations lower than the conditioned stimulus. This was demonstrated in both the Fischer-344 and Wistar strains. The nerve-transected rats also generalized the aversion to ammonium chloride, but so did sham-operated control rats.

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