



Different Characteristics of Gustatory Responses Between the Greater Superficial Petrosal and Chorda Tympani Nerves in the Rat

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Abstract

The integrated responses to gustatory stimuli applied to the soft palate were recorded from the greater superficial petrosal nerve (GSP) and were compared with those from the chorda tympani nerve (CT) innervating the anterior part of the tongue in the rat. Stimuli included various concentrations of NaCl, sucrose, HCl and quinine hydrochloride, and 0.5 M of six sugars. The inhibitory effects of amiloride on the responses to sodium salts, including various concentration of NaCl, 0.1 M sodium acetate and 0.01 M sodium saccharin, were also tested. Both the phasic and tonic responses to sugars in the GSP were significantly larger than those in the CT, whereas both responses to NaCl in the GSP were significantly smaller than those in the CT. Although amiloride at 50 μ M significantly depressed the phasic and tonic responses to NaCl with a wide range of concentration in the CT, little inhibitory effect was observed in the GSP. The tonic response to sodium acetate, when dissolved in amiloride solution, was depressed to 15% of the control in the CT, and slightly but significantly depressed to 70% in the GSP. These response characteristics of the GSP may play important roles in the processing of gustatory information. *Chem. Senses* 22: 133–140, 1997.

Introduction

Histological studies in mammals, including man, have demonstrated that several subpopulations of taste buds are distributed on the tongue and throughout the oral cavity (Fish *et al.*, 1944; Guth, 1957; Lalonde and Eglitis, 1957). Among these subpopulations, the soft palate and the nasoincisor duct contain taste buds innervated by the greater superficial petrosal nerve (GSP), a branch of the facial nerve. In the rat, the number of taste buds on the palate, including the nasoincisor duct, was reported to range from 220 (Kaplick, 1953) to 227 (Miller, 1977), which is

similar to that of 179 (Fish *et al.*, 1944) and 187 (Miller, 1975) indicated on the fungiform papillae of the anterior tongue innervated by the chorda tympani nerve (CT), also a branch of the facial nerve. In the hamster, 88 taste buds were estimated to be dispersed on the soft palate, whereas 130 were reported on fungiform papillae of the tongue (Miller and Smith, 1984).

Although taste buds are widely distributed over the soft palate, little is known concerning their gustatory function compared to those on the tongue. The first electro-

physiological recording from the GSP in the rat revealed that gustatory stimulation of the soft palate with sucrose produced larger neural responses compared to those in the CT (Nejad, 1986). Similarly in the hamster, stimulation of the soft palate with various sugars produced robust responses in the GSP (Harada and Smith, 1992). These neurophysiological data suggest that the GSP plays an important role in mediating sweet taste information.

Behavioral experiments indicated that the GSP was important in perception of sucrose taste by showing that the rat with transection of the GSP alone or with a combined transection of both the GSP and the CT exhibited a significant decrease in mean lick ratio to sucrose solutions (Krimm *et al.*, 1987). The GSP was also shown with a conditioned taste aversion paradigm in the hamster to contribute greatly to the taste of sucrose (Harada, 1992). The degree of the conditioned taste aversion to 0.1 M sucrose significantly decreased when the GSP and/or the CT were sectioned bilaterally. The order of the sectioning effects was GSP + CT > GSP ≥ CT > sham.

There are currently no reports, other than those by Nejad (1986) in the rat and Harada and Smith (1992) in the hamster, of electrophysiological recordings from the GSP. Additional studies are necessary to understand the gustatory function of these palatal taste receptors. The present study clarifies the response characteristics of the GSP sensitivity not only for sugars, but also for sodium salts by using amiloride.

Methods

Animals

Data were obtained from 17 adult, male Sprague–Dawley rats weighing between 170 and 280 g (210.8 ± 31.1 g). Each rat was anesthetized deeply with Nembutal (Abot, contains 50 mg/ml sodium pentobarbital, 1 ml/kg body wt, i.p.). The surgical level of anesthesia was maintained by a supplemental dose (0.2 ml/kg) of Nembutal.

Surgical procedures

The surgical procedure to dissect the GSP was almost the same as described before (Harada, 1992; Harada and Smith, 1992). Briefly, the head of the animal was fixed with a non-traumatic head-holder made of Plexiglas that allowed the soft palate to be exposed for stimulation. The area of the nasoincisor duct innervated by the GSP was covered by the

head holder and sealed with petroleum jelly. An incision was made ventrally along the angle of the right mandible. The ventral wall of the right tympanic bulla was removed, and the tensor muscle was cut at the tendon attached to the malleus and removed carefully. The cochlea was left intact, a layer of a part of the temporal bone overlying the GSP was removed. The GSP was dissected free from the surrounding tissue and transected at its exit from the geniculate ganglion.

Electrophysiological recording

The exposed GSP was placed on a 100 μ m Ag–AgCl hook electrode, and an indifferent electrode was placed on the inner wall of the bulla. These electrodes were soaked in petroleum jelly mixed with an equal amount of liquid paraffin. The animal was grounded by an alligator clip attached to the surgical margin. Neural activity from the whole nerve was led to a high impedance probe (JB-101J, Nihon Kohden) and an AC amplifier (ABV-11, Nihon Kohden), monitored on an oscilloscope and an audio monitor, and was recorded on a PCM data recorder (RD-111T, TEAC) for later analysis. Responses of the whole nerve were integrated (RC = 0.3 s, EI-600G, Nihon Kohden) and these integrated responses were displayed on a thermal array recorder (RTA-1100M, Nihon Kohden) at a speed of 1 mm/s.

Neural responses from the CT were also recorded. The rat CT, which runs along the surface of the lamina of the malleus and spans the gap between the process of the incus and the tympanic bone, was cut proximally and recorded by the same method as described for the GSP.

Stimulation

Taste stimuli were delivered by a computer-controlled system. An outlet of polyethylene tubing (2.5 mm i.d.) was placed adjacent to the soft palate or to the anterior portion of the tongue for application of taste stimuli and rinsing water at a flow rate of 2 ml/s. Distilled water (DW) constantly flowed over the palate or tongue, and was switched to one of the stimulus solutions for 10 s by a three-way electromagnetic valve controlled by a micro-computer (PC9801RX, NEC). Stimulus solutions were made with reagent-grade chemicals (Nacalai Tesque, Inc.) in DW. The stimuli were 0.5 log step concentration series of sucrose (0.001–1.0 M), NaCl (0.0001–1.0 M), HCl (0.00001–0.01 M), quinine hydrochloride (QHCl, 0.00003–0.01 M), 0.1 M sodium acetate, 0.01 M sodium saccharin, and 0.5 M sugars consisting of sucrose (Suc), lactose (Lac),

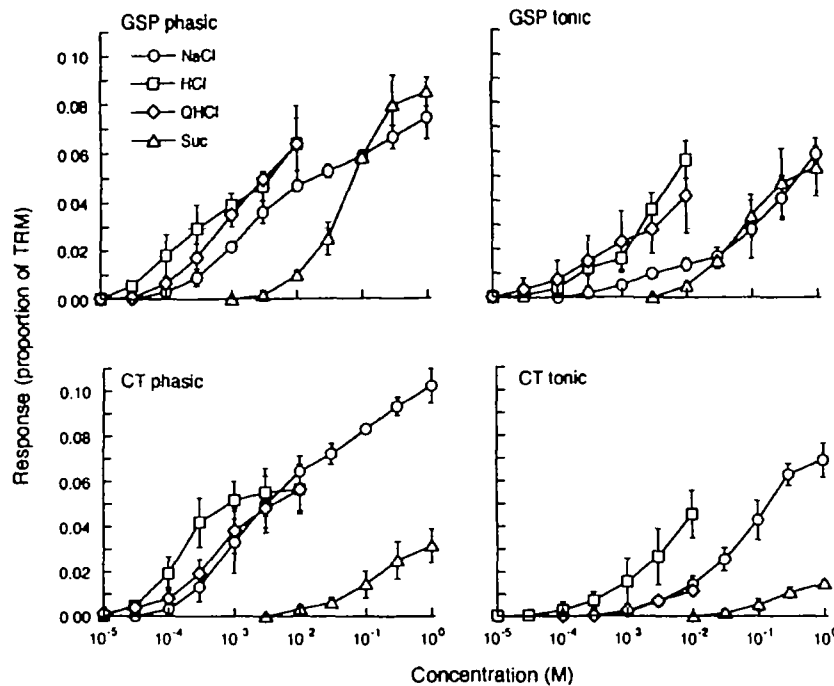


Figure 1 Mean concentration–response function to NaCl, HCl, QHCl and sucrose (Suc) in the GSP and CT. Each response is expressed as a portion of the total response magnitude (TRM) for each nerve (see text for explanation). Responses of the GSP are shown at the top of the figure and those of the CT at the bottom. Phasic responses are on the left and tonic responses are on the right. Error bars show SD of the means. Means were calculated from five preparations in the GSP and seven in the CT.

maltose (Mal), D-fructose (Fru), D-glucose (Glu) and D-galactose (Gal). Sugar solutions were prepared weekly and stored at 5°C. All stimuli and rinsing water were presented to the tongue or palate at room temperature.

Data analysis

The phasic portion of the integrated response to 0.1 M NaCl was used as a standard. All of the responses recorded from a given preparation were calculated relative to the magnitude of the response to 0.1 M NaCl. This standard solution was applied just prior to and subsequent to each concentration series, and between every three or four stimulations with 0.1 M salts or 0.5 M sugars. The height of the peak of the initial phasic response and the height of the tonic portion of the integrated response at 10 s after stimulus onset were used as measures of the response magnitude to each stimulus. To compare the magnitude of responses between the CT and GSP, total response magnitudes were calculated (Harada and Smith, 1992). That is, mean response magnitudes to the concentration series of sucrose, NaCl, HCl and QHCl were derived from all the preparations of each nerve; the total response magnitudes (TRMs) for the GSP and for the CT were obtained by

summation of all these means. The mean response to each stimulus in each nerve was then expressed as a proportion of the TRM for that nerve. This proportion comprised the relative response magnitude for each stimulus. In this way, the relative responsiveness of the GSP and the CT to every stimulus could be assessed, although the absolute magnitudes of the responses in the two nerves could not be compared. For each of the concentration series, the responses in the two nerves (GSP and CT) were compared with a two-way analysis of variance (nerve versus concentration). Differences in the responses of the GSP and the CT to the 0.1 M salt series, and to the 0.5 M sugar series were analyzed using independent measures *t*-tests.

Results

Responses to four basic taste stimuli

Stimulation with various taste solutions applied to the soft palate produced robust GSP responses (Figure 1). Integrated responses in the GSP to sucrose were significantly larger than those from the CT (Figures 1, 2 and 5). The estimated electrophysiological threshold of the

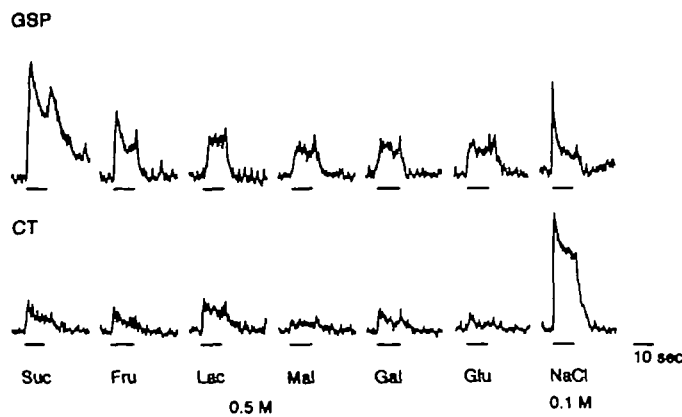


Figure 2 Integrated responses of the GSP and CT to six 0.5 M sugars and to 0.1 M NaCl. Stimuli were applied for 10 s.

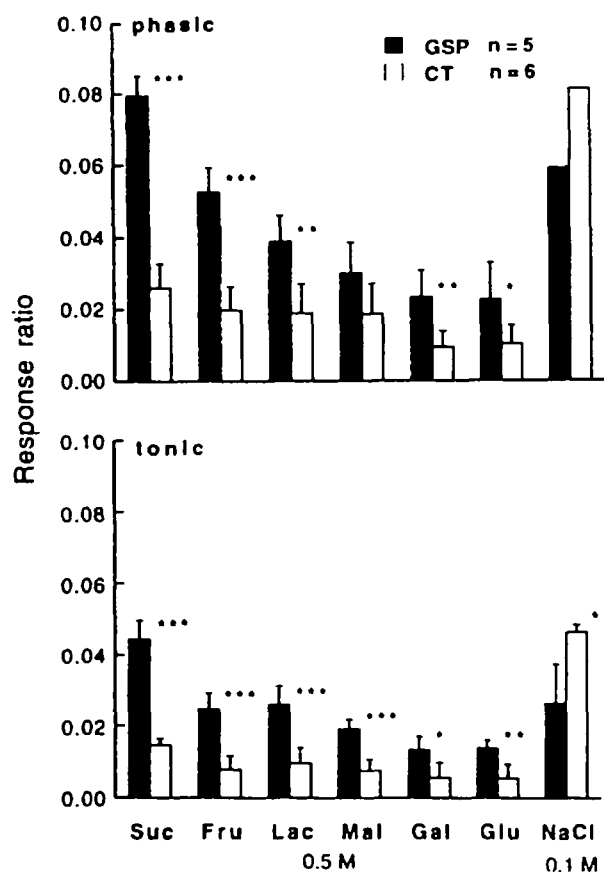


Figure 3 Comparisons of mean phasic and tonic responses of the GSP (open bars; $n = 5$) and CT (solid bars; $n = 6$) to 0.5 M sugars. Error bars show SD of the means. Asterisks indicate statistically significant difference between the two nerves (two-tailed t -test; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

phasic response of the GSP to sucrose was about a 0.5 log unit lower (0.001 M) than that for the CT (0.003 M). The magnitudes of the GSP responses to sucrose increased more steeply with an increase in concentration than that for

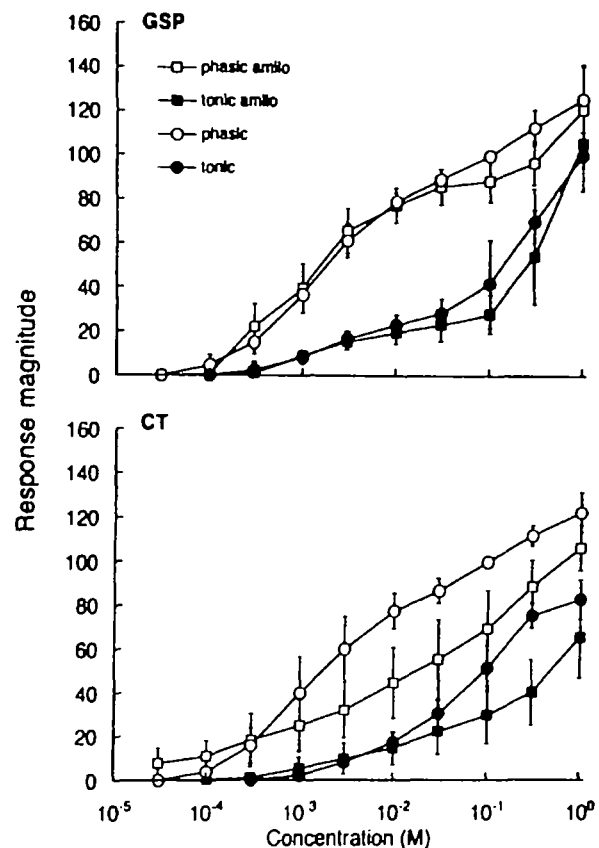


Figure 4 Mean concentration-response functions for NaCl solutions made up with DW and with 50 μ M amiloride solution in the GSP and CT. Responses are expressed as percentages to the magnitude of phasic responses to 0.1 M NaCl in DW. Solvents of DW and amiloride are symbolized by circles and squares respectively. Open marks indicate phasic responses, and filled ones tonic responses. Error bars show SD of the means. Means were calculated from five and four preparations for the GSP and CT respectively.

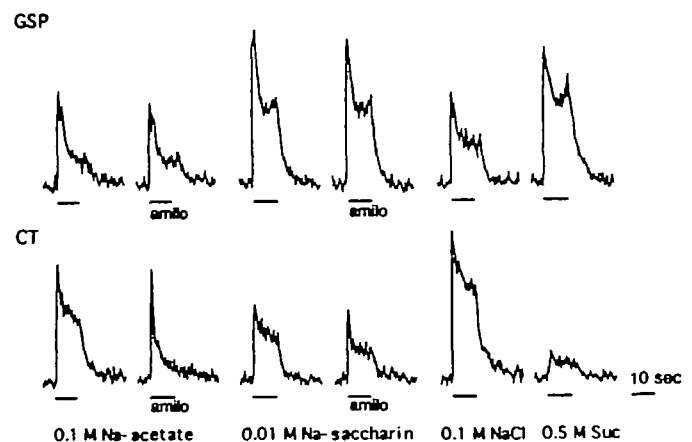


Figure 5 Integrated responses of the GSP and CT to 0.1 M sodium acetate, 0.1 M sodium acetate made up with DW and with 50 μ M amiloride, 0.01 M sodium saccharin; 0.01 M sodium saccharin contained 50 μ M amiloride, 0.1 M NaCl, and 0.5 M sucrose. Stimuli were applied for 10 s.

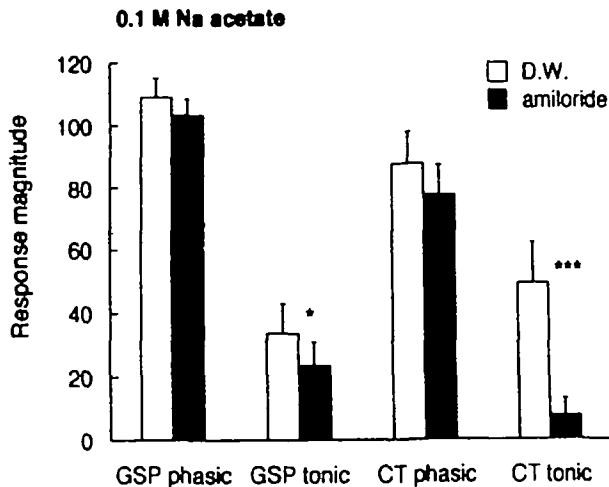


Figure 6 Comparisons of effects of amiloride on 0.1 M sodium acetate in the GSP and CT. The solvents are DW (open bar) or 50 μ M amiloride (solid bar). Ordinate shows mean phasic and tonic responses of the GSP ($n = 4$) and CT ($n = 6$). Error bars show SD of the means. Asterisks indicate statistically significant difference (two-tailed t -test; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

NaCl, and exceeded the NaCl response above 0.3 M with slight saturation of both the phasic and tonic responses. In contrast, the CT phasic response to sucrose was only 30% of that for NaCl, even when tested at 1.0 M. The responses of both the CT and GSP to NaCl increased monotonically up to 1.0 M; threshold to NaCl was ~ 0.0001 M in both cases. The tonic response of the GSP to NaCl rose continuously up to 1.0 M, while the tonic responses of the CT to NaCl was saturated above 0.3 M. Threshold (0.00001 M) for HCl was approximately the same in both nerves. Although the phasic CT response to HCl saturated at 0.001 M, the GSP responses to HCl increased monotonically with an increase in concentration up to 0.01 M, and showed no tendency to saturate. Both phasic and tonic responses to QHCl increased monotonically with an increase in concentration.

A two-factor factorial ANOVA between the two nerves (Table 1) indicated that both phasic and tonic components of the response to sucrose were highly significantly larger in the GSP than in the CT. In contrast, both phasic and tonic responses to NaCl in the GSP were highly significantly smaller than those in the CT. Although no significant difference existed for the phasic responses to HCl and QHCl between the two nerves, the tonic responses were significantly larger in the GSP than in the CT for the two chemicals.

Responses to sugars

All six sugars tested produced larger responses relative to

Table 1 Result of ANOVA for concentration–response function of four basic taste stimuli in the GSP ($n = 5$) and CT ($n = 7$)

	NaCl	HCl	QHCl	Suc
Phasic	GSP < CT*** $P < 0.0001$ $F = 41.3$	NS $P = 0.360$ $F = 0.945$	NS $P = 0.747$ $F = 0.110$	GSP > CT*** $P < 0.0001$ $F = 118$
Tonic	GSP < CT * $P = 0.0151$ $F = 8.58$	GSP > CT ** $P = 0.0047$ $F = 13.9$	GSP > CT*** $P < 0.0001$ $F = 91.7$	GSP > CT*** $P < 0.0001$ $F = 80.4$

Statistical significances are shown with *** $P < 0.001$; $P < 0.01$; * $P < 0.05$; NS, no significance.

0.1 M NaCl, in the GSP than in the CT (Figures 2 and 3). The phasic responses of the GSP to Suc and Fru ($P < 0.0001$), Lac ($P = 0.0034$), Gal ($P = 0.0040$), Glu ($P = 0.0283$) were significantly larger than those recorded from the CT. Similarly, the tonic responses of the GSP to Suc, Fru and Mal ($P < 0.0001$), Lac ($P = 0.0005$), Mal ($P < 0.0001$), Lac ($P = 0.0005$), Glu ($P = 0.0017$) and Gal ($P = 0.0108$) were significantly larger than those of the CT.

Apparently sucrose produced prominent phasic responses among the six sugars in the GSP (Figures 2 and 3), and there were highly significant differences in phasic responses between sucrose and the other sugars (two-tailed t -test; $P < 0.001$). Also the ranking of the response magnitudes for the six sugars is more significant in both phasic and tonic responses of the GSP ($W = 0.922$ and 0.905 respectively) than in those of the CT ($W = 0.712$ and 0.698) (Table 2).

Inhibitory effects of amiloride in response to sodium salts

Although amiloride depressed both phasic and tonic CT responses, no such effect occurred for recording from the GSP (Figure 4). A two-factorial ANOVA between the two nerves for phasic and tonic responses to DW versus amiloride revealed that response to NaCl in DW was significantly larger than that in amiloride solution for both phasic ($P = 0.0117$) and tonic CT response ($P = 0.0339$), while there was no significant effect for the GSP responses (phasic, $P = 0.4336$; tonic, $P = 0.2895$).

Amiloride significantly depressed the tonic responses of the GSP ($P = 0.0182$) and of the CT ($P = 0.0006$) to sodium acetate and sodium saccharin; however, no such effects was indicated for phasic responses of both the GSP and CT to either compound (Figures 5 and 6).

Table 2 Rank orders of responses to six sugars at 0.5 M

Nerve	Rank order										W	P	n	
GSP (phasic)	Suc	*** >	Fru	** >	Lac	* >	Mal	≥	Gal	≥	Glu	0.922	<0.0003	5
GSP (tonic)	Suc	** >	Lac	≥	Fru	* >	Mal	* >	Glu	≥	Gal	0.905	<0.0004	5
CT (phasic)	Suc	* >	Fru	≥	Lac	≥	Mal	* >	Glu	≥	Gal	0.712	<0.0007	6
CT (tonic)	Suc	** >	Lac	≥	Fru	≥	Mal	≥	Gal	≥	Glu	0.698	<0.0037	6

W is the Kendall coefficient of concordance. Asterisks indicate statistically significant differences between neighbouring two stimuli (two-tailed t-test; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Discussion

Chemical stimuli applied to the soft palate of the rat produced robust neural responses in the GSP. Among the concentration–response curves for each of the four basic taste stimuli in both the GSP and CT, those for sucrose in the GSP showed a most remarkable increase in response with an increase in concentration (Figure 1). The phasic responses to sucrose were significantly larger in the GSP than those in the CT, while the phasic responses to NaCl were larger in the CT than those in the GSP. Such reversal relations of the responsiveness of NaCl and sucrose between the GSP and CT are consistent with those in the hamster (Harada and Smith, 1992). In contrast, the tonic responses to HCl and QHCl in the CT were significantly larger in the GSP than in the CT, although there was no significant difference between the two nerves for phasic responses to these stimuli. This is inconsistent with the result in the hamster (Harada and Smith, 1992), in which QHCl showed significantly larger responsiveness in the CT than that in the GSP. These results revealed that the functional properties for these four stimuli in the soft palate are different among species.

Not only sucrose, but also five other sugars produced larger responses than those observed in the CT. Rank order of the response magnitudes for six sugars in the hamster GSP was slightly different from that in the CT, where Gal produced a relatively larger response in the GSP than in the CT (Harada and Smith, 1992). In the rat the relative effectiveness of the sugars recorded from the GSP was similar to that from the CT. The rat GSP, however, produced significantly larger phasic responses, especially for sucrose, than the GSP in the hamster (Harada and Smith, 1992). Such high responsiveness to sugars in the GSP of the rat is

consistent with the previous report (Nejad, 1986). The GSP also innervates another population of ~66 taste buds in the nasoincisor ducts (NID), where approximately one-third of those are located on the soft palate (Miller and Spangler, 1982). Neurons within the nucleus of the solitary tract responded well to stimulation of the NID with the preferable stimuli, such as Suc, Fru, and Glu (Travers and Norgren, 1987), confirming the specificity for sugars in the rat GSP.

Amiloride is known to be a potent inhibitor of sodium transport in various epithelia. Amiloride was shown to suppress taste responses to NaCl and LiCl in various species of animals, including rat (Schiffman *et al.*, 1983; Heck *et al.*, 1984; Brand *et al.*, 1985; DeSimone and Ferrell, 1985), hamster (Herness, 1987; Hettinger and Frank, 1990), monkey (Hellekant *et al.*, 1988) and even frog (Yoshii *et al.*, 1986). Although such suppressive effects on the response to NaCl in the CT were confirmed in the present experiment, the effects were quite small in recordings from the GSP (Figures 4 and 6).

Formaker and Hill (1988) demonstrated that tonic responses in the rat CT to non-halogenated sodium salts were greatly reduced to <4% of the original responses after treatment of the tongue with a 100 μ M amiloride solution. Similar results were obtained in the present experiment (i.e. the tonic response to sodium acetate in amiloride solution was as little as ~15% of that in the amiloride-free solution). In contrast, the tonic response to sodium acetate in amiloride solution was reduced to 70% of that in DW, this reduction being statistically significant ($P < 0.05$). It was revealed that 32 single fibers of the rat CT were divided into 18 high and 14 low amiloride sensitive fibers (Ninomiya and Funakoshi, 1988). It was also shown in the hamster that N- and H-fiber types responded well to 0.1 M NaCl (Hettinger

and Frank, 1990). Also, 10 μ M amiloride completely inhibited responses of sodium-selective N fibers and had minimal effect on responses of electrolyte-sensitive H fibers. Thus, sodium-sensitive fibers in the GSP may be more similar to the H- rather than N-fibers. A lack of the amiloride effect was shown in the glossopharyngeal nerve (GL) in mice (Ninomiya *et al.*, 1991) and rats (Formaker and Hill, 1991). Taken together, the order of the amiloride effect is CT > GSP > GL.

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