GUSTATORY SYSTEM OF THE SOFT PALATE IN MAMMALS

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Abstract

Histological experiments have revealed that numerous taste buds distribute on the soft palate in mammals including man. There exist 220 taste buds on the soft palate with 17% of total number in the rat, and 100 taste buds with 13.8% of the total in the hamster. Those taste buds are innervated by the greater superficial petrosal nerve (GSP) branch of the VIIth nerve. Electrophysiological recordings from the GSP in the rat and hamster showed that taste stimulation with sweet substances on the soft palate produces robust responses on the GSP nerve. Behavioral experiment in the rat and hamster revealed that transection of the GSP resulted in significant decrease of the sensitivity for sucrose. Neural recordings from the rat GSP indicate that the GSP produced robust responses not only to sugars but also to various amino acids. In the rat chorda tympani, L-amino acids are more stimulatory than the D-forms, while the GSP responds better to D-amino acids compared to enantiomers. Histological experiments in the hamster and rat revealed that postnatal development and maturation of taste buds on the soft palate preceded those on the other loci in the oral cavity including anterior and posterior part of the tongue. Also, it was reported that there exist more than 400 taste buds inhuman fetus. These importance of the gustatory system of the soft palate is discussed in this review.

Key words

soft palate, taste bud, development, facial nerve

I. Introduction

Histological studies both in man and animals have demonstrated that taste buds are distributed on the tongue and throughout the oral cavity within several subpopulations of taste buds [1-11]. The fungiform papillae on the anterior portion of the tongue contains taste buds and in the rostral part of the foliate papillae on the side of the tongue are innervated by the chorda tympani (CT) branch of the VIIth nerve. Taste buds located on the soft palate and in the naso-incisor ducts and are innervated by the greater superficial petrosal nerve (GSP) branch of the VII nerve. The glossopharyngeal (IXth) nerve innervates taste buds on the vallate and foliate papillae at the posterior portion of the tongue, and the superior laryngeal nerve (SLN) innervates taste buds on the laryngeal surface of the epiglottis and on the aryepiglottal folds. Although taste buds are widely dispersed over the soft palate,

little has been known for their gustatory function compared to those on the tongue. To elucidate the importance of the soft palate in gustatory system of mammals, psychophysical, neurophysiological, histological, and behavioral data are discussed in this review.

Ⅱ. Gustatory sensation of the soft palate in man

According to Miller[9], the first description for the presence of gustatory sensation on the human soft palate is by the publication of the memories of Brilliat-Savarin[12] in 1825. A scientific report for this aspect, however, was late by Kiesow[13] in 1894. He demonstrated that all of the four basic sensation, i.e. sweet, salty, sour, and bitter, apparently occurres on the soft palate in human adult, and not only on the soft palate but also throughout the oral cavity in infant. Henkin and Christiansen[14] also showed that after anesthesia of the human tongue the detection and recognition thresholds for sour and bitter substances significantly increased, while the salty and sweet sensation were unchanged. After complete anesthesia of the palate thresholds for salt and sweet were essentially unchanged, but resulted in a diminution in sensitivity to sour and bitter. They concluded that the palate plays an important role in bitter and sour sensation.

Collings[15] tested taste recognition thresholds and sensation magnitudes as a function of the molecular concentration for different taste among four loci on the tongue and soft palate in human subjects. She obtained results that the slopes of psychophysical functions were not significantly different on the palate, but thresholds for urea and quinine were lower on the soft palate than the other region. Nilsson[16] also tested taste acuity at the apex and base of the tongue and on the hard and soft palate using both an electric and four basic taste stimuli. He could not confirm the high sensitivity for sour and bitter on the soft palate reported previously[14-15]. However, in spite the wide inter-individual range of the threshold values for taste sensation on the soft palate, for one subject the threshold for bitter were lower than on the base of the tongue, and for one other subject the threshold for sour was lowest on the soft palate. Hammond et al.[17] investigated the effects of palatal compromise such as surgery, cleft of palate, and trauma, to show that the soft palate contributes to bitter and salty sensations to a greater degree than sweet and sour sensations.

In conclusion, in human adults, the gustatory system on the soft palate should play an important role for bitter sensation, and may be for salty or sour sensation, as well. However, it is unclear concerning gustatory sensitivity for infants although numerous taste buds are observed on the soft palate[3].

Ⅲ. Taste buds distribution in the human soft palate

Whether taste buds are distributed on the soft palate or not had long been discussed since the appearance of the first description by Hoffmann[18] in 1875. Gairns[19] investigated by autopsies on human subjects ranging in age from 17 to 62 years and found no taste buds on the soft palate. Also in a relatively recent paper Wood and Kraus[20] found no taste buds on the soft palate examined 60 human prenated specimens in age

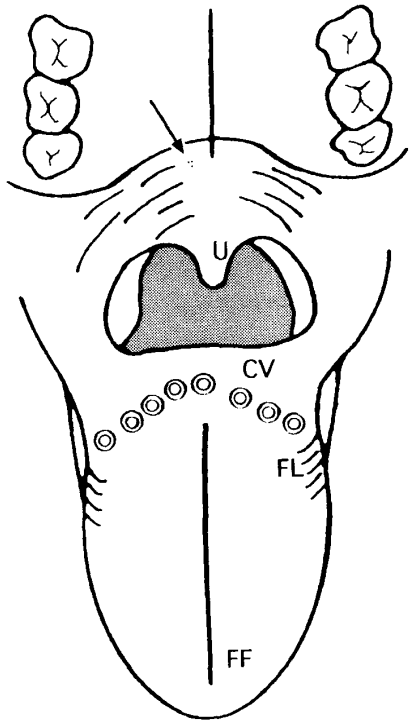

Figure 1 : The location of the three taste buds on the soft palate in a human subject of 78-year-old. U; uvula, CV; circumvallate papillae, FL; foliate papillae, FF; fungiform papillae.

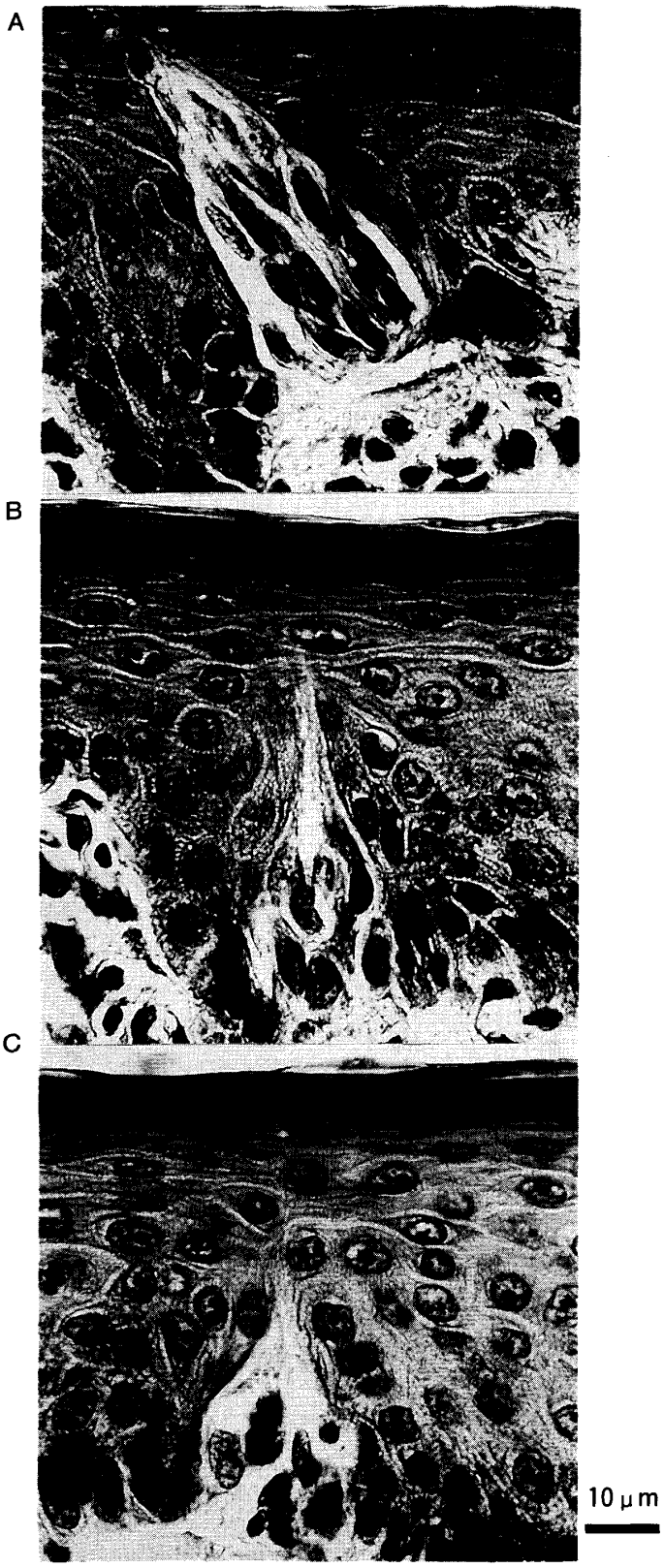

Figure 2 : Microscopic photos of three taste buds observed on the right soft palate shown in Figure 1.

from 7 weeks to birth. However, Lalonde and Eglitis[3] supplied quantitative information on the number and distribution of taste bud on the soft palate. Their study from a single human newborn revealed the presence of 419 taste buds on the soft palate. Nilsson[5] revealed the occurrence of taste buds in the palatal mucosa from autopsy materials in four of seven subjects aged 25-44 years. He concluded that the difference among these results are based on the scarcity of the taste buds and mortal autolysis. Recently, we examined 10 μm serial paraffin sections of right half of a soft palate aged 78 years and found three taste buds on the midline region of the soft palate shown in Figure 1. A clear taste pore was observed in one of the three taste buds (Figure 2; A), but not observed in rest of them (Figure 2; B and C). On the other hand, many psychophysiological experiments have been reported that there exist taste sensation on the soft palate in man as cited above[12-17]. Therefore, at least it might be certain that there functional taste buds exist through life span on the soft palate in human. More precise experiment should be notified in this issue.

Ⅳ. Taste buds distribution in animals

The distribution of taste buds on the soft palate has been investigated comprehensively in the rat. Kutuzov and Sicher[6] observed numerous taste buds on the terminal ridge behind the posterior rugal field of the hard palate in the rat (Figure 3). Kaplick[7] also observed 30 taste buds on this ruge, which he called "Geschmacksstreifen (GS)", and 60 taste buds in the naso-palatin ducts of the rostral hard palate. Distribution of taste buds on the central palatal area was reported by Cleaton-Jones[8]. Quantitative information for the distribution of taste buds and their innervation was supplied by Miller[10,21-22]. In his intensive work[10], there were 22-44 taste buds per unilateral GS with a mean 33.6 taste buds per side, and the posterior field of the soft palate averages more than 80 per rat. Quantitative taste bud distribution in the rat reported formerly were summarized in Table 1[9]. Also, quantitative distribution of taste buds on the soft palate in the hamster was shown by Miller and Smith[10]. The palate contained 100 taste buds divided among the soft palate (88) and the incisal papillae (12) (Table 2). Our

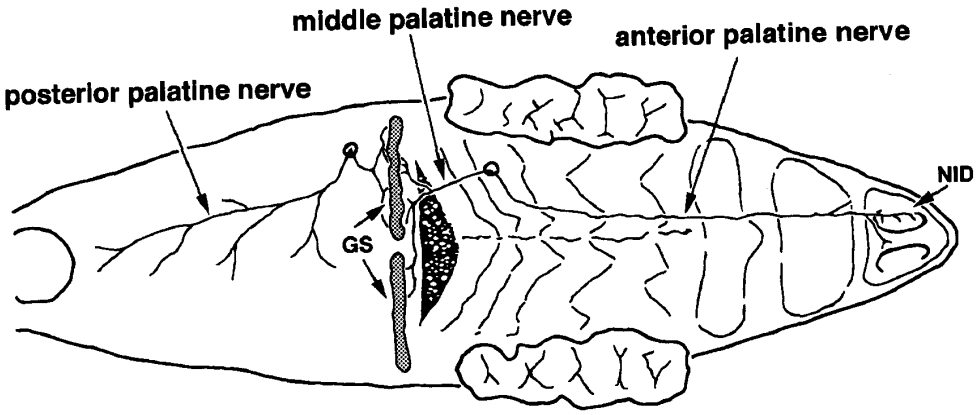

Figure 3 : Distribution of branches of the GSP on the palate of the rat[21]. GS ; Geschmacksstreifen, NID ; nasal incisal duct.

histological experiment showed that dissection of the GSP resulted in severe degeneration of taste buds on the soft palate in the hamster[26] (Figure 4), which made sure that those taste buds are innervated by the GSP. In the monkey, numerous taste buds were found in aggregates confined to 0.15 to 0.3 mm wide, round island of keratinizing epithelium of the soft palate[23].

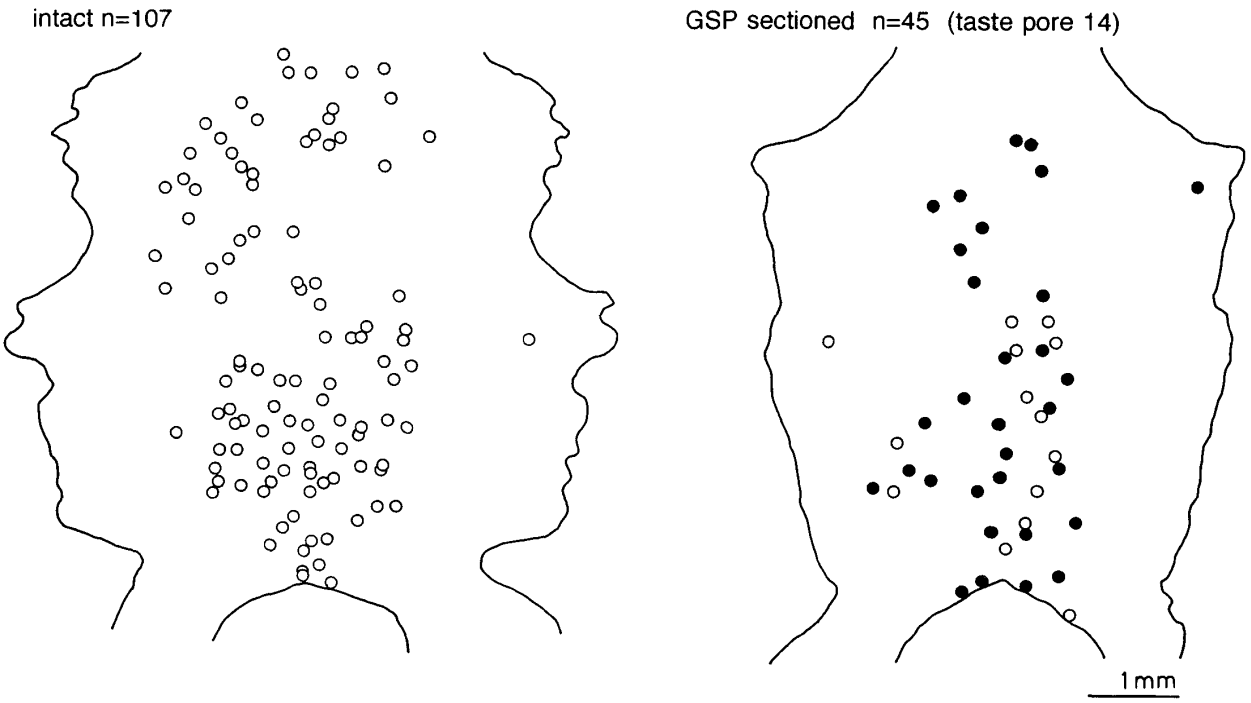

Figure 4 : Taste bud distribution on the soft palate with intact GSP (left) and one month after GSP sectioned hamster (right). Open circle indicates taste buds with taste pore, closed circle without pore[23].

Table 1 : Total taste bud distribution in the rat[9] (partly modified.)

Region	Number of taste buds	Source	Estimated mean per animal	Percent of total
Fungiform	178.8 mean total (N=103)	Fish *et al.*[1]		
	187 mean total (N=10)	Miller and Preslar[73]		
	93 mean per side (N=3)	Oakley[74]	185	15%
Foliate	231 per side (N=4)	Oakley[75]	460	36%
Circumvallate	375 mean total (N=8)	Guth[2]		
	292 mean total (N=8)	Kennedy[76]	350	28%
Palate	165 estimated total of soft palate and NID	Kaplick[7]		
	156 mean soft palate only (N=6)	Cleaton-Jones[8]		
	225 soft palate and NID	Kaplick[7]	220	17%
Epiglottis	21-91 range total per animal (N=25)	Fishman[77]	50	4%
Total			1,265	100%

Table 2 : Taste bud distribution in the hamster[10]

Total Hamster Taste Buds	723	100%
Fungiform	130	18.0%
Sublingual Organ	5	0.7%
Foliate	230	31.8%
Buccal Wall	10	1.4%
Vallate	168	23.2%
Palate	100	13.8%
Incisal Papilla only	12	1.7%
Soft Palate only	88	12.1%
Epiglottis	70	9.7%
Nasopharynx	10	1.4%

V. Innervation of the palate taste buds

Palatal taste buds are innervated by the GSP nerve branched from the facial nerve (VIIth cranial nerve) in the geniculate ganglion. The palatine distribution of the GSP in the rat are shown by Miller et al.[21] in Figure 3 which was identified from the homologous innervation in mouse shown by Rhinehart[25]. Degeneration studies by Miller and Spangler[22] revealed that only 34 of 277 total taste buds on the palate remained 20-22 days after bilateral transection of the GSP, and they concluded that 85% of the palatal taste buds are innervated by the GSP. Our histological examination in the hamster[26] revealed that transection of the GSP caused severe degeneration of taste buds on the soft palate (Figure 4). Mean number of taste bud on the soft palate one month following sectioning the GSP was 44.3 ± 4.0 (S.D., n=3), which was significantly smaller than those in intact animal (117.7 ± 8.3, n=3). However, the number of remained taste buds (37.6%) was larger than in the rat (15%)[22]. Sectioning the CT in the hamster resulted in much smaller degeneration of taste buds on the tongue (143.3 ± 17.0, n=3) against that in intact hamster (174.0 ± 5.6, n=3)[26], although the number of taste buds observed taste pore was 54.3 ± 15.0 in the CT dissection against the 101.0 ± 4.6 in the group with intact GSP. These data suggest that the remained taste buds after the GSP nerve transection cannot be identified as they were innervated by different nerves.

VI. Electrophysiological recordings from the GSP in the rat

Regardless of these histological data, the great majority of information about the processing of taste quality has been based on input from the fungiform papillae via the CT nerve in different animals[27-44], to some extent, the glossopharyngeal nerve[27,45-48] and the superior laryngeal nerve[49-52]. Neural recordings from the GSP were reported only from the rat[53,55] and hamster[54]. The first electrophysiological recording from the GSP in the rat made by Nejad[53] in 1986. He revealed that the response profile in the rat GSP for four basic taste stimuli is quite different from that

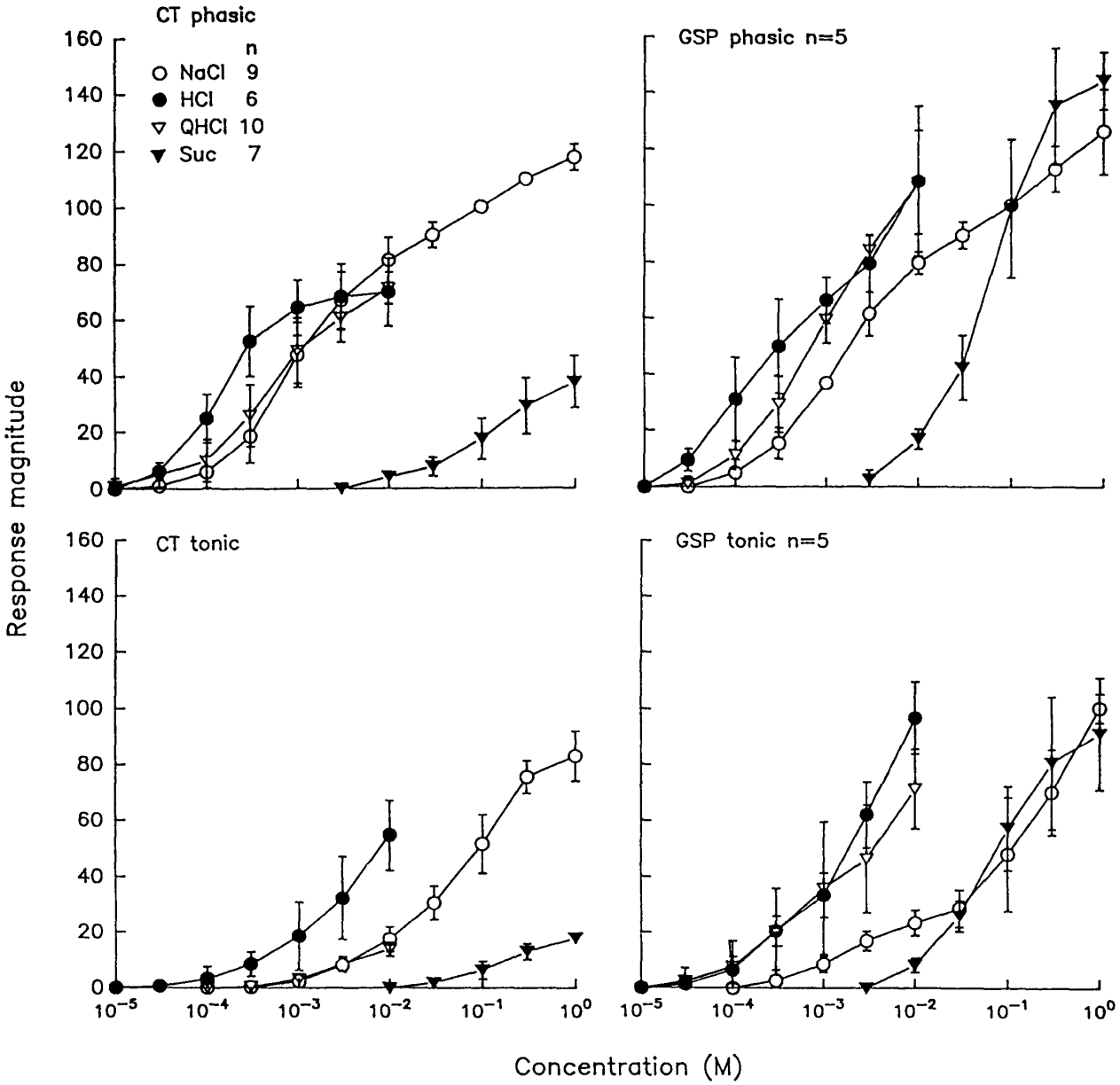

Figure 5 : Mean concentration-response functions for the four basic taste stimuli in the GSP and CT nerves of the rat. The phasic response to 0.1 M NaCl was used as standard 100. Error bar shows SD of the mean.

in the rat CT although the origin of both nerves are VIIth nerve. In the rat GSP, sucrose produced the greatest neural response among the four taste qualities, whereas, NaCl produced the greatest response in the CT. Mean integrated responses in the CT and GSP nerve of the rat to the concentration series of the four basic taste stimuli are shown in Figure 5. In the figure, phasic responses of both nerves are shown at the top of the figure and tonic responses at 10 sec after the stimulation onset are shown at the bottom. Thresholds for the phasic and tonic responses to sucrose in both GSP and CT nerves were around 0.003 M. However, in the GSP, sucrose response increase in steeper slope with concentration increase, whereas that the rate of increase in the CT was much smaller than that in the GSP, and only 30% even at 1 M. In order to compare the responsiveness for four basic taste stimuli between the two nerves, total response magnitudes

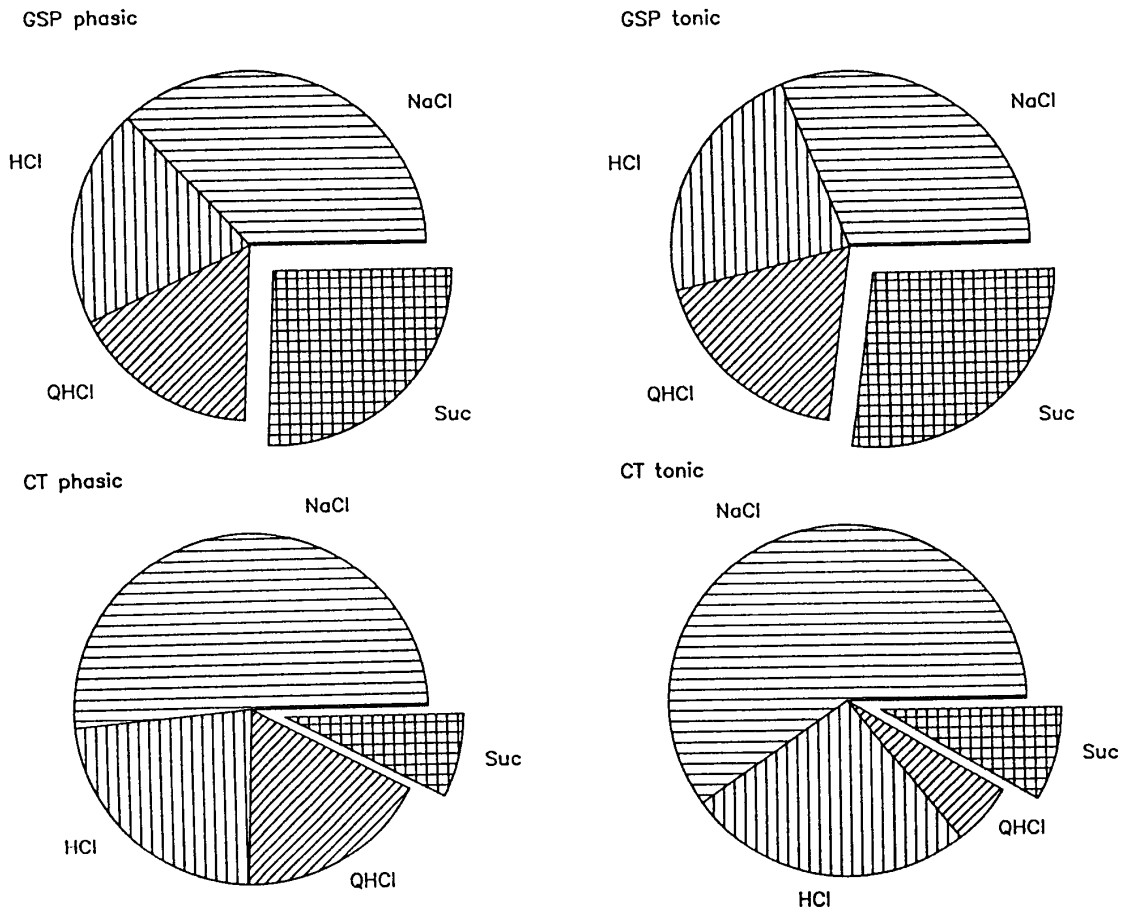

Figure 6 : Response ratio of total response magnitudes[55] for each stimuli of four basic taste stimuli in the GSP and CT of the rat. Data were calculated from the data in Figure 5.

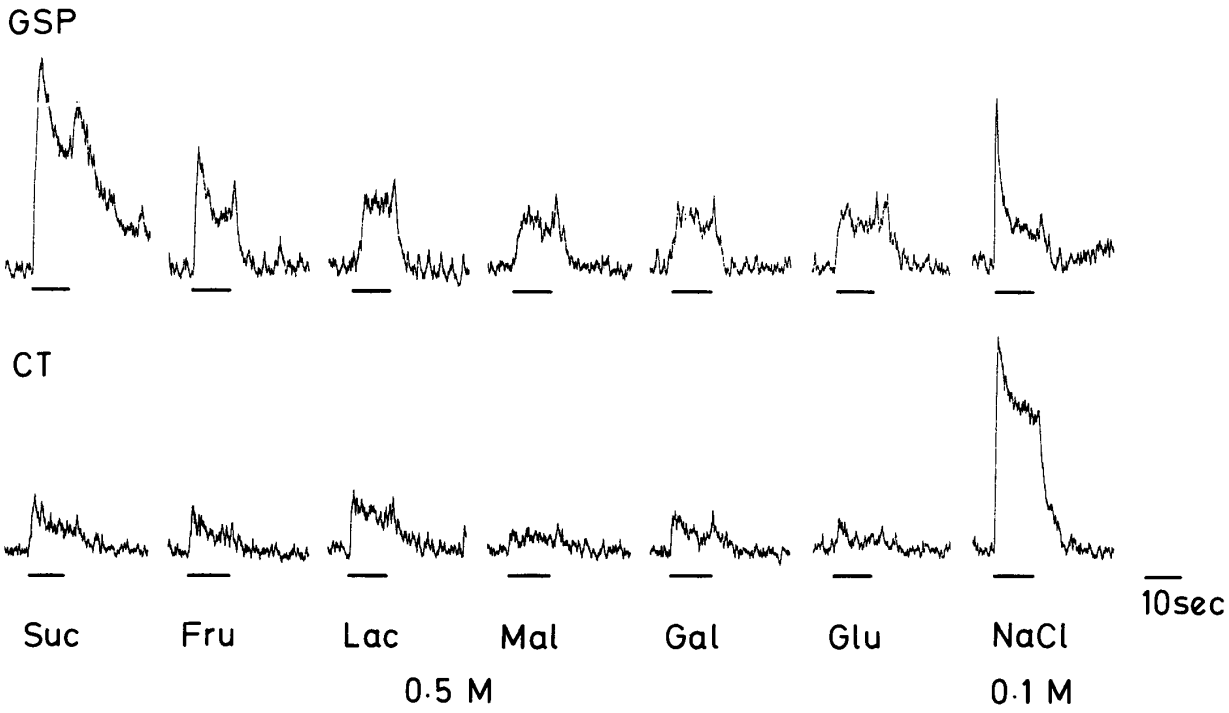

Figure 7 : Typical integrated taste responses of a CT nerve and a GSP nerve to six 0.5 M sugars and 0.1 M NaCl standard. Stimuli are applied for 10 sec duration shown by the horizontal bar below each response. Integration time constant was 300 msec.

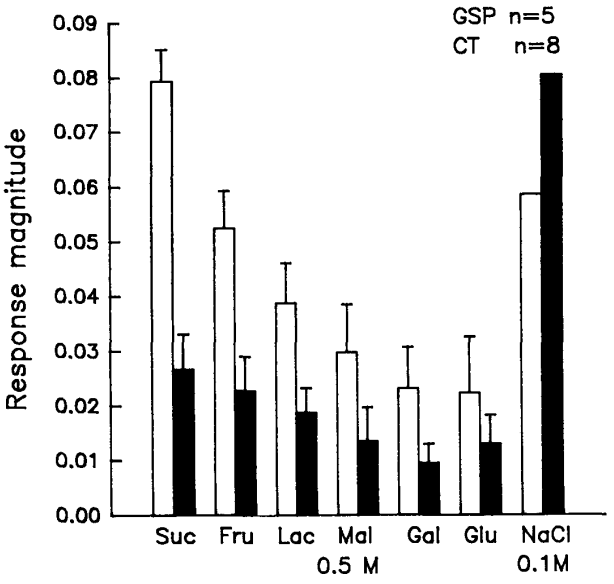

Figure 8 : A comparison of the mean phasic responses of the GSP (open bars) and CT (close bars) to the 0.5 M sugars in the rat. Error bars show SD.

(TRM) were calculated by summating all of the response magnitudes for each stimulation with the limited concentration range (NaCl 0.0001 - 1 M, sucrose 0.003 - 1 M, HCl 0.00001 - 0.01 M, quinine-HCl 0.000003 - 0.01 M). Figure 6 shows the ratio of each TRM against the total of TRM showing the large responsiveness for sucrose in the GSP rather than in the CT.

Integrated responses from a GSP and CT to six sugars at 0.5 M are shown in Figure 7, and mean relative response magnitudes for them are shown in Figure 8. All of the six sugars, especially sucrose, produced large responses in the GSP. Generally, amiloride has a potent depression effect on the Na response in the CT. In the CT, tonic response to 0.1 M Na-acetate is markedly depressed to base line level when dissolved in 0.00005 M amiloride solution, and tonic response to 0.01 M Na-saccharine is also inhibited to two-third of distilled water solution (Figure 9; bottom). On the contrary, in the GSP, amiloride showed no clear effects on responses to both Na-acetate and Na-saccharin (Figure 9; top). These recordings suggest that taste buds

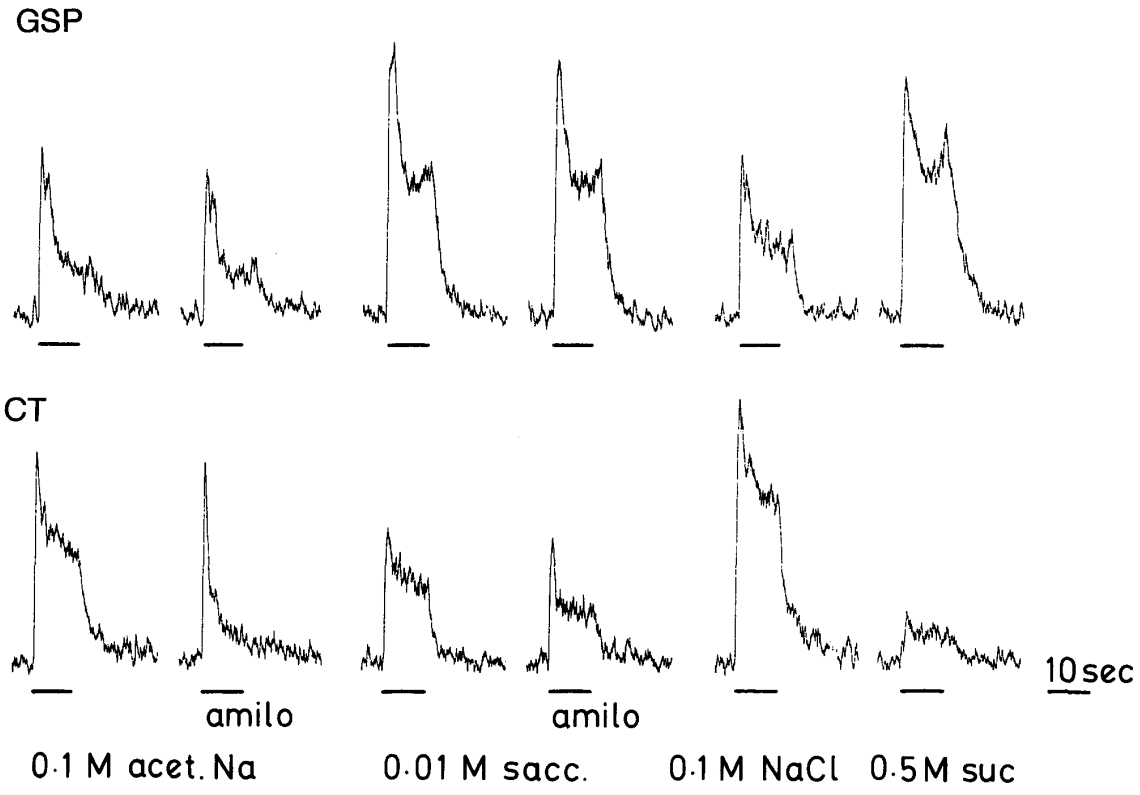

Figure 9 : Effects of 0.00005 M amiloride solved in the stimulus solution of 0.1 M Na-acetate and 0.01 M saccharin on integrated responses from one GSP and one CT of rats.

on the soft palate posses not only high sensitivity for sweet substances but also have different transduction mechanisms from that of the tongue.

Ⅶ. Neural responses to amino acid in the GSP of the rat

The amino acid is one of the essential nutrient for all organisms and their importance as taste stimuli has been recognized and investigated in several kinds of animals including man. Psychophysiological studies in man have addressed structure activity relationships for the taste of amino acids. D-amino acids have been reported to produce generally sweet taste while L-forms produce either sweet, bitter, or no taste sensation[57-58]. In mammals, several investigators have reported stimulatory effectiveness for amino acids by neural recording from the CT[56-57,59,62-70] or geniculate ganglion[60-61]. These results have revealed that several amino acids have prominent sweet taste component. Although the GSP have strong sensitivity for sweet substances as mentioned above, nothing is known for the sensitivity for amino acids in this nerve. Thus neural responses to various L- and D-amino acids were recorded and compared between the GSP and CT nerves in the rat.

In the rat CT, basic amino acids HCl salts (L-Arg-HCl, L-Lys-HCl, and L-His-HCl) at 0.1 M produced robust phasic and succeeding tonic response that were quite similar to those for 0.1 M NaCl[56,62-63,65-67]. A comparison of the phasic responses to L- and D- amino acids in the CT and GSP nerve are shown in Figure 11. The responses to D-basic amino acids HCl salts were similar to enantiomer, and differences between the two forms were no significant. However, in the GSP, D-His-HCl produced a significantly larger response than L-His-HCl. The free base D-His was also more stimulatory than L-His in the GSP. Multiple unit responses of fine strands of the GSP showed that the units which responded sucrose specifically responded to free base His (Figure 12). All eleven L-neutral amino acids (Asn, Ser, Gln, Met, Thr, Phe, Leu Val Pro at 0.1 M and Trp at 0.05 M) produced only 30% - 40% of relative response magnitudes in both the CT and GSP, and there was strongly significant correlation ($p < 0.01$) between the two nerves (Table 3). In the CT, each response to D-neutral amino acids (Asn, Ser, Gln, Ala, Met, and Thr at 0.1 M) was significantly smaller than that to each enantiomer, only 0.05 M D-Trp producing a significantly larger response than that to L-Trp in this nerves. In the GSP, in contrast to that, most of the D-neutral amino acids produced significantly larger responses than the L-neutral amino acids (Table 3). Only L-Pro produced a larger response than the enantiomers. Effects of gurumarin which is extracted from Gymnema sylvestre and which specifically suppresses sweet taste in the rat[78] tested in the CT and GSP. After the treatment for 15 min with 20 μg/ml gurmarin, responses to sucrose decreased 50% in the CT. The suppression effect, in the GSP, was so strong that responses to 0.5 M sucrose or 0.01 M Na-saccharin decreased to 20% - 30%, and most of the responses to neutral amino acids of both forms were affected, with some exceptions, such as D-Trp (Figure 13).

These results suggest that the strong stimulatory effectiveness induced by D-amino acids in the rat GSP depends on strong responsiveness to sweet substances, and that the receptor sites or transduction mechanisms for amino acids might be different from those of the other loci of the soft palate.

Ⅷ. Neural responses in the GSP of the hamster

Recordings from the GSP in the hamster performed by Harada and Smith was the second precise report after the first report by Nejad in the rat. Figure 14 shows the mean integrated responses to the concentration series of the four basic taste stimuli. 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 on the right. Although the threshold for the phasic response to sucrose in the GSP was about a half log unit higher than in the CT, the relative response magnitude for 1.0 M sucrose in the GSP was larger than that in the CT. The difference in sucrose response between the two nerves is even more apparent in the tonic response. Responses of one GSP and one CT nerve to six 0.5 M sugars and to the 0.1 M NaCl standard are shown in the Figure 15. The sugars did not elicit pronounced phasic responses in either nerve. All six of the sugars, however, produced larger

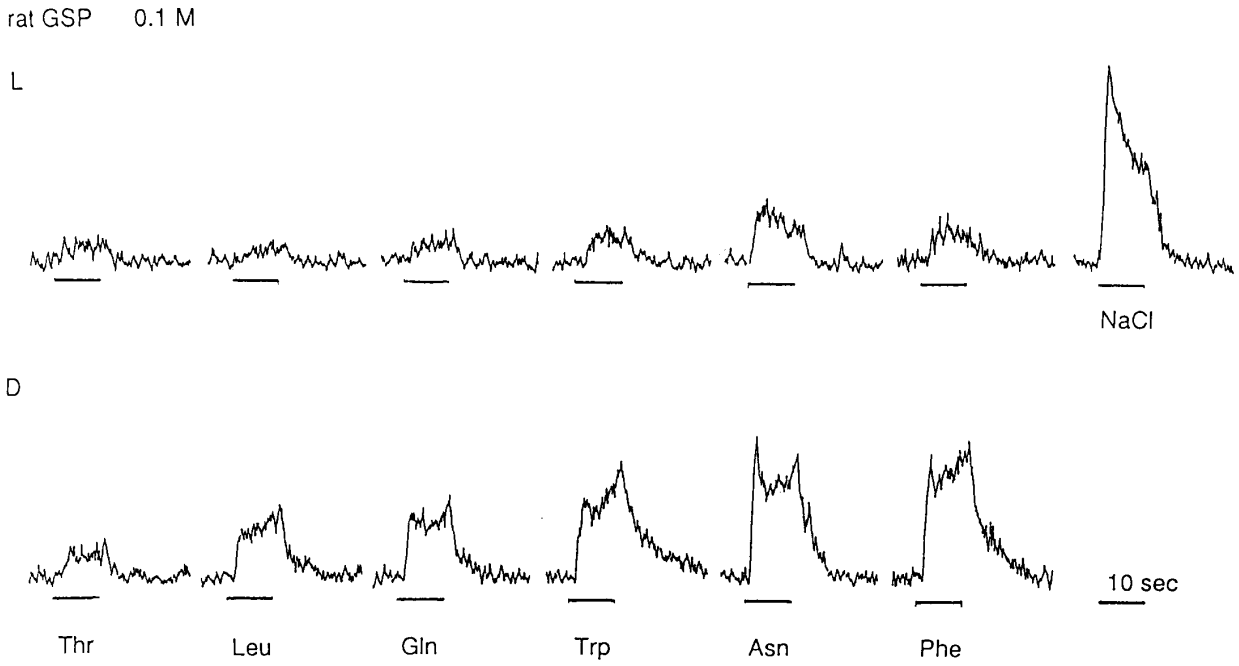

Figure 10 : Integrated responses of a GSP nerve to six 0.1 M L- and D-form amino acids and the 0.1 M NaCl in a rat.

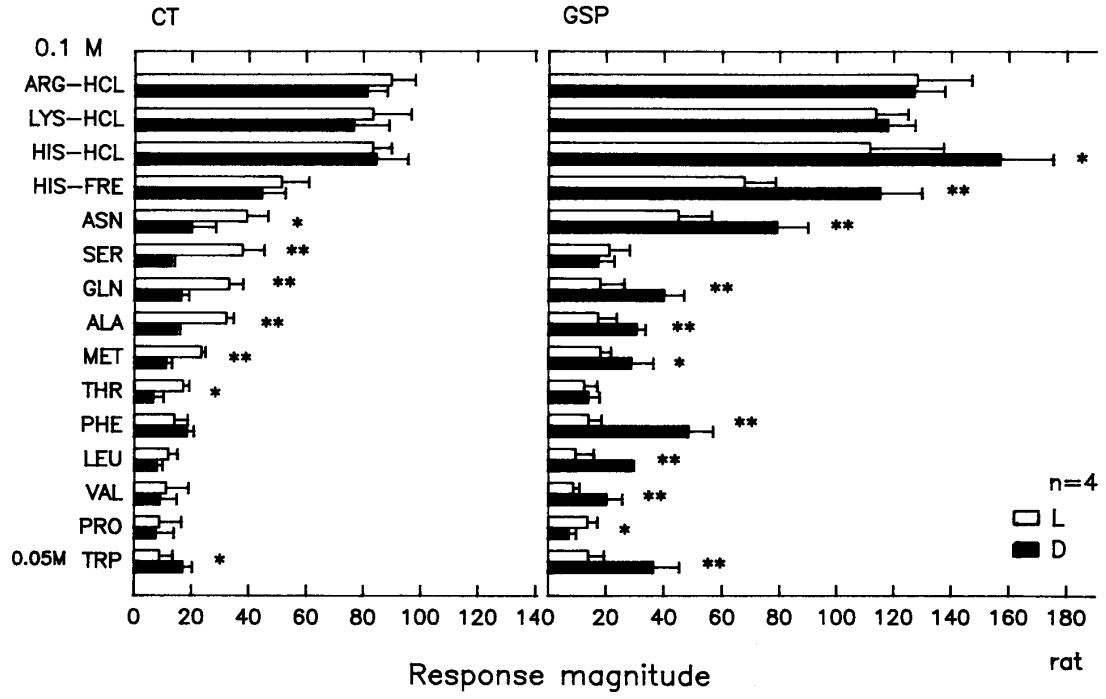

Figure 11 : A comparison of the mean phasic responses to L- and D-amino acids in the CT and GSP of the rat, which are relative response magnitude to phasic response of 0.1 M NaCl as a standard. Error bars show SD. Asterisks indicate statistically significant differences (two tailed *t*-test ** $p < 0.01$; * $p < 0.05$).

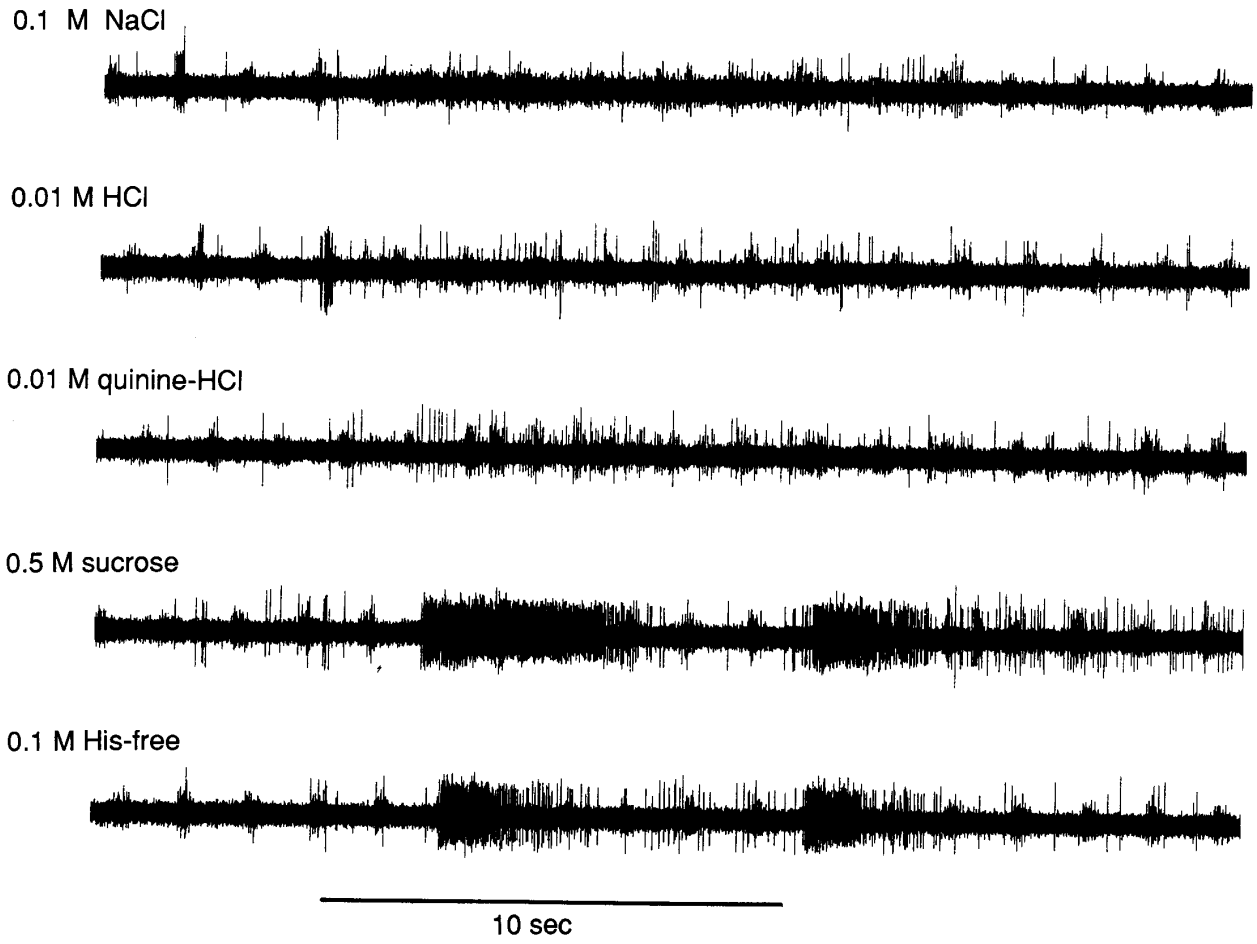

Figure 12 : Responses recorded from a fine strand of a GSP nerve of a rat to four basic taste stimuli and 0.1 M L- His free-base.

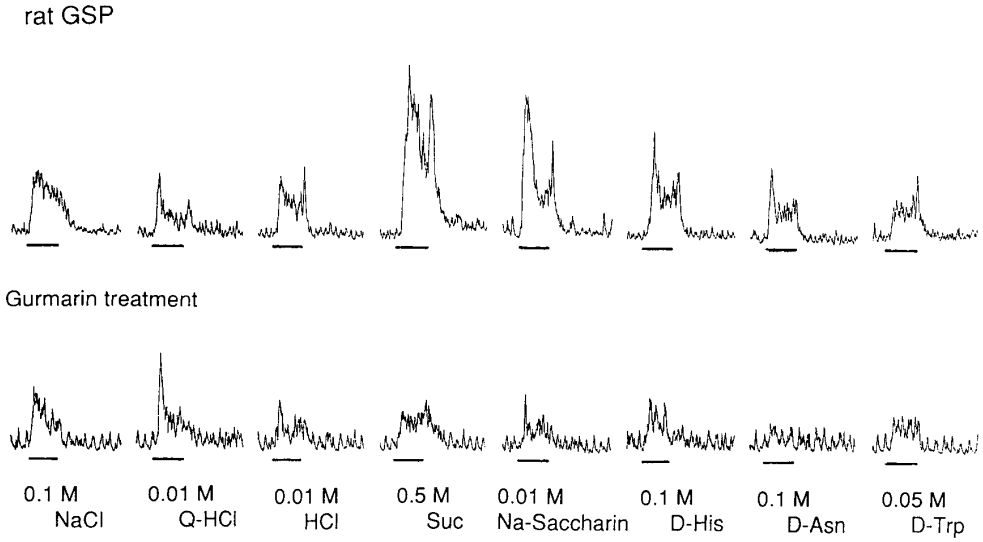

Figure 13 : Integrated responses to the four basic taste stimuli, Na-saccharin and three D-amino acids and those after the treatment for 15 min with 20 μg/ml gurumarin.

Table 3 : Correlalion coefficient between responses to L-vs D-amino acids in the GSP or CT, and the GSP vs CT.

		basic	neutral
L vs D	GSP	0.3353	0.7611**
	CT	0.9713*	0.4741
GSP vs CT	L-form	0.9754*	0.7290**
	D-form	0.6326	0.8422**
	n	4	11

*$p<0.05$, **$p<0.01$

responses in the GSP than in the CT, relative to the phasic response to 0.1 M NaCl. In fact, compared to the tonic responses to 0.1 M NaCl, in each nerve which are smaller in the GSP, the response to the sugars were much larger than that in the GSP; sugar responses were more than twice of the tonic response to NaCl in the GSP but less than half of the tonic response to NaCl in the CT (Figure 15). The mean relative responses to each of these stimuli in the two nerves are shown in Figure 16. These response ratios, as mentioned above, were derived from the data normalized to the phasic response to 0.1 M NaCl and then expressed as a portion of the TRM (as defined above). There were significant differences ($p < 0.05$) between the CT and GSP in both the phasic and tonic portions of the sugar responses, except for the initial phasic response to glucose. In every instance, the relative responses to these sugars was larger in the GSP than in the CT nerve. Since there was little pronounced phasic response to the sugars, the differences between the two nerves are markedly evident on both the phasic and tonic response measures, indicating that the sugars are around twice as effective on the soft palate as they are on the anterior portion of the tongue compared to the control, the phasic response to 0.1 M NaCl.

Ⅸ. Discussion

Most of the knowledge about the neurophysiological mechanisms in peripheral gustatory nerves was based on the response profiles from the CT innervating anterior part of the tongue. Although histological data apparently indicate the existence of numerous taste buds on the soft palate in mammals, functions of those taste buds had been remained unknown for a long time. Recent electrophysiological studies in the rat and hamster have enclosed the importance of the gustatory input from the soft palate taste buds in mammals. This importance is also revealed by behavioral experiments. In the rat, bilateral section of the GSP nerve results in a dramatic reduction in licking of sucrose solution[71]. Also, we demonstrated that transection of the GSP and/or CT nerves in the hamster resulted in a significant reduction of the conditioned taste aversion for sucrose. The order of the sectioning effects was GSP + CT > GSP ≧ CT > sham (Table 4). These reports suggest that the GSP plays an important role for mediating sweet taste information.

On the other hand, in the hamster, there are almost as many as taste buds on the soft palate as in 120-day-old hamsters, although there are presumative buds, showing no clear taste pore[11]. In rats, it is reported that immature taste buds are present on the soft palate of 1-day-old and mature taste buds are evident at 12 days postnatally[72]. Recently, we quantitatively examined postnatal development of taste buds on the soft palate and the tongue in the rat. There exist 200 taste buds on the soft palate at birth as many as in 3-week-old although taste pore were observed in 50 taste buds (Figure 17; top). On the contrary, less than 100 taste buds, without observation of taste pore, existed in fungiform papillae on the anterior tongue in new born rats, and the number of taste buds postnatally increased during 4 weeks reached to the maximum of 200 (Figure 17, bottom). Human newborns have been reported to possess a numeral number of taste buds on the soft palate[19]. Considering these number of taste buds on the soft palate and the strong responsiveness for sweet including many amino acids, gustatory function of the soft palate should play an important role on the ingestion of milk during early development in postnatal stage.

Table 4 : Effect of nerve transection on conditioned taste aversion[26]

	GSP+CT	GSP	CT	sham
GSP+CT	—	**4.167**	**5.486**	**8.546**
GSP		—	1.282	**4.467**
CT			—	**3.229**

Significant t-values are shown in underlined bold face type ($p < 0.01$) or in bold face type ($p < 0.05$).

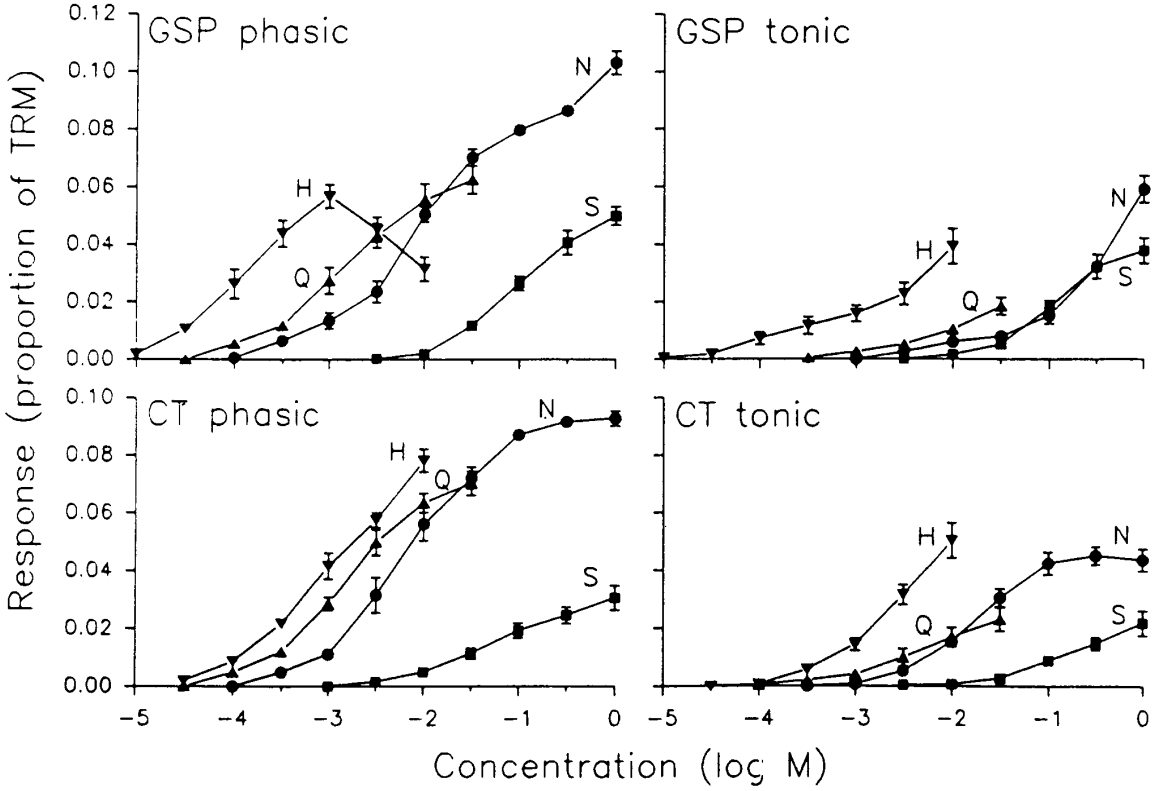

Figure 14 : Mean concentration-response functions to four basic taste stimuli in the GSP and CT nerves of the hamster. Responses are expressed as a proportion of the TRM for each nerve. Error bar shows SE.

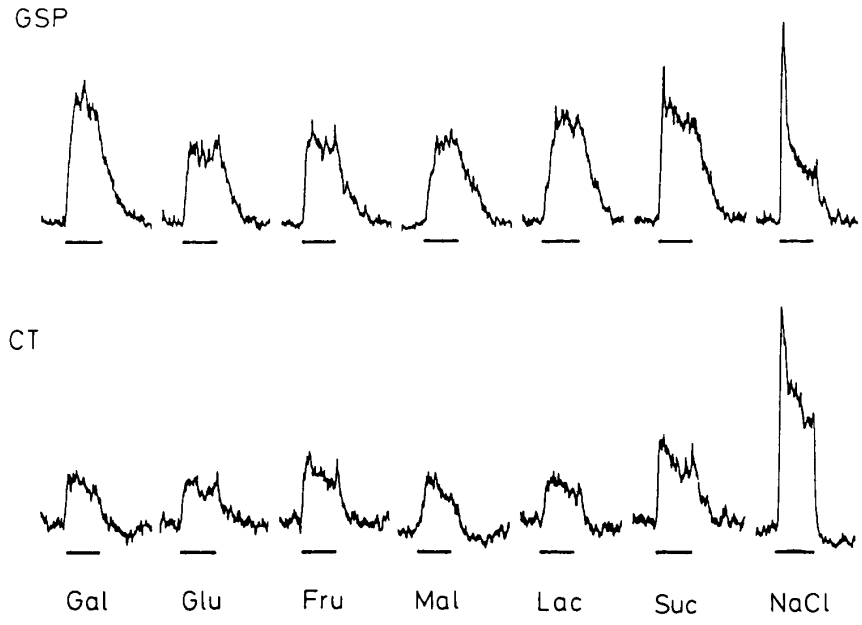

Figure 15 : Integrated responses of one GSP and one CT of hamsters to six 0.5 M sugars and to the 0.1 M NaCl standard.

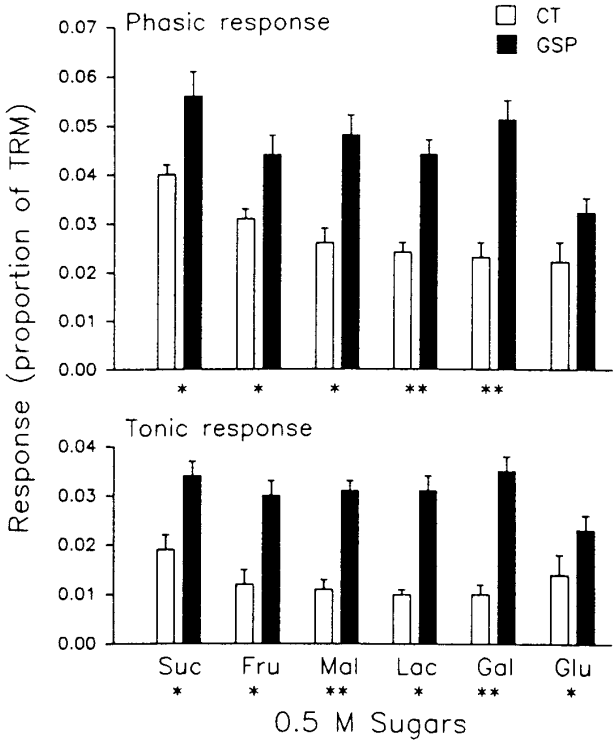

Figure 16 : A comparison of the mean phasic and tonic responses of the CT (open bars; n=6) and GSP (solid bars; n=6) to the 0.5 M sugars. Error bars show SE. Asterisks indicate significant difference (two tailed t-test; ** $p < 0.01$, ** $p < 0.05$).

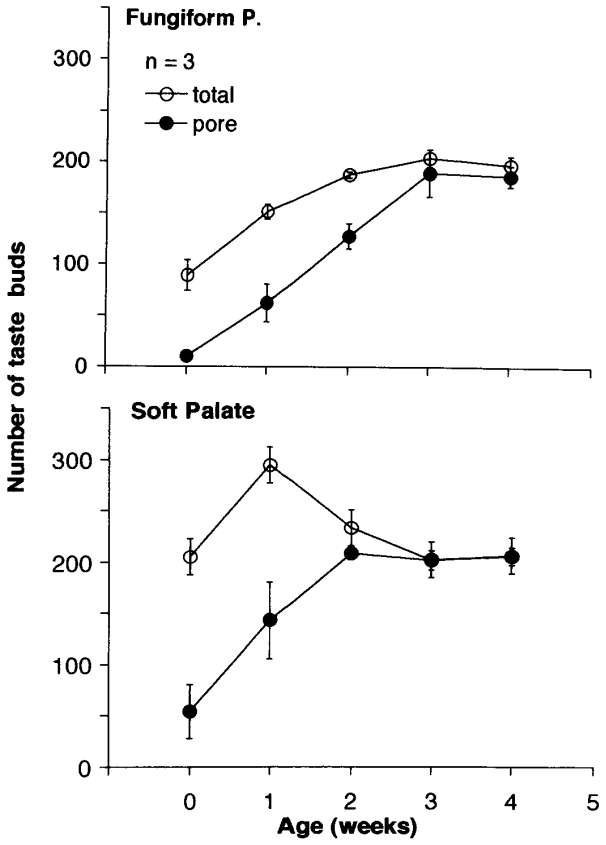

Figure 17 : Postnatal changing of numbers of taste bud distributed on the tongue (upper) and the soft palate (bottom) in the rat. Open circle shows total taste buds and closed circle shows taste buds with pores. Error bars inditate SD.

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References

1) Fish, H., Malone, P. and Richter, C.: The anatomy of the tongue of the domestic Norway rat. I. The skin of the tongue; the various papillae; their number and distribution. Anat. Rec. 89, 429-440, 1944

2) Guth, L.: Effects of glossopharyngeal nerve transection on the circumvallate papillae of the rat. Anat. Rec. 128, 715-731, 1957

3) Lalonde, E. and Eglitis, J.: Number and distribution of taste buds on the epiglottis, pharynx, soft palate and uvula in a human new born. Anat. Rec. 181, 91-95, 1961

4) Ponzo, M.: Sulla presenza di organi del gustonella parte laringea, della faringe, nel tratto cervicale del esofago e nell palato duro del feto umano. Anat. Anz. 31, 570-575, 1907

5) Nilsson, B.: The occurrence of taste buds in the palate of human adults as evidenced by light microscopy. Acta Odontol. Scand. 37, 253-258, 1979

6) Kutuzov, H. and Sicher, H.: Anatomy and function of the palate in the white rat. Anat. Rec. 114, 67-84, 1952

7) Kaplick, M.: Uber Vorkommen, Verteilung und Histologische Beziehungen der Geschmacksknos-

pen am Mundach einiger Sauger, besonders der Nagetier. Zeit. Zell. 38, 571-590, 1953

8) Cleaton-Jones, P.: Histological observations in the soft palate of the albino rat. J. Anat. 110, 39-47, 1971

9) Miller, I. J. Jr.: Gustatory receptors of the palate. In: Katsuki, Y., Sato, M., Takagi, S. and Oomura, Y. (eds), Food Intake and Chemical Senses. University of Tokyo Press, Tokyo, pp.173-185, 1977

10) Miller, I. J. and Smith, D. V.: Quantitative taste bud distribution in the hamster. Physiol. Behav. 32, 275-285, 1984

11) Belecky, T. L. and Smith, D. V.: Postnatal development of palatal and laryngeal taste buds in the hamster. J. Comp. Neurol. 293, 646-654, 1990

12) Brillat-Savarin, J. A.: The Physiology of Taste; Thoughts on Transcending Gastronomy. Privately published 1825 (in French) Translated by Fisher, M. F. K., The Physiology of Taste. New York: Alfred A. Knopf, 1971

13) Kiesow, F.: Beiträge zur physiologischen Psychologie des Geschmackssinnes. Philos. Stud. 10, 329-368, 1894

14) Henkin, R. I. and Christiansen, R. L.: Taste localization on the tongue, palate, and pharynx of normal man. J. Appl. Physiol. 22, 316-320, 1967

15) Collings, V. B.: Human taste response as a function of locus of stimulation on the tongue and soft palate. Percept. Psychophys. 16, 169-174, 1974

16) Nilsson, B.: Taste acuity of the human palate. I. Studies with electrogustometry and taste solutions on young adults. Acta Odontol. Scand. 35, 51-62, 1977

17) Hammond, R., Beder, O. E. and Ratener, P. E.: Palatal receptor contribution to and effects of palatal alteration on taste acuity thresholds. J. Proth. Dent. 49, 121-125, 1983

18) Hoffman, A: Über die Verbreitung der Geschmacksknospen beim Menschen. Virschows Arc. Path. Anat. 62, 516-530, 1875

19) Gairns, F. W.: The sensory nerve endings of the human palate. Quart. J. Exp. Physiol. 40, 40-48, 1955

20) Wood, P. J. and Kraus, B. S.: Prenatal development of the human palate. Arch. oral Biol. 7, 137-150, 1962

21) Miller, I. J., Jr., Gomez, M. M. and Lubarsky, E. H.: Distribution of the facial nerve to taste receptors in the rat. Chem. Senses Flav. 3, 397-411, 1978

22) Miller, I. J., Jr. and Spangler, K. M.: Taste bud distribution and innervation on the palate of the rat. Chem. Senses 7, 99-108, 1982

23) Harada, S., Kohriyama, S. and Kasahara, Y.: Decrease of taste discrimination for sucrose after bilateral sections of the greater superficial petrosal nerve. Proc. 25th Symp. on Taste & Smell, pp.305-308, 1991

24) Klien, P. B. and Shroeder, H. E.: Epithelial differentiation and taste buds in the soft palate of the monkey, Macaca irus. 196, 181-188, 1979

25) Rhinehart, D. A.: The nerves facialis of the albino mouse. J. Comp. Neurol. 30, 81-125, 1918

26) Harada, S.: Effects of transection of the greater superficial petrosal and the chorda tympani nerves on conditioned taste aversion to sucrose in the hamster. Jpn. J. Oral Biol. 34, 690-700, 1992

27) Pfaffmann, C.: Gustatory afferent impulses. J. Cell. Comp. Physiol. 17, 243-258, 1941

28) Beidler, L. M.: Properties of chemoreceptors of tongue of rat. J. Neurophysiol. 16, 595-607, 1953

29) Pfaffmann, C.: Gustatory nerve impulses in rat, cat and rabbit. J. Neurophysiol. 18, 429-440, 1955

30) Fishman, I. Y.:Single fiber gustatory impulses in rat and hamster. J. Cell. Comp. Physiol. 49, 319-334, 1957

31) Ogawa, H., Sato, M., and Yamashita, S.: Gustatory impulse discharges in response to saccharin in rats and hamsters. J. Physiol. 204, 311-329, 1969

32) Ogawa, H., Sato, M., and Yamashita, S.: Varidity in impulse discharges in rat chorda tympani fibers in response to repeated gustatory stimulation. Physiol. Behav. 11, 469-479, 1973

33) Ogawa, H., Sato, M. and Yamashita, S.: Multiple sensitivity of chorda tympani fibers of the rat and hamster to gustatory and thermal stimuli. J. Physiol. 199, 223-240, 1968

34) Sato, M., Ogawa, H., and Yamashita, S.: Response properties of macaque monkey chorda tympani fibers. J. Gen. Physiol. 66, 781-810, 1975

35) Frank, M.: An analysis of hamster afferent taste

nerve response function. J. Gen. Physiol. 61, 588-618, 1973
36) Smith, D. V. and Frank, M.: Cross adaptation between salts in the chorda tympani nerve of the rat. Physiol. Behav. 8, 213-220, 1972
37) Smith, D. V. and Bealer, S. L.: Sensitivity of the rat gustatory system to the rate of stimulus onset. Physiol. Behav. 15, 303-314, 1975
38) Smith, D. V., Steadman, J. W. and Rhodine, N.: An analysis of the time course of gustatory neural adaptation in the rat. Am. J. Physiol. 229, 1134-1140, 1975
39) Smith, D. V., Bealer, S. L. and Buskirk, R. L.: Adaptation and recovery of the rat chorda tympani response to NaCl. Physiol. Behav. 20, 629-636, 1978
40) Frank, M., Bieber, S. L. and Smith, D. V.: The organization of taste sensibilities in hamster chorda tympani nerve fibers. J. Gen. Physiol. 91, 861-896, 1988
41) Cheal, M.: Taste responses of the chorda tympani nerve in the mouse. Physiol. Behav. 19, 175-177, 1977
42) Nagai, T. and Ueda, K.: Stochastic properties of gustatory impulse discharges in rat chorda tympani fibers. J. Neurophysiol. 45, 574-592, 1981
43) Harada, S., Marui, T. and Kasahara, Y.: Analysis of the initial taste responses from rat chorda tympani nerve. Jpn. J. Oral Biol. 25, 566-170, 1983
44) Ninomiya, Y., Tonosaki, K. and Funakoshi, M.: Gustatory neural response in the mouse. Brain Res. 244, 370-373, 1982
45) Pfaffmann, C., Fisher, G. and Frank, M.: The sensory and behavioral factors in taste preferences. In Hayashi, T.(ed.), Olfaction and Taste II, Pergamon Press Ltd., London, pp. 361-381, 1967
46) Oakley, B., Jones, L. B. and Kaliszewski, J. M.: Taste responses of the gerbil IXth nerve. Chem. Senses Flav. 4, 79-87, 1979
47) Shingai, T. and Beidler, L. M.: Interstrain differences in bitter taste response in mice. Chem. Senses 10, 51-55, 1985
48) Hanamori, T., Miller I. J., Jr. and Smith, D. V.: Gustatory responsiveness of fibers in the hamster glossopharyngeal nerve. J. Neurophysiol. 60, 478-498, 1988
49) Storey, A. T.: A functional analysis of sensory units innervating epiglottis and larynx. Exp. Neurol. 20, 366-383, 1968
50) Storey, A. T. and Johnson, P.: Laryngeal water receptor initiating apnea in the lamb. Exp. Neurol. 47, 42-55, 1975
51) Shingai, T. and Beidler, L.: Response characteristics of three taste nerve in mice. Brain Res. 335, 245-249, 1985
52) Smith, D. V. and Hanamori, T.: Organization of gustatory sensitivities in hamster superior laryngeal nerve fibers. J. Neurophysiol. 65, 1098-1114, 1991
53) Nejad, M.: The neural activities of the greater superficial petrosal nerve of the rat in response to chemical stimulation of the palate. Chem. Senses 11: 283-293, 1986
54) Harada, S., Kohriyama, H., Shimura, G., R. Mochizuki, Y. and Y. Kasahara: Properties of responses from the greater superficial petrosal nerve to gustatory stimulation on the soft palate in the rat. Proc. 25th Jpn. Symp. Taste and Smell, 325-328, 1991
55) Harada, S. and Smith, D. V. : Gustatory responses of the hamster's soft palate. Chem. Senses 17, 37-51, 1992
56) Harada, S., Enomoto, S. and Kasahara, Y.: Gustatory responses from the GSP nerve to L- and D-amino acids applied on the soft palate in the rat. In Kurihara, K. edt: Olfaction & Taste XI, Springer-Verlag, 1993 (in press)
57) Solms, J., Vuatas, L., and Egli, H.: The taste of L- and D-amino acids. Experientia 21, 692-694, 1965
58) Schiffman, S. S., Sennewald, K., and Gagnon, J.: Comparison of taste qualities and thresholds of D- and L-amino acids. Physiol. Behav. 27, 51-59, 1981
59) Halpern, B. P., Bernard, R. A., and Kare, M. R.: Amino acids as gustatory stimuli in the rat. J. Gen. Physiol. 45, 681-701, 1962
60) Boudreau, J. C., and Nelson, T.: Chemical stimulus determinants of cat geniculate ganglion chemoresponsive groupiunits discharge. Chem. Senses Flav. 2, 353-374, 1977
61) Boudreau, J. C., Oravec, J. J., and Hoang, N. K.:

Taste system of goat geniculate ganglion. J. Neurophysiol. 48, 1226-1242, 1982

62) Pritchard, T. C., and Scott, T. R.: Amino acid as taste stimuli. I. Neural and behavioral attributes. Brain Res. 253, 81-92, 1982

63) Pritchard, T. C., and Scott, T. R.: Amino acids as taste stimuli. II. Quality coding. Brain Res. 253, 93-104, 1982

64) Harada, S., Marui, T., and Kasahara, Y.: Amino acdis as taste stimuli in the mouse. Proc. 16th Jpn. Symp. Taste and Smell. pp. 123-126, 1982

65) Harada, S., Marui, T., and Kasahara, Y.: Gustatory stimulatory effectiveness of basic amino acids in rat and mouse. Proc. 17th Jpn. Symp. Taste and Smell. pp. 61-64, 1983

66) Harada, S., Marui, T., and Kasahara, Y.: Gustatory responses to amino acids from mouse chorda tympani nerve. Proc. 18th Jpn. Symp. Taste and Smell. pp. 149-152, 1984

67) Harada, S., Marui, T., and Kasahara, Y.: Neural and behavioral responses to amino acid in mice and rats. Olfaction and Taste IX, ed. by Roper, S. D., and Atema, J., The New York Acad. Sci., pp.345-346, 1987

68) Iwasaki, K., Kasahara, T., and Sato, M.: Gustatory effectiveness of amino acids in mice: behavioral and neurophysiological studies. Physiol. Behav. 34, 531-542, 1985

69) Kasahara, T., Iwasaki, K., and Sato, M.: Taste effectiveness of some D- and L-amino acids in mice. 39, 619-624, 1987

70) Ninomiya, Y., Nomura, T., and Katsukawa, H.: Genetically variable taste sensitivity to D-amino acids in mice. Brain Res. 596, 349-352, 1992

71) Krimm, R. F., Nejad, M. S., Smith, J. C., Miller, I. J. and Beidler, L. M.: The effects of bilateral sectioning of the chorda tympani and the greater superficial petrosal nerves on the sweet taste in the rat. Physiol. Behav. 41, 495-501, 1987

72) Mistretta, C. M.: Topographical and histological study of the developing rat tongue, palate, and taste buds. In J. F. Bosma (ed): Third Symposium on Oral Sensation and Perception: The Mouth of the Infant, Springfield, IL: Charles C. Thomas, pp.163-187, 1972

73) Miller, I. J., Jr., and Preslar, A: Spatial distribution of rat fungiform papillae. Anat. Rec. 181, 679-684, 1975

74) Oakley, B.: Reformation of taste buds by crossed sensory nerves in the rat's tongue. Acta Physiol. Scand. 79, 88-94, 1970

75) Oakley, B.: On the secification of taste neurons in the rat tongue. Brain Res. 75, 85-96, 1974

76) Kennedy, J.: The effects of transection of glossopharyngeal nerve on the taste buds of the circumvallate papillae of the rat. Arch. Oral Biol. 17, 1197-1207, 1972

77) Fishman, I.: Unpublished data.

78) Imoto, T., Miyasaka, A., Ishima, R., and Akasaka, K.: A novel peptide isolated from the leaves of Gymnema sylvestre: I. Characterization and its suppressive effect on the neural responses to sweet taste stimuli in the rat. Comp. Biochem. Physiol. 100A, 309-314, 1991