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Broad Tuning of Rat Taste Cells for Four Basic Taste Stimuli

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Abstract

The breadth of responsiveness of rat taste cells to the four basic taste stimuli was studied using the entropy measure (*H*) proposed by Smith and Travers. *H* values range from 0.0 for narrow tuning to 1.0 for broad tuning. Based on the responses of depolarizing receptor potentials of 26 rat taste cells to the four basic taste stimuli, taste cells were classified into nine NaCl-best, four Q-HCl (quinine-HCl)-best, 10 HCl-best and three sucrose-best cells. NaCl-best cells were narrowly tuned to the four basic taste stimuli, but the other three stimuli-best cells were broadly tuned to the stimuli. In all, 85% of the taste cells responded to more than one of four basic taste stimuli. The mean *H* values for NaCl-best, Q-HCl-best, HCl-best and sucrose-best cells were 0.285, 0.832, 0.781 and 0.796 respectively. The mean *H* value for all 26 taste cells was 0.621. This was larger than *H* in rat gustatory fibers. Transformation of large *H* values in taste cells into small *H* values in taste fibers may be due to a non-random interaction between taste cells and taste fibers during the synaptic formation. Broad tuning properties of rat taste cells suggest that the across-taste cell response pattern may play an important role in taste quality coding mechanisms. **Chem. Senses 22: 287–293, 1997.**

Introduction

Taste neural pathways differ a little between lower mammals such as rats and higher mammals such as monkeys (Yamamoto, 1984). Either lower or higher mammals possess taste areas in the nucleus of the solitary tract, the thalamus and the cerebral cortex. However, there is the pontine taste area between the gustatory zone of the nucleus of the solitary tract and the thalamic taste area in lower mammals (Yamamoto, 1984).

Analyses of electrical activities of the primary gustatory fibers and the neurons in a variety of central taste areas indicate that most of the peripheral and central gustatory neurons show multiple sensitivity for four basic taste stimuli (Pfaffmann, 1955; Erickson *et al.*, 1965; Ogawa *et al.*, 1968; Doetsch and Erickson, 1970; Frank, 1973; Smith *et al.*, 1983; Yamamoto *et al.*, 1984; Travers *et al.*, 1987). There are two theories regarding taste quality coding mechanisms, across-neuron response pattern theory (Erickson *et al.*, 1965) and labeled line theory (Frank, 1973, 1991; Nowlis and Frank, 1977; Frank *et al.*, 1988). The former emphasizes that each piece of taste quality information is due to spatial activities across many broadly tuned neurons in the peripheral and central taste pathways, and the latter

emphasizes that four kinds of gustatory quality information are carried by four classes of best-stimulus mediated gustatory neuron responses.

Receptor potentials in mammalian taste cells in response to four basic taste stimuli were first recorded in rats and hamsters by Kimura and Beidler (1961), who found that a taste cell shows a multiple sensitivity for four basic taste stimuli. The electrical properties and the responsiveness of rat taste cells to four basic taste stimuli have been investigated in detail (Ozeki and Sato, 1972; Sato and Beidler, 1982, 1983a,b). It has been found that most of the rat taste cells respond to more than one of the four basic taste stimuli and that responsiveness of the taste cells to a stimulus is independent of those to the other three stimuli.

Smith and Travers (1979) have proposed a method to analyse quantitatively response breadth of neurons to gustatory stimuli. They used the entropy (H) in the information theory to compare the breadth of responsiveness of gustatory neurons at various levels of taste pathways. The purpose of this study is to re-analyse tuning patterns of the rat taste cells for four basic taste stimuli according to Smith and Travers' theory (1979).

Materials and methods

Eleven female Sprague–Dawley rats weighing 250–410 g were used in the experiments. The experimental methods employed have been mentioned in previous papers (Sato and Beidler, 1982, 1983a,b). Briefly, the following approaches were taken. After the animals were anesthetized with an i.p. injection of urethane (1 g/kg body wt), intracellular recordings from taste cells within taste buds of the fungiform papillae were made using glass capillary microelectrodes having a resistance of 30–70 MΩ. An indifferent Ag–AgCl electrode was inserted into the forelimb muscles. All the experiments were carried out at a room temperature of 25–27°C.

Taste stimuli used were 0.5 M NaCl, 0.02 M quinine-HCl (Q-HCl), 0.01 M HCl and 0.5 M sucrose. All solutions were prepared with distilled water. The tongue surface was adapted to and rinsed with distilled water. Stimulus solutions and distilled water were dripped on the tongue surface at a rate of 1.4 ml/min.

The breadth of responsiveness measure H (entropy) was calculated for each taste cell according to the formula

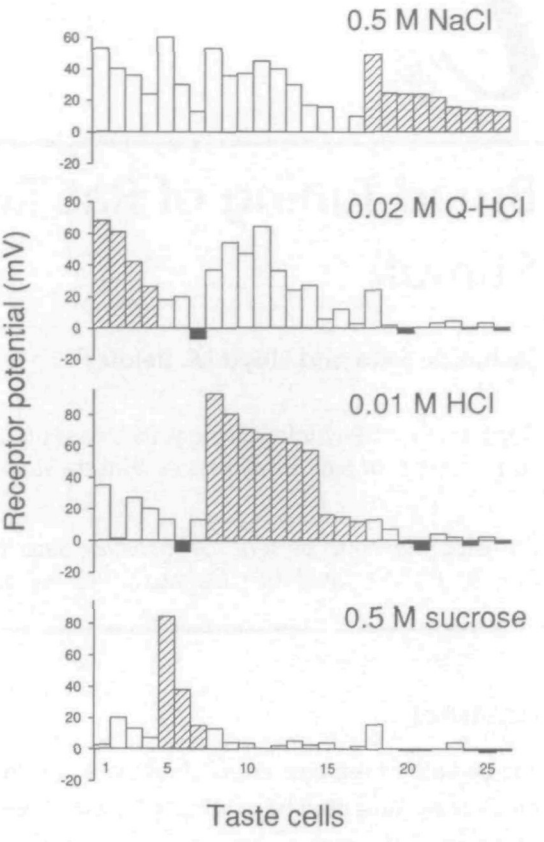

Figure 1 Receptor potential profiles of 26 rat taste cells in response to the four basic taste stimuli. Taste cells were grouped in four best-stimulus categories [NaCl-best, quinine-HCl (Q-HCl)-best, HCl-best and sucrose-best]. Best responsive taste cells for a certain stimulus were shown by shadowed blocks. Black blocks indicate hyperpolarizing receptor potentials. Taste cells were adapted to and rinsed with distilled water.

$$H = -K\sum_{i=1}^{4} p_i \log p_i$$

where K is a scaling factor = 1.661 and p_i is the proportion of the response to stimulus i against the total response to all four taste stimuli (Smith and Travers, 1979). The value of H ranges from 0.0 to 1.0.

Results

By inserting a microelectrode into a taste cell through the taste pore, we could identify 26 taste cells responding to basic taste stimuli with a depolarization or a hyperpolarization. The mean amplitude of resting potentials of 26 taste cells adapted to distilled water was –51 ± 3 mV (mean ± SEM) with a range of –22 to –80 mV. The response profiles of 26 taste cells to 0.5 M NaCl, 0.02 M Q-HCl, 0.01 M HCl and 0.5 M sucrose are shown in Figure 1. If the amplitudes of receptor potentials are ignored, most of the

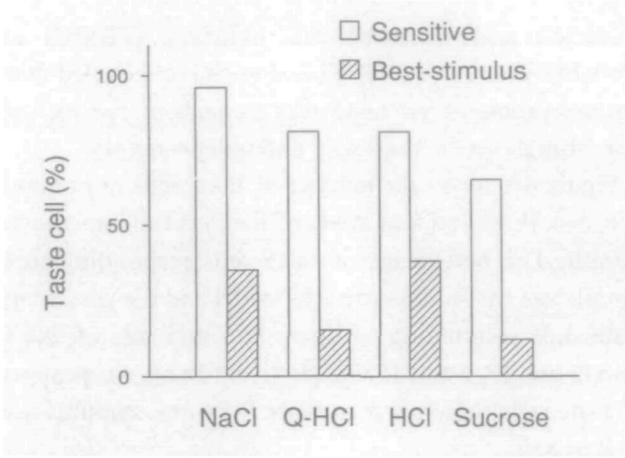

Figure 2 Percentage of taste cells sensitive and best responsive to each of the four basic taste stimuli. The percentage was calculated from number of depolarized taste cells to 26 taste cells tested.

taste cells responded to more than one of the four taste qualities with depolarizations. A certain taste cell did not change the membrane potential to some of the four basic taste stimuli, or responded with a hyperpolarizing receptor potential. The mean amplitudes of responses of all 26 taste cells to 0.5 M NaCl, 0.02 M Q-HCl, 0.01 M HCl and 0.5 M sucrose were 26 ± 3, 22 ± 5, 25 ± 6 and 9 ± 4 mV respectively. Although responding to more than one of the basic taste stimuli, taste cells which possessed a maximal depolarizing response to a certain stimulus were regarded as the stimulus-best cells. In Figure 1, the nine NaCl-best cells were nos 18–26, the four Q-HCl-best cells nos 1–4, the 10 HCl-best cells nos 8–17 and the three sucrose-best cells nos 5–7.

Figure 2 illustrates the percentage of taste cells which were sensitive (empty blocks) and best responsive (shadowed blocks) to each of the four basic stimuli. The taste cells which showed no change in the resting potential or a hyperpolarizing response to a certain stimulus were regarded as insensitive cells for the stimulus because these taste cells might not contribute to impulse generation in gustatory nerve fibers. The percentage of sensitive taste cells was decreased in the order of NaCl > Q-HCl ≈ HCl > sucrose. The percentage of best responsive cells was 12–15% for Q-HCl and sucrose but 35–38% for NaCl and HCl. Figure 3 illustrates the mean amplitudes of receptor potentials to each of the four taste stimuli in four classes of best responsive taste cells. NaCl-best cells (A) showed smaller responses of <15% of the NaCl response for the other three stimuli. However, each of Q-HCl-best (B), HCl-best (C) and sucrose-best cells (D) showed larger responses of >40% for one or two of the other three stimuli. In Q-HCl-best cells a

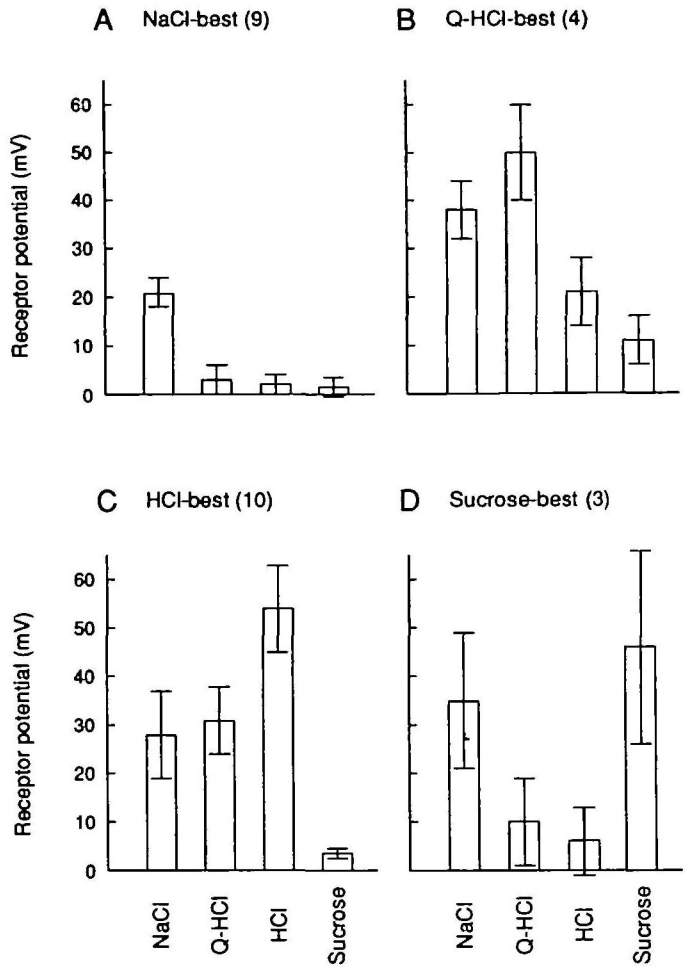

Figure 3 Mean amplitudes of depolarizing responses to each of the four basic taste stimuli in four classes of stimulus-best taste cells. Numerals within parentheses are number of stimulus-best taste cells tested. Vertical bars are SEM.

NaCl response showed 78% of the response for Q-HCl. Also, in HCl-best cells the mean amplitudes of responses to NaCl and Q-HCl were as large as 51 and 57% of HCl response respectively. Sucrose-best cells responded well to NaCl. These indicate that best responsive taste cells have mostly broad tuning. The mean amplitude of resting potentials in the nine NaCl-best cells was –38 ± 2 mV. The resting potentials in the four Q-HCl-best cells, 10 HCl-best cells and three sucrose-best cells were –59 ± 4 mV, –53 ± 6 mV and –68 ± 11 mV respectively. The resting potentials of the NaCl-best cells were significantly smaller than those of the other three stimuli-best cell ($P < 0.05$).

If the sensitivity of a taste cell to any one of the four basic taste stimuli is independent of the sensitivities to the other three kinds of stimuli, the probability of evoking taste cell responses to any pair of the four taste stimuli would be given

by the product of the probability of obtaining the response to each stimulus. The response probability for each stimulus can be estimated by the proportion of responding taste cells to the total number of taste cells tested. Table 1 shows the probability of occurrence of depolarizing responses in taste cells to all six pairs of the four basic taste stimuli and the predicted and obtained numbers of taste cells depolarized by the pairs. No statistical differences were seen between the predicted and observed cell numbers (Fisher's exact probability test, $P > 0.05$). Therefore, it is concluded that the responsiveness of rat taste cells to each of the four basic taste stimuli occurs randomly and independently.

Table 1 Numbers responding with depolarizations to all six pairs of the four basic taste stimuli in 26 taste cells

Pair of taste stimuli	Probability	Number of taste cells		*P*
		Predicted	Observed	
NaCl + sucrose	0.962 × 0.654	16.4	17	0.05
NaCl + HCl	0.962 × 0.962	24.1	20	0.05
NaCl + Q-HCl	0.962 × 0.808	20.2	20	0.05
Sucrose + HCl	0.654 × 0.962	16.4	16	0.05
Sucrose + Q-HCl	0.654 × 0.808	13.7	16	0.05
HCl + Q-HCl	0.962 × 0.808	20.2	20	0.05

The rat tongue was adapted to distilled water. The taste stimuli used were 0.5 M NaCl, 0.02 M quinine-HCl (Q-HCl), 0.01 M HCl and 0.5 M sucrose. The probabilities of obtaining a depolarization to each stimulus were 0.962 (NaCl), 0.808 (Q-HCl), 0.962 (HCl) and 0.654 (sucrose). *P* was calculated with Fisher's exact probability test.

Figure 4A shows the number of taste cells responding to one, two, three and four kinds of the four fundamental taste stimuli. The percentage of taste cells responding to four stimuli was 58% of 26 taste cells tested and the percentage of taste cells responding to three, two and one of the four stimuli was 23, 4 and 15% respectively. In all, the proportion of taste cells responding to more than one stimulus was as high as 85%.

The distribution of entropy H showing a range of response tuning in taste cells is shown in Figure 4B. Eight taste cells (31%) had a response breadth <0.6 in H value and 18 taste cells (69%) showed a large H value of >0.7. In general, many taste cells had a broad breadth of responses. Taste cells having the small amplitude of resting potentials below –45 mV generally showed a small H value of 0.174 ± 0.081 (n = 8) with a range of 0.000–0.543, but taste cells having the large amplitude of resting potentials above –45 mV showed a large H value of 0.815 ± 0.012 (n = 18) with a range of 0.752–0.944. Figure 5 shows the mean H for four kinds of best responsive taste cells. Nine NaCl-best cells had a mean H of 0.285 ± 0.120. Seven of nine NaCl-best cells had a small resting potential below –45 mV and a mean H of 0.128. The other two NaCl-best cells showed a larger resting

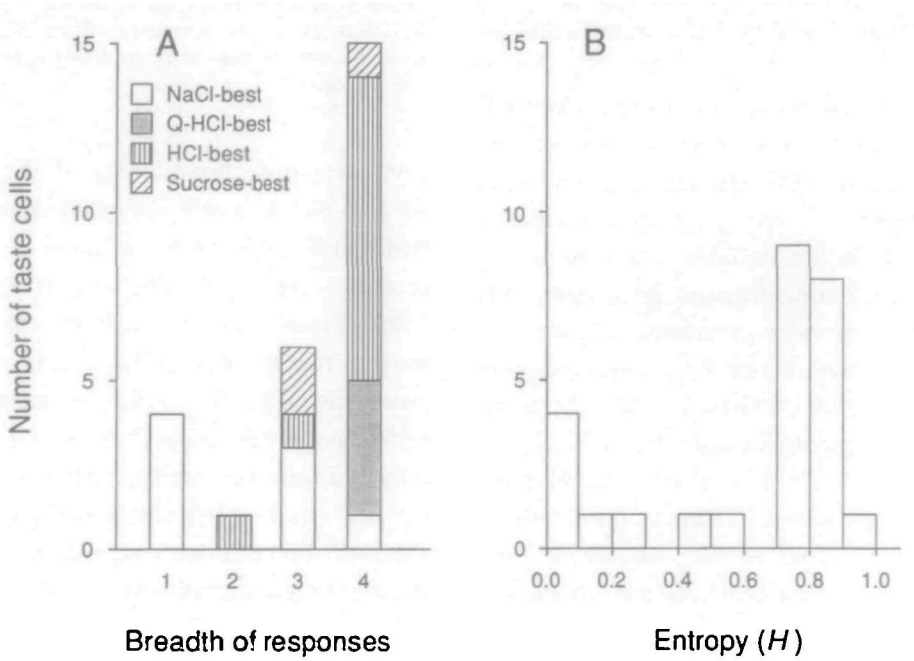

Figure 4 **(A)** Number of taste cells responding to one, two, three and four of the four basic taste stimuli. **(B)** Number of taste cells having various entropy values, *H*, for four basic taste stimuli. Data were obtained from 26 taste cells.

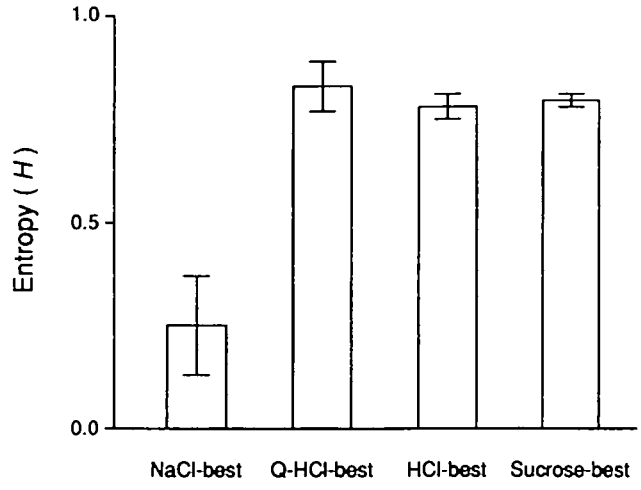

Figure 5 Mean magnitudes of entropy values to the four basic taste stimuli in nine NaCl-best taste cells, four Q-HCl-best taste cells, 10 HCl-best taste cells and three sucrose-best taste cells. Vertical bars are SEM.

potential of –50 mV and –55 mV and a larger *H* of 0.774 and 0.898. The mean *H* values from four Q-HCl-best, 10 HCl-best and three sucrose-best cells were 0.832 ± 0.060, 0.781 ± 0.034 and 0.796 ± 0.017 respectively. One HCl-best cell having a small resting potential of –38 mV showed a small *H* of 0.495. The *H* values of the other 16 cells of Q-HCl-best, HCl-best and sucrose-best types ranged from 0.752 to 0.944. The mean *H* values of total 26 taste cells were 0.621 ± 0.065. On average, NaCl-best cells showed a narrow tuning breadth, but the other stimuli-best cells showed a broad tuning breadth.

Discussion

A mathematical expression of entropy from information theory can provide a measure of the breadth of tuning of gustatory neurons in response to the four basic taste stimuli (Smith and Travers, 1979). The entropy measure (*H*) means the breadth of gustatory responsiveness. As described in the Materials and methods section, the *H* values range from 0.0, representing a specificity to one of the four basic stimuli, to 1.0, representing an equal response to all the four stimuli. Only depolarizing receptor potentials were used for calculation of *H*. Since negative values like hyperpolarizing receptor potentials become invalid for a calculation, these potentials were treated as zero values because the hyperpolarizations do not contribute to generation of gustatory neural impulses. The mean *H* values calculated from chorda tympani fiber impulses in the rat, the hamster and the mouse for four basic taste stimuli are in the order of HCl-best fibers (0.708) > sucrose-best fibers (0.403) ≈ NaCl-best fibers (0.409) > Q-HCl-best fibers (0.377) (Travers *et al.*, 1987). These values in monkey taste fibers are much smaller (M. Sato *et al.*, 1994). In the present experiments, *H* values from the receptor potentials of rat taste cells are in the order of Q-HCl-best cells (0.832) > sucrose-best cells (0.796) ≈ HCl-best cells (0.781) > NaCl-best cells (0.285). Comparison of *H* values of primary gustatory afferent responses and that of the taste cell responses indicates that *H* values of Q-HCl-best and sucrose-best taste cells are much larger than those of these stimuli-best gustatory fibers. The *H* value is large in both HCl-best gustatory fibers and HCl-best taste cells. The *H* value in NaCl-best taste cells in the rat is smaller than that in NaCl-best gustatory fibers in the rodent.

The amplitude of receptor potentials for NaCl in NaCl-best taste cells in the rat was much smaller than those for NaCl in the other three stimuli-best taste cells. In the present study, the amplitudes of resting and receptor potentials in 80% of all NaCl-best taste cells were much smaller than those of the other three stimuli-best taste cells. It is well accepted that receptor potentials in taste cells in response to NaCl stimuli are generated by activation of ion channels situated at the taste receptive membrane and that the amplitude of the receptor potentials becomes larger with increasing magnitude of the membrane potential (T. Sato *et al.*, 1994, 1995; Lindemann, 1996). Therefore, the small amplitude of receptor potential and the small *H* value in NaCl-best taste cells may be due to the small amplitude of resting potential under which various kinds of ion channels involved with the receptor potential are inactivated (Fox *et al.*, 1987; Hille, 1992). If a larger population of rat taste cells was examined, characteristic NaCl-best cells having the large response amplitude and the large *H* value, like cell no. 18 in Figure 1, might be obtained.

A possible mechanism by which a large value of *H* in rat taste cells is transformed into a smaller value of *H* in the gustatory fibers must be considered. A single gustatory fiber in rats branches below the fungiform papillae and innervates several fungiform papillae, each of which has one taste bud at the top (Beidler, 1969; Pfaffmann, 1970; Miller, 1971; Miller *et al.*, 1978). It is suggested that each taste bud in the fungiform papillae has a few functional taste cells which synapse with gustatory fibers (Royer and Kinnamon, 1994). Probably, one gustatory fiber in the

rat synapses with several to a few tens of taste cells. If four classes of best responsive taste cells (Figure 3) are randomly synaptically connected with one gustatory nerve fiber, most of the gustatory fibers might respond well to the four basic stimuli. This results in a larger value of H in gustatory nerve fibers than in taste cells. However, this is not the case. Therefore, the different pattern of synaptic connection may exist between taste cells and gustatory fibers. This view has already been suggested by some researchers (T. Sato, 1972; M. Sato, 1973). The statistical examination of responsiveness of taste cells suggests that independent and random occurrence of taste cell responses to each of the four basic taste stimuli exists in the frog (Sato, 1972, 1980) and the rat (Ozeki and Sato, 1972; Sato and Beidler, 1983a; Sato, 1986). The same finding was obtained in the present study. On the other hand, the independent responsiveness between taste stimuli is not always seen in gustatory fibers of rats and hamsters (Ogawa *et al.*,1968; Sato *et al.*, 1969) and of monkeys (Sato *et al.*, 1975). Dependent occurrence between HCl and Q-HCl responses was found in rat gustatory fibers (Ogawa *et al.*, 1968). Therefore, it is likely that non-random functional connection may occur between taste cells and fibers. Taste cells having similar sensitivity may be innervated by single gustatory fibers. An electron microscopic study shows that morphologically similar taste cells are innervated by one gustatory fiber in the rabbit and the mouse (Royer and Kinnamon, 1994). Even though one fiber innervates several taste cells having a similar response, a large value of H in taste cells may not be transformed into a smaller H value in taste fibers.

It is suggested that >100 frog gustatory cells are innervated by a single gustatory fiber (Sato *et al.*, 1983). When only one taste cell in the frog taste disk was electrically stimulated by an intracellular microelectrode inserted into the cell, no impulses appeared in gustatory fibers (T. Sato and Y. Okada, unpublished data). However, when several taste cells in the frog taste disk were electrically stimulated by an extracellular microelectrode, a few im- pulses appeared in a gustatory fiber (T. Sato and Y. Okada, unpublished data). This experiment suggests that summation of large depolarizing receptor potentials elicited in several taste cells to produce large generator potentials at postsynaptic nerve terminals is necessary for generation of impulses in a frog gustatory fiber. If this is the case in rat taste system, the following possibility is considered. The summation of smaller depolarizations in several taste cells evoked by non-best-taste stimuli may not reach the threshold to generate impulses in a gustatory fiber innervating several cells. This is one possible explanation that larger H values in taste cells are transformed into small H values in gustatory fibers in rats.

ACKNOWLEDGEMENTS

This study was supported in part by an NSF Grant GU-2612 in USA and by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sports and Culture in Japan.

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Received on November 8, 1996; accepted on December 17, 1996