

Conductance Change Associated with Receptor Potentials of Gustatory Cells in Rat

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ABSTRACT The electrical properties of gustatory cells and cells which do not respond to chemical stimuli in the taste bud of fungiform papillae in rats were studied by means of intracellular microelectrodes. Neither of these cell types showed spike electrogenesis. Gustatory cells showed a depolarization, the receptor potential, associated with an increase in the membrane conductance in response to NaCl, sucrose, and HCl, whereas quinine produced a decrease in the conductance together with an increase in the receptor potential magnitude. The reversal point of the receptor potential in response to NaCl or KCl was close to zero membrane potential, but in the case of quinine it was at a more negative potential level than the resting potential. From these results two receptive processes are postulated in the gustatory cell membrane. When the gustatory cells were stimulated for a long duration by concentrated NaCl or sucrose, receptor potentials showed adaptation with decrease in magnitude, but adaptation of the responses to HCl and quinine were hardly detected. Adaptation of the receptor potential was not correlated with conductance change.

INTRODUCTION

Concerning the initial receptive mechanism of taste stimuli it has been proposed that stimulating substances are adsorbed onto the microvillus membrane in gustatory cells (Beidler, 1954) and that, following adsorption, the gustatory cell elicits the receptor potential. Subsequently, depolarization of gustatory cells in response to various chemicals has been demonstrated by Kimura and Beidler (1961) in rats and hamsters and by Sato (1969) in frogs. Recently, Ozeki and Sato (1971) reported the results of experiments on the responses of gustatory cells in the fungiform papillae of rats to taste stimuli representing the four taste qualities, and their experiments confirmed the earlier results by showing that single gustatory cells possess multiple sensitivity to the stimuli.

In the present study, described below, the electrical properties of the cells, located in the taste bud of the fungiform papillae, were studied by passing currents intracellularly. From examination of both conductance changes associated with receptor potentials induced by the four basic gustatory stimuli and the relationships between the receptor potential amplitude and the steady membrane potential level, two kinds of receptive processes are postulated after the gustatory stimulants have been adsorbed onto the microvillus membrane of the cell. One occurs in response to NaCl, sucrose, and HCl and the other is that produced by quinine. Conductance changes during adaptation of the responses to the four gustatory stimuli are also described. Some of the results have already been communicated (Ozeki, 1970).

METHODS

Adult female rats of the Sprague-Dawley strain were used. Each rat, anesthetized with an intravenous injection of sodium amobarbitone (50 mg/kg body weight) into the tail, was fixed on a stereotaxic table with a head holder and the trachea was cannulated. In order to stop small muscular movements of the tongue, the hypoglossal nerves on both sides were cut under the jaw. The tongue was pulled out and pinned at the tip onto a plastic plate. The tongue was usually soaked in saline, containing 0.0414 M NaCl, which is the average sodium concentration in rat saliva (Hiji, 1969).

Procedures of inserting microelectrodes into the gustatory cells of the rat and recording methods have been fully described elsewhere (Ozeki and Sato, 1971). When currents were passed through the intracellular microelectrode a Wheatstone bridge circuit was used. The input resistance of cells at rest was estimated from the steady level of electrotonic potentials less than 10 mv in magnitude induced by hyperpolarizing pulses of 100 msec duration, applied intracellularly. Within this hyperpolarization a straight line relationship between applied currents and electrotonic potentials was obtained. Most microelectrodes were filled with 3 M KCl; the resistance of the electrodes was 30–50 M Ω . Microelectrodes filled with 2 M KCl and 1 M K citrate were used on some occasions, with no difference in results. 0.3 M NaCl, 0.5 M sucrose, 0.01 N HCl, and 0.02 M quinine hydrochloride were used as the four basic gustatory stimuli. In a few cases 0.5 M NaCl was used as one of the stimuli. Taste solutions were applied slowly to the tongue at a rate of about 1 ml/50 sec with an injection syringe (Ozeki and Sato, 1971). In the cases where adaptation was examined, solutions were applied more slowly to the tongue at a rate of about 1 ml/70 sec. After stimulation of the tongue it was rinsed with the saline.

The experiments were performed at temperatures ranging from 23° to 25°C.

RESULTS

Electrical Properties of Cells in Fungiform Papillae

Electrical properties of about 150 cells in the taste bud of fungiform papillae distributed on the surface of the anterior two-thirds of the tongue were studied

and two kinds of cells were observed in the papillae; one is the responsive cell responding to four basic gustatory stimuli and the other is the nonresponsive cell, as reported by Ozeki and Sato (1971). The former cells are considered gustatory cells and depolarizations produced in the cell are receptor potentials. The resting potential of both types of cells varied from 18.7 to 85.0 mv and the values were distributed unimodally within this range. The resting potential of gustatory cells was 40.1 ± 14.4 mv (mean \pm SD of 120 cells) and

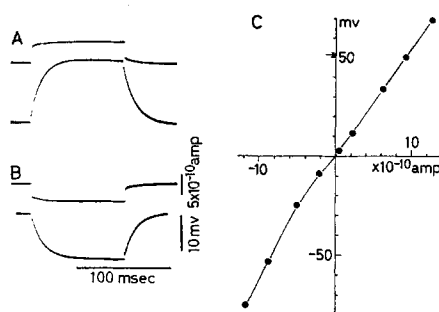


FIGURE 1

FIGURE 1. Electrotonic potentials and current-voltage relationship in a gustatory cell. Electrotonic potentials induced in a gustatory cell by a depolarizing pulse (A) and a hyperpolarizing pulse (B). Upper traces represent currents, and lower traces show electrotonic potentials. (C) Current-voltage relationships. The arrow indicates zero membrane potential. This cell responded to NaCl, sucrose, and HCl but not to quinine hydrochloride.

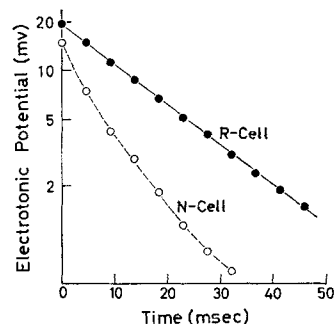


FIGURE 2

FIGURE 2. Time-course of decay of electrotonic potentials in a gustatory cell (solid circles and *R-Cell*) and a nonresponsive cell (open circles and *N-Cell*). Ordinate: magnitude of electrotonic potential plotted on a logarithmic scale. Abscissa: time. The gustatory cell responded to NaCl, HCl, and sucrose but not to quinine hydrochloride. The resting potential and the input resistance were -57 mv and 80.5 M Ω in the gustatory cell and -34.5 mv and 17.1 M Ω in the nonresponsive cell.

that of nonresponsive cells was 43.2 ± 11.5 mv (18 cells). The input resistance of cells varied widely from 10 to 300 M Ω and the values for gustatory cells and nonresponsive cells were 81.2 ± 54.9 M Ω (132 cells) and 58.5 ± 39.9 M Ω (21 cells), respectively. However, the differences found between the two types of cells were not statistically significant. The cells showing large resting potentials tended to have a large input resistance but the correlation between them was poor.

The slope of the relationship between the applied current and the membrane potential change was constant for currents causing depolarization. Neither gustatory cells nor nonresponsive cells examined showed graded or all-or-none spike electrogenesis in response to depolarization. For currents producing hyperpolarization, the slope of the current-voltage relationship was

not the same in all cells and became nonlinear for hyperpolarizations of more than 30 mv from the resting level. This is illustrated in Fig. 1.

The electrotonic potential had rising and falling times of several tens of milliseconds (Fig. 1). The decay of the electrotonic potentials in 32 gustatory cells out of 42 was a simple exponential function (Fig. 2, *R-Cell*). In the other 10 cells, however, the decay was more complex. The time constant of the falling phase of the electrotonic potential in the former cells, calculated from changes in the membrane potential in the hyperpolarizing direction of less than 20 mv, was 15.5 ± 6.7 msec (32 cells). No significant difference in the responses to the four basic gustatory stimuli between these two kinds

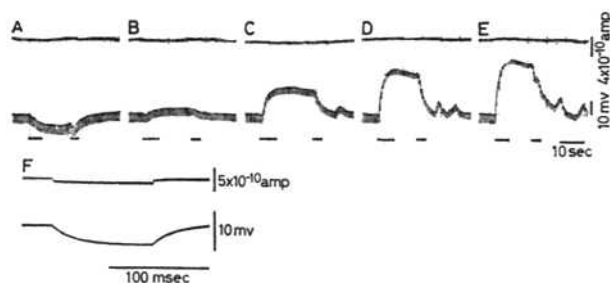


FIGURE 3. Upper figures (A)–(E): receptor potentials produced by 0.03 (A), 0.1 (B), 0.3 (C), 1.0 (D), and 2.0 M (E) NaCl. Electrotonic potentials induced by repetitive application of square pulses were superimposed on receptor potentials. In (A)–(E) top traces represent monitored currents, while lower traces show electrotonic potentials recorded from a gustatory cell. Lower figure (F): electrotonic potential which can be seen as a small pulse in (A)–(E). The electrotonic potential recorded from the resting cell and the monitored current applied to the cell are demonstrated with an elongated time scale. The cell responded to four kinds of gustatory stimuli. The first signal marker in (A)–(E) and also in Figs. 4, 6, and 8 indicates the time of flow-in of the stimulating substance and the second one shows flow-in of the saline.

of cells could be observed. In nonresponsive cells the decay in 7 out of 11 cells examined could not be approximated to a simple exponential function (Fig. 2, *N-Cell*). In the remaining four cells it was a simple exponential function and the time constant of the cells was 11.2 ± 2.1 msec. The difference between the mean time constant of gustatory cells and that of nonresponsive cells was not significant ($0.2 < P < 0.3$). The proportion of gustatory cells showing a simple exponential time-course of the membrane transient was higher in gustatory cells than in nonresponsive cells.

Conductance Change During Gustatory Stimulation

Membrane conductance during gustatory stimulation was studied by passing short hyperpolarizing constant current pulses through the recording electrode and measuring the voltage drop across the membrane (Fig. 3 F, recorded

at rest). As indicated by the changes in amplitude and time-course of small electrotonic potentials (Fig. 3 A-E), membrane conductance increased during the depolarizing response to NaCl. This suggests that depolarizations of the gustatory cell elicited by NaCl solutions of various concentrations are produced as a result of a decrease in the membrane resistance of cells. As shown in Fig. 4 A, B, a similar conductance change in gustatory cells elicited by sucrose and HCl was observed. However, when the cell was stimulated by quinine, changes in the membrane resistance showed an entirely opposite

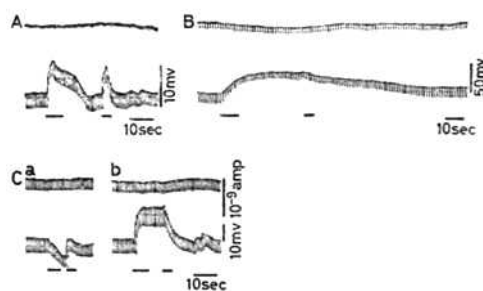


FIGURE 4

FIGURE 4. Changes in the magnitude of electrotonic potentials associated with responses to 0.5 M sucrose (A), 0.01 N HCl (B), and 0.002 and 0.02 M quinine hydrochloride (Ca and Cb, respectively). Records (A), (B), and (C) were obtained from three different cells. The cell A responded to NaCl, sucrose, and HCl but not to quinine hydrochloride. The cells B and C responded to NaCl, HCl, and quinine hydrochloride but not to sucrose. FIGURE 5. Relationships between the relative conductance change and the magnitude of receptor potentials produced by NaCl (open and solid circles), sucrose (open squares), HCl (solid squares), and quinine hydrochloride (open and solid triangles). The ordinate represents the relative conductance calculated as a ratio of the input resistance of the cell at rest (R_{rest}) over that at the steady state of receptor potentials (R_{rp}), while the abscissa indicates the magnitude of receptor potentials. Solid circles correspond to the cell in Fig. 3. Open and solid squares and open triangles correspond to cells in Fig. 4.

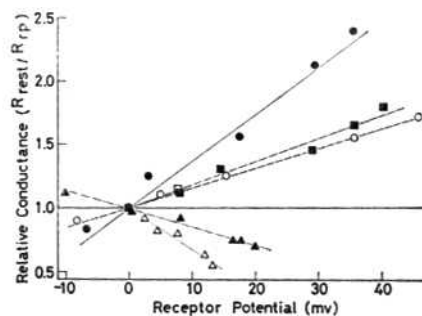


FIGURE 5

tendency from that found with NaCl, sucrose, and HCl, as shown in Fig. 4 C (see Ozeki, 1970). A similar conductance decrease in the cell during the depolarizing response to quinine with the saline was also observed.

The relationships between the conductance change and the receptor potential of cells induced by four kinds of gustatory stimuli are presented in Fig. 5. The ordinate indicates the relative conductance change, calculated from the resistance at rest over the resistance in the excited state, while the abscissa represents the potential change from the resting level. Relative conductance changes have a linear relationship with amplitudes of receptor potentials. Those produced by sucrose, NaCl, and HCl have a positive slope, whereas the relationship for quinine has a negative slope. The slope of the

line varied from one cell to another mainly due to variations in the input resistance of each gustatory cell. In gustatory cells with a large input resistance, the slope of the line was proportionally steeper.

The results indicate that the mechanisms underlying the conductance change in the gustatory cell can be classified into two kinds; one is the mechanism which produces the receptor potential in response to NaCl, sucrose, and HCl, and the other is a process of a different kind which is activated by quinine and which shows an opposite conductance change from that produced in response to NaCl, sucrose, and HCl.

Adaptation of Gustatory Response

When the gustatory cell was stimulated for a long duration by concentrated NaCl solutions, the receptor potentials showed gradual adaptation with decreased amplitude of depolarization. An example of adaptation of responses is shown in Fig. 6. In this figure, although the amplitude of the receptor potential induced by 0.5 M NaCl stimulation decreased to only 85% of its peak amplitude after 50 sec continuous stimulation, the amplitude of the potential elicited by 2 M NaCl decreased to 16% of its peak amplitude after the same period. The amplitude of the receptor potential in response to 2 M NaCl 50 sec after stimulation became smaller than that obtained by 0.5 M NaCl. With high concentrations of NaCl the observed adaptation was proportionally great, as shown in Fig. 7 A, where the cell was stimulated by NaCl in the order of 0.5, 1, and 2 M. In this figure the maximum amplitude of the response to 1 M NaCl is smaller than that obtained by 0.5 M NaCl, probably because the cell was stimulated by 1 M NaCl before it recovered sufficiently from the after-effect of the preceding stimulation. There was a considerable variation in rate of adaptation among different gustatory cells. Adaptation of the receptor potential in response to sucrose was larger than that in the NaCl response (Fig. 4). However, the potentials in response to HCl and quinine showed little adaptation.

As shown in Fig. 7 A and B, during the adaptation process a decrease in the membrane conductance was also observed, but the amplitude of the depolarization decreased more prominently than did the conductance. A further difference between the adaptation of the potential and conductance change was that even though the adaptation, as indicated by the amplitude decrease of the receptor potential, was influenced by the concentration of NaCl, the rate of relative conductance change in single gustatory cells was independent of the concentration (Fig. 7 B). In a few cells the membrane conductance increased during the adaptation. This indicates that the adaptation process cannot be explained by resistance changes across the membrane only.

Recovery of the conductance decreased during the stimulation took a long time after cessation of stimulation, although the potential had recovered to the original level. In one gustatory cell it took 120 sec after cessation of stimulation by 0.5 M NaCl, 160 sec after 1 M NaCl, and 180 sec after 2 M NaCl.

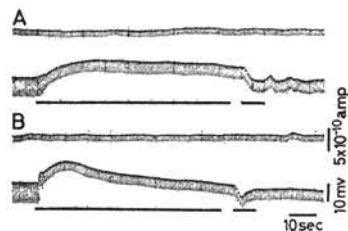


FIGURE 6

FIGURE 6. Changes in the magnitude of electrotonic potentials during the receptor potentials induced by NaCl stimulation. The membrane responses to constant square pulses are shown before, during, and after stimulation. Stimulus concentrations: 0.5 M in (A) and 2 M in (B). The cell responded to NaCl, quinine hydrochloride, and HCl but not to sucrose.

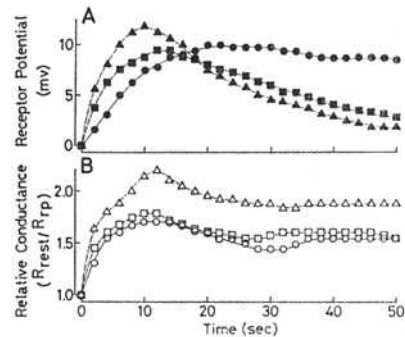


FIGURE 7

FIGURE 7. Time-course of adaptation of the receptor potential and of the relative conductance change during responses to 0.5 M (open and solid circles), 1 M (open and solid squares), and 2 M (open and solid triangles) NaCl. Stimulations of the cell were made in the order of 0.5, 1, and 2 M NaCl and intervals between successive stimulations were 2 and 5 min. (A) Plot of amplitude of receptor potential vs. time after application of each stimulus. (B) Relative conductance change of receptor potentials in (A) vs. time after application of each stimulus. Ordinate represents the relative conductance calculated as a ratio of the input resistance of the cell at rest (R_{rest}) over that at the state of receptor potential (R_{rp}). Circles and triangles were taken from records shown in Fig. 6.

Interaction of Gustatory Stimuli and Membrane Potential Change

In the experiment illustrated in Fig. 8, different intensities of steady currents were passed through the impaling microelectrode, and 0.3 M NaCl was applied to the cell as stimuli. The figure shows that depolarizing currents decrease the magnitude of the receptor potential, whereas the reverse happens with hyperpolarizing currents.

As shown in Fig. 9 A, the relationship between the magnitude of receptor potentials following gustatory stimulation and the steady potential induced by the applied currents is approximately linear. In Fig. 9 B, the lines obtained with different NaCl concentrations converged approximately at zero

membrane potential. This suggests that for these responses the potential at which the response reverses polarity, during displacement of the membrane potential with applied current, does not vary with change in stimulus intensity. The mean value and standard deviation of the reversal potential obtained with 0.3 M NaCl from six cells was 2.4 ± 12.6 mV, ranging from

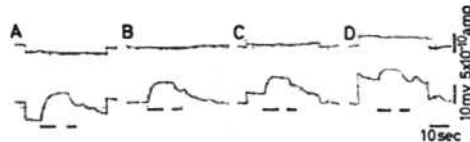


FIGURE 8. Receptor potentials in response to 0.3 M NaCl recorded at various membrane potential levels from a single gustatory cell. In (A) the cell had been hyperpolarized by a constant current of 1.7×10^{-10} amp, while in (C) and (D) it had been depolarized by currents of 0.6 and 2.5×10^{-10} amp before application of NaCl solution. The cell responded to NaCl and HCl.

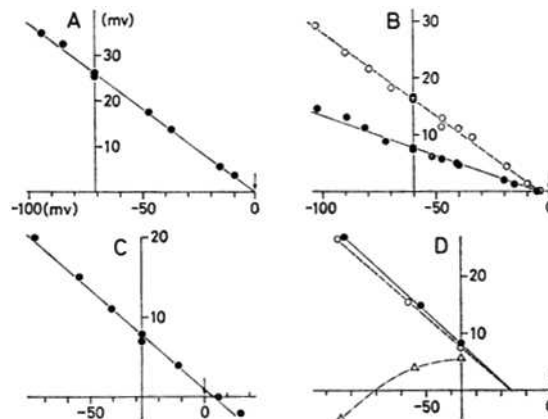


FIGURE 9. Relationships between the amplitude of receptor potentials in response to NaCl, KCl, and quinine hydrochloride and the steady membrane potential. (A) Relationship for the response to 0.3 M NaCl obtained from the experiment shown in Fig. 8. (B) Relationships for responses to 0.3 M (solid circles) and 0.6 M (open circles) NaCl. (C) Relationship for the response to 0.5 M KCl. (D) Relationships for responses to 0.3 M NaCl (solid circles), 0.3 M KCl (open circles), and 0.02 M quinine hydrochloride (open triangles). Ordinate: peak amplitude of the receptor potential induced by a constant amount of gustatory stimuli; abscissa: membrane potential. The resting potentials are indicated by vertical lines.

-16 to +22 mV. Relationships similar to those for NaCl were obtained between the amplitude of receptor potentials in response to 0.5 and 0.3 M KCl and the steady potential level changed by applied currents, as shown in Fig. 9 C and D. The reversal potential for KCl was also close to zero membrane potential and the values obtained with 0.5 and 0.3 M KCl in two

different cells were +3.5 mv (C) and -17 mv (D). Relationships similar to these were also observed in the response to HCl and sucrose. When the gustatory cell was depolarized at a steady potential level by the treatment of the cell with cocaine or FeCl_3 , reversal of the polarity of the response to NaCl has been observed by Tateda and Beidler (1964). From these results they proposed that the response to NaCl was related to a certain equilibrium potential of the cell membrane.

However, the relationship between the amplitude of the receptor potential in response to quinine and the steady potential level was entirely different from that for NaCl. The receptor potential did not converge to zero membrane potential, but the polarity of the receptor potential was reversed at a more negative potential level than the resting potential, as shown in Fig. 9D. As shown by Ozeki (1970), the amplitude of the receptor potential in response to quinine increased by only a few millivolts, regardless of the change in the membrane potential to a more depolarized level than the resting potential. In three cells, which were responsive to both NaCl and quinine and had resting potentials of 36, 24.5, and 26.4 mv, reversal potentials for NaCl and quinine were -16 and -72 mv, +22 and -112 mv, and 0 and -50 mv, respectively. The reversal potential in gustatory cells responding to quinine only has not yet been examined, because the proportion of such cells is small in the fungiform papillae of rats (Ozeki and Sato, 1971).

The observation that the reversal potential for the response to quinine is different from those for NaCl, sucrose, and HCl may be correlated with a difference in conductance change of the cell membrane between the responses to quinine and to the other three kinds of stimuli, and supports the conclusion that two kinds of receptive processes exist in a single gustatory cell.

DISCUSSION

In the present study an attempt has been made to examine the electrogenesis of the gustatory cell in response to stimuli representing the four basic taste qualities. By recording membrane potentials intracellularly from cells in the fungiform papillae and also by applying currents to the cell, it has been found that two kinds of cells exist; one is the gustatory cell and the other is the nonresponsive cell.

The surface dimension of the gustatory cell, which is an oblate spheroid according to the histological pictures of Kolmer (1927), is about $3.2 \times 10^{-5} \text{ cm}^2$, ranging from 2.5 to $3.7 \times 10^{-5} \text{ cm}^2$. From this value and the mean input resistance, the approximate value of the specific membrane resistance of gustatory cells, R_m , can be calculated. R_m in gustatory cells was found to be 2.6 kohm cm^2 . By assuming the same value for the surface area of non-responsive cells, their R_m value came to be 1.9 kohm cm^2 . Consequently, the

specific membrane capacity, C_m , of cells can be calculated by dividing the time constant of the falling phase of electrotonic potentials by R_m . The values of C_m thus obtained were $6.0 \mu\text{F}/\text{cm}^2$ in gustatory cells and $5.6 \mu\text{F}/\text{cm}^2$ in nonresponsive cells. The values of R_m and C_m in these cells are similar to those of twitch muscle fibers of the iliofibularis of the frog (Adrian and Peachey, 1965).

The fact that electrotonic potentials of a majority of gustatory cells decayed with a simple exponential function probably means that the cells have few interconnections with neighboring cells. As Tomita (1966) pointed out about the smooth muscle response to intracellular stimulation, the behavior of the electrotonic potential in the cell may be mimicked qualitatively due to the three-dimensional current spread through electrotonic interconnections with neighboring cells. However, in a number of nonresponsive cells examined the falling phase was not a simple exponential function. Therefore, it is possible that such cells have interconnections with neighboring cells. Although morphological analysis to classify cells in the fungiform papillae of rats into type I and type II cells, or gustatory and supporting cells (Farbman, 1965), has been made, it is difficult at the present stage to correlate the difference in the time-course of decay of electrotonic potentials of the two kinds of cells with the morphological difference between gustatory and supporting cells or between type I and type II cells. The fact that a relatively large number of gustatory cells shows an exponential decay of the falling phase of the electrotonic potentials indicates that they may be in a simpler morphological situation than are nonresponsive cells.

The electrical effects of NaCl, sucrose, and HCl stimulation on the gustatory cell membrane are similar to the effect of acetylcholine on the motor end plate of the skeletal muscle (Fatt and Katz, 1951) in that there is an increase in conductance across the membrane. Consequently the receptor potential in the gustatory cell may be produced by an increase in ionic permeabilities of the cell membrane to some ions, possibly sodium, potassium, or chloride. During the adaptation phase of gustatory cells in response to NaCl, the conductance change of the cell membrane is no longer correlated with the amplitude change of the receptor potential. This suggests that the adaptation is not produced simply by a change in conductance of the membrane due to a change in permeability to some specific ions, but is elicited by changes in the permeabilities of two or three ions and by an inactivation of the mechanism producing conductance changes.

On the other hand, in the cells responding to quinine, the receptor potential may be produced mainly by a decrease of resting potassium conductance with an ionic mechanism similar to the generation of slow excitatory postsynaptic potential in frog sympathetic ganglion cells (Weight and Votava, 1970). If such a mechanism occurs, the decrease in potassium per-

meability must be partially independent of the membrane level, since the amplitude of the receptor potential was hardly affected by depolarization of the membrane. However, on steady hyperpolarization the amplitude of the receptor potential was reduced, suggesting that within this membrane potential range the decrease in potassium permeability produced by quinine is smaller than that occurring at the normal membrane potential. Below a critical level of hyperpolarization, the polarity of the receptor potential was reversed, so that an increase in potassium permeability must occur. Falk (1961) pointed out that quinine had the action of a local anesthetic on the action potential in frog muscle fibers and that 0.02% quinine hydrochloride produced a slow fall of the resting potential and decreased the overshoot of the action potential. These facts suggest that quinine reduces potassium permeability of the membrane. Therefore, conductance changes induced by quinine in gustatory cells may be identical with the effect of quinine on the muscle fiber membrane. Whether or not all bitter stimuli induce similar action to that of quinine has not yet been examined. Although the concentrated KCl showed similar taste quality to that of quinine (Sato et al., 1969), KCl produced the same action on gustatory cell membrane as NaCl.

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Note Added in Proof After this paper was submitted, Ozeki and Ōura (unpublished observations) observed the ultrastructure of the gustatory cell of rat by electron microscopy. They obtained the following results: the surface dimension of the gustatory cell, which was a rather prolate spheroid, was calculated to be $6.6 (\pm 0.9) \times 10^{-6} \text{ cm}^2$ (mean \pm SD of four cells). From this value and the mean input resistance, the approximate value of the specific membrane resistance of the gustatory cell, R_m , was 536 ohm cm^2 . Consequently, the specific membrane capacity, C_m , of cells was 28.9 $\mu\text{F}/\text{cm}^2$.

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