The Receptor Potential of the Taste Cell of the Rat

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ABSTRACT The electrical responses of the taste cell of the rat to chemical stimuli were studied by means of microelectrode techniques. Although large positive potential changes in the taste cell were usually elicited by taste stimuli, the response was a small negative potential change with respect to surrounding tissues if the microelectrode was thrust deeply into the taste bud. Both $FeCl_3$ and cocaine produced a positive change in the steady potential. If this new potential is larger than a certain equilibrium potential, reversal of the polarity of the potential change caused by a taste stimulus is observed. Gamma-aminobutyric acid and acetylcholine had no effect on the receptor steady potential nor on the receptor responses elicited by taste stimuli.

INTRODUCTION

Kimura and Beidler (1956, 1961) reported that slow potential changes were elicited in the taste cells of rats and hamsters by several kinds of chemical stimuli, and that one taste cell may respond to as many as four major taste substances: sucrose, alkali salts, HCl, and quinine, although the ratios of the responses to these substances were different in each cell. It was also reported that the relation between the magnitude of response and the concentration of the chemical stimulus was similar to that obtained from the neural response in the chorda tympani nerve. It was assumed from these electrophysiological findings that the slow potentials associated with the taste receptors might be the potentials that are related to the generation of the action potentials in the innervating nerve. However, since there was no histological evidence of the impalement of the cell by the electrode and only limited physiological evidence, further study is needed. For example, if the tip of the electrode remains between the sensory cells in the taste bud, no response would be expected, or if the tip of the electrode remains near the cell membrane, small responses with reversed polarity may be expected (Tomita, 1956). If it is assumed that these slow potential changes are elicited in the taste cell, some of the inhibitors

of taste neural activity may change the magnitude of the steady potentials of the cells. Results of such experiments may also elucidate the taste mechanism in the sensory cell and the transmission of the excitation from the cell to the nerve endings. These are the problems which form the subject of the present study.

MATERIAL AND METHODS

The methods used in the present study were similar to those of the previous study (Kimura and Beidler, 1956, 1961). Albino rats were anesthetized by intraperitoneal

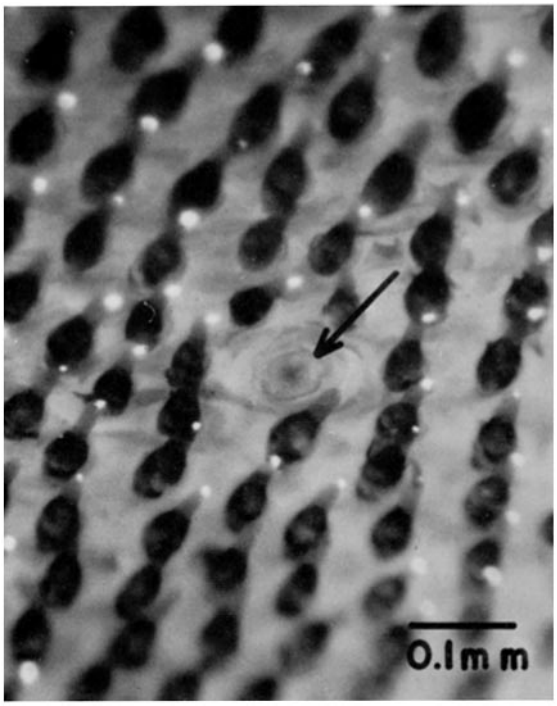

FIGURE 1. Photograph of the rat tongue surface showing white fungiform papilla with taste pore in its center after methylene blue was applied to tongue surface. Arrow shows taste pore. Large black dots are filiform papillae.

injection of nembutal (1 ml/kg). The head of the rat was immobilized with a holder, and the tongue pulled out from the mouth and pinned to the bottom of the flow chamber.

A glass pipette microelectrode, whose tip was about 0.5 micron and which was filled with 3 M KCl solution, was inserted into a fungiform papilla under a dissecting binocular microscope with the aid of a micromanipulator. Methylene blue solution, by which not only the papillae but also the taste pores were clearly locallized (Fig. 1), was often applied to the tongue before insertion of the microelectrode. The micro-

electrode was used as an active recording electrode, while an indifferent metal electrode was thrust into the neck. Recording electrodes were connected to a MacNichol type preamplifier (1954) which was followed by a D. C. amplifier, a cathode ray oscilloscope, and a Sanborn recorder.

Stimulating solutions were flowed gently on the tongue, avoiding movement of the electrode and tongue. The tongue was washed with tap water after each stimulation.

RESULTS

The microelectrode was inserted into the fungiform papilla until a sudden negative potential change (30 to 50 mv) occurred and then the microelectrode

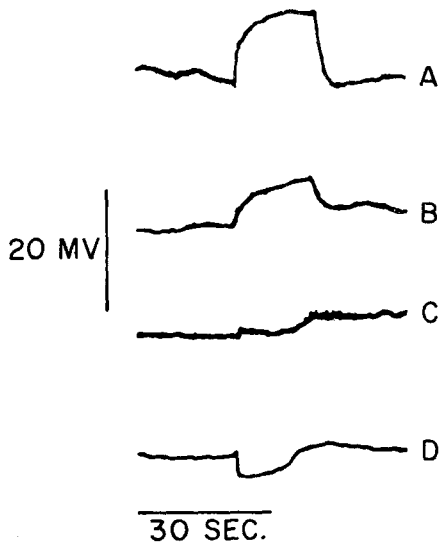

FIGURE 2. Responses of taste cells to 1.0 M NaCl obtained from different depths in the taste bud. Record A obtained from cell near surface of tongue and B, C, D, were obtained after inserting the electrode deeply, step by step. Steady potentials for A, B, C, and D were 50, 45, 95, and 85 mv respectively.

was immobilized. If this negative potential was maintained at the same level for several minutes, sapid solutions were applied to the tongue. Slow positive deflections of the steady potential were elicited by the chemical stimuli (Fig. 2). The microelectrode was then slowly thrust deeper into the papilla, until the steady potential again changed suddenly. While the tip of the electrode was kept in this new position, the chemical stimuli were again applied on the tongue and the slow potential changes recorded (without regard to direction of the change of the steady potential). In Fig. 2 the response to 1.0 M NaCl alone is shown and the steady potentials for the records A, B, C, and D were 50, 45, 95, and 85 mv, respectively.

The sudden changes in potential with electrode penetration suggest that the tip of the electrode moved from one cell to another, each of different sensitivity and steady potential. When the electrode was inserted deeply into the papilla, no responses to chemical stimuli were observed. However, before reaching the layer of no responses, small responses with reversed polarity of

potential changes were sometimes recorded (Fig. 2). These responses suggest that the electrode tip was outside, but yet very near, the sensory cell.

The size of the responses to four basic taste substances, 1.0 M NaCl, 1.0 M sucrose, 0.01 M HCl, and 0.02 M quinine hydrochloride, varied from one cell to another. The results are similar to those reported by Kimura and Beidler (1961).

Distilled water and NaCl concentrations less than 0.01 M sometimes elicited a positive deflection of the potential similar to that observed with high con-

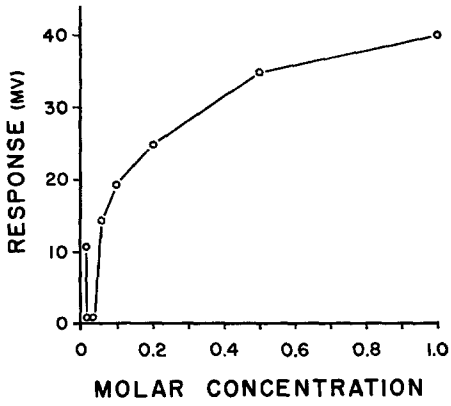

FIGURE 3. Magnitude of change in receptor potential as a function of NaCl concentration.

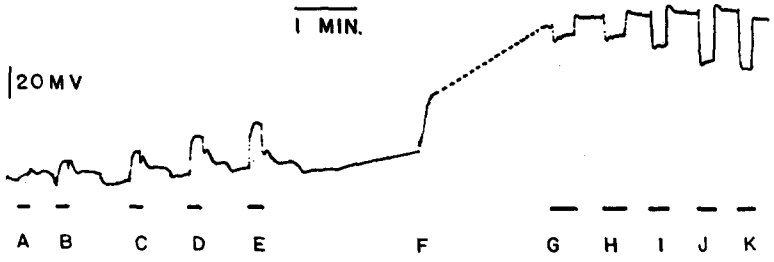

FIGURE 4. Responses to various concentrations of NaCl (A and G, 0.05 M; B and H, 0.1 M; C and I, 0.25 M; D and J, 0.5 M; E and K, 1.0 M) before and after application of cocaine at F. Each bar on the bottom of the record shows the duration of stimulus application.

centration of NaCl, while relatively low concentrations (0.01 to 0.02 M) of NaCl caused almost no response or a negative deflection of the potential change. In Fig. 3, the magnitudes of such responses to NaCl are plotted against concentration. The resulting curve is similar to that derived from the responses of the salt fiber of the frog by Koketsu and Kimura (1953) and from the responses of the salt fiber of the cat obtained by Cohen, Hagiwara, and Zotterman (1955), although no appreciable water response was observed in the neural activity of the chorda tympani nerve of the rat (Beidler, 1953; Pfaffmann, 1955; Zotterman, 1956).

It is known that cocaine will abolish human taste sensation (Moncrieff, 1946). One per cent cocaine applied to the surface of the tongue inhibited the neural response of the chorda tympani nerve of the rat to taste stimuli within 1 minute. One per cent cocaine also elicited a positive deflection of the steady potential of the taste cell, the magnitude of which varied from cell to cell (20 to 60 mv). After washing the tongue with water, the new potential that had been elicited by cocaine remained for a few minutes and then recovered gradually to the original level.

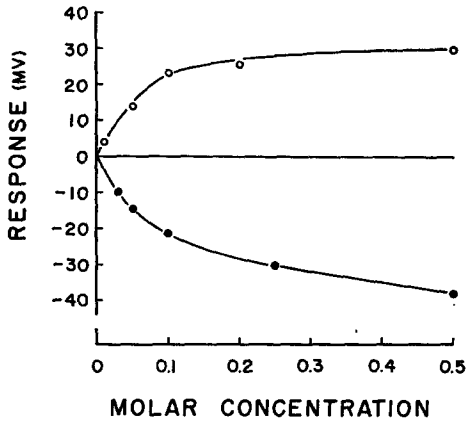

FIGURE 5. The magnitudes of receptor responses as a function of NaCl concentration. Open circles show the responses before application of cocaine and closed circles after cocaine application.

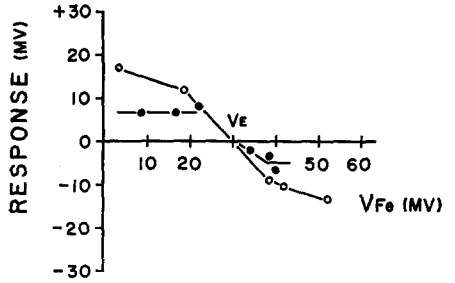

FIGURE 6. The magnitudes of receptor responses to 1.0 M NaCl (open circles) and 0.25 M NaCl (closed circles) as a function of the potential change produced by $FeCl_3$.

While the tongue was being washed with 1 per cent cocaine, various concentrations of NaCl dissolved in 1 per cent cocaine were applied to the tongue. Fig. 4 shows the responses to various concentrations of pure NaCl solution before application of cocaine and the responses to various concentrations of NaCl dissolved in 1 per cent cocaine after application of cocaine. Under the effect of cocaine, the responses to NaCl reversed polarity, and the response magnitude increased according to the concentration of NaCl (Fig. 5).

$FeCl_3$, which normally has a depressing effect on the taste response, was applied to the surface of the tongue for 5 to 10 minutes. The effect of $FeCl_3$ was similar to that of cocaine. 0.06 M $FeCl_3$ solution produced a large positive deflection of the steady potential, which remained for a longer period even

after washing with water. Since recovery from the displacement of the potential caused by $FeCl_3$ was slow, the change of the polarity of the responses to NaCl could be observed for some time before recovery was complete.

In Fig. 6 the sizes and polarities of the slow potential change produced by NaCl are plotted against the potential change elicited by $FeCl_3$. The reversals of the polarities of the responses to 1.0 M and 0.25 M NaCl occurred when the potential elicited by $FeCl_3$, V_{Fe}, reached a certain value, V_E. That is, the slow potential of the maximal response to high concentrations of NaCl alone tended towards V_E, which has a value of 30 mv for this cell (Fig. 5). Therefore, if V_{Fe} is larger than V_E, the response to NaCl is the negative deflection from V_{Fe}, and if V_{Fe} is smaller than V_E, the response to NaCl is positive.

Excitation elicited in the taste cell is transmitted to the taste nerve endings in either a chemical or electrical manner. Landgren, Liljestrand, and Zotterman (1954) assumed that acetylcholine transmitted excitation from the taste receptor cells to the nerve endings. In the present study acetylcholine (1 mg/ml) applied to the surface of the tongue, did not cause any change in either the steady potential or the magnitude of response to NaCl in the taste cell. This result is not in disagreement with their assumption. Gamma-aminobutyric acid (1 mg/ml) also did not change either the response to stimuli or the steady potential although it did inhibit the neural response to NaCl recorded from the glossopharyngeal nerve of the frog. Therefore, gamma-aminobutyric acid may abolish transmission from the taste cell to the nerve ending but does not interfere with excitation of the taste cell.

DISCUSSION

In the present study, the authors paid particular attention to localization of the tip of the electrode since the taste cells are embedded under the epithelium. According to electron microscopical findings (de Lorenzo, 1958; Trujillo-Cenoz, 1957), and microscopical findings (*cf.* Kimura and Beidler, 1961), the diameters of the taste buds of the rabbit are about 50 micra and of the taste cells, 10 micra. Therefore, it is quite probable that if the microelectrode were thrust through or near the taste pore, it would be inserted into the taste bud. By using Bultitude's histological technique (1958), the tip of the electrode was localized after recording the responses. The results showed that the tip of the electrode was inside the taste bud. By this technique, however, it is difficult to know whether or not the tip of the electrode is in the sensory cell because the diameter of the colored spot is about 20 micra which is larger than the diameter of the sensory cell. Moreover, a slight movement of the tip of the electrode during an experiment causes widespread marking. However, if the tip of the electrode is once thrust into the taste bud, it may stay in the taste cell because the cells in the taste bud are very compact. Thus, if the electrode was thrust deeper after the electrode recorded responses to chemical stimuli,

the polarity of the slow potential change elicited by chemical stimuli reversed and the size of the responses became very small. Such a reversal of polarity and decrease in size of the response may occur when the tip of the electrode leaves the cell. Tomita (1956) recorded simultaneously the intracellular and extracellular receptor potentials of the eccentric cell of the *Limulus* eye and his results showed that the receptor potentials recorded extracellularly were smaller than those recorded intracellularly. The polarity of the former potentials was opposite to the latter.

When the recording microelectrode is inside the taste cell, the steady potential measured is related to, but not necessarily equal to, the resting potential of the cell.

Gamma-aminobutyric acid is considered to be an inhibitor of post-synaptic excitation (Kuffler and Eyzaguirre, 1955). In the recent study, neither the steady potential nor the taste cell responses elicited by NaCl were changed by application of gamma-aminobutyric acid, but the neural response of the glossopharyngeal nerve of the frog to chemical stimuli was depressed. Also acetylcholine, excess of which depresses the neural response of the glossopharyngeal nerve of the frog (Landgren, Liljestrand, and Zotterman, 1954), did not change the steady potential and taste cell response to chemical stimuli. These substances may not inhibit the response of the receptor, but may abolish the transmission of excitation from the taste cell to the nerve endings as suggested by Landgren *et al.* (1954).

On the other hand, cocaine and $FeCl_3$ both changed the magnitude and polarity of the responses of the taste cell. The relation between the slow potential change elicited by NaCl and the potential change elicited by cocaine or $FeCl_3$ resembles in some ways that between the inhibitory polarization and stretch depolarization obtained from the stretch receptor of the crayfish by Kuffler and Eyzaguirre (1955).

The response of the receptor cell to a stimulus is believed to be the result of the adsorption of the stimulating ions or molecules to the receptor microvilli surfaces which changes the molecular configuration of the surface and thus increases the membrane permeability (Beidler, 1961).

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