Monoamines of Taste Buds in the Fungiform and Foliate Papillae of the Mouse

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Summary. After administration of monoamine precursors, taste buds in the fungiform and foliate papillae of the mouse were observed by means of electron microscopy and fluorescence histochemistry. The taste buds in the fungiform papillae differed in the ultrastructure of their apical regions from those in the foliate papillae, which contained the same taste buds as those described in the circumvallate papillae. The gustatory cells in both the fungiform and foliate papillae were capable of taking up monoamine precursors, although this ability was greater in the latter papillae. The results suggest that, not only in the circumvallate papillae but also in both the foliate and fungiform papillae, monoamines might be involved in neurotransmission from the gustatory cells to the nerves.

In recent studies on taste buds in the mouse circumvallate papillae, we have demonstrated that the gustatory cells in these tissues are capable of taking up monoamine precursors and storing corresponding amines in their dense-cored vesicles. We have also suggested that monoamines might act as neurotransmitters between the gustatory cells and the nerves in the taste buds (TAKEDA, 1977; TAKEDA and KITAO, 1980).

In rats and rabbits, taste buds in the fungiform papillae have been found to differ in the ultrastructural features of their apical regions from those in the circumvallate papillae; however, those in the foliate papillae have been found to be basically similar to those of the circumvallate papillae (MURRAY and MURRAY, 1970; MURRAY, 1973; TAKEDA and HOSHINO, 1975).

Using mice, this study compares the ultrastructural features of taste buds in both the fungiform and foliate papillae with those in the circumvallate papillae, and tries to ascertain whether taste bud cells in the fungiform and foliate papillae are capable of taking up monoamine precursors.

MATERIALS AND METHODS

Adult dd-mice were injected intraperitoneally with 100 mg/kg 5-hydroxy-L-tryptophan (5-HTP) or 100 mg/kg L-3, 4-dihydroxyphenylalanine (L-DOPA), 1 hr before killing. Two hours before killing, each animal was pretreated with 200 mg/kg nialamide (one of the monoamine oxidase inhibitors). Some mice received only 200 mg/kg nialamide, 1 hr before killing. Untreated mice were used as controls.
Fig. 1 and 2. The apical region of a taste bud from a foliate papilla in a mouse treated with 5-HTP. Type-I cells (1) contain many dense granules. The content of a granule is being released into the pore (double arrows, Inset). A type-II cell (2) contains numerous vesicles and smooth-surfaced endoplasmic reticulum. Type-III cells (3) contain small dense-cored vesicles. Numerous vesicles (V) occur in the pore, being embedded in an amorphous dense substance. Fig. 1. ×23,000; Fig. 2. ×20,000; Inset ×40,000
**Fluorescence microscopy:** Small blocks containing fungiform and foliate papillae were excised, quenched by liquid nitrogen and freeze-dried at $-40^\circ C$ for 4 days. They were exposed to paraformaldehyde vapor at $80^\circ C$ for 2 hr (FALCK et al., 1962). The tissues were then embedded in paraffin wax within a vacuum, sectioned at $6 \mu m$ and examined by fluorescence microscope.

**Electron microscopy:** The mice were perfused through the left ventricle with a phosphate buffered ice-cold mixture of 4% glutaraldehyde and 2% paraformaldehyde. The fungiform and foliate papillae were excised, immersed in the same fixative for 1 hr at $4^\circ C$ and postfixed in 1% osmium tetroxide for 1 hr. After embedding in Epon 812, ultrathin sections were cut out, stained with uranyl acetate followed by lead citrate, and examined by electron microscope.

**RESULTS**

The ultrastructure of taste buds in the foliate papillae closely resembled that in the circumvallate papillae (TAKEDA, 1976). Three distinct types of cells, I, II and III, were recognized in the taste buds. The type-I cell contained numerous dense granules (100–200 nm in diameter) just below the apical end of the cytoplasm. The contents of the granules were released into the pore by a process known as exocytosis (Fig. 1). The type-II cell was characterized by an abundance of variously sized vesicles and smooth-surfaced endoplasmic reticulum (Fig. 2). The type-III (gustatory) cell contained large dense-cored vesicles (80–100 nm) scattered throughout the cytoplasm. Afferent synaptic contacts were found between the type-III cells and the nerve terminals. Small clear vesicles (30–60 nm) were accumulated at the membrane densities of the synaptic contacts (Fig. 3). At the apex, slender cytoplasmic processes of taste bud cells protruded from the pore (Fig. 1). Numerous vesicles (40–80 nm) with a moderately dense content occurred among the processes of cells in the pore, being embedded in an amorphous dense substance (Fig. 1, 2).

The taste buds in the fungiform papillae differed in the ultrastructure of their apical regions from those in the foliate papillae. The apex of each type of cells terminated in short microvilli which never reached the outer surface. The taste pore was narrow and deep, and contained numerous vesicles (40–80 nm in diameter) with a moderately dense content. No dense substance was observed among the vesicles in the pore. The dense granules in the apical cytoplasms of the type-I cells were rod-shaped and low in density, instead of being round and more highly dense as those in the foliate papillae (Fig. 6).

In both untreated and nialamide treated mice, no specific fluorescence appeared in the taste buds of the foliate and fungiform papillae. After administration of 5-HTP, a number of yellow fluorescent cells appeared in the taste buds of the foliate papillae (Fig. 8). Similarly, green fluorescent cells were observed in the taste buds of the foliate papillae following an injection of L-DOPA (Fig. 9). The fluorescence was observed from the basal to the apical region of the cell.

In the taste buds of the fungiform papillae, green fluorescent cells appeared after administration of L-DOPA (Fig. 11), although the intensity of their fluorescence tended to be weaker than that in the foliate regions. Furthermore, the intensity of yellow fluorescence in the mice treated with 5-HTP was very weak (Fig. 10).

In the foliate papillae following an injection of 5-HTP, the type-III (gustatory) cells underwent ultrastructural changes. Small dense-cored vesicles (30–60 nm) appeared
Fig. 3. A synaptic contact between a gustatory cell and a nerve terminal (N) from a foliate papilla in an untreated mouse. Small clear vesicles (arrows) are gathered towards the presynaptic membrane. LV large cored vesicles. ×40,000

Fig. 4. A synaptic contact between a gustatory cell and a nerve terminal (N) from a foliate papilla in a mouse treated with 5-HTP. Small (arrows) and large cored vesicles (LV) are seen along the synaptic membrane. ×45,000

Fig. 5. Cytoplasm of a gustatory cell from a foliate papilla in a mouse treated with 5-HTP. There are scattered large and small dense-cored vesicles. N nerve terminal. ×40,000
scattered throughout the cytoplasm (Fig. 1, 2, 5) and were also found to intermingle with small clear vesicles (30-60 nm) accumulated at the presynaptic membranes in the gustatory cells (Fig. 4). The electron densities of large dense-cored vesicles (80-100 nm) became denser as compared with untreated mice (Fig. 4, 5). Gustatory cells in the fungiform papillae treated with 5-HTP also contained small dense-cored vesicles, though they were fewer in number than those in the foliate papillae (Fig. 7). Large cored vesicles (80-100 nm) with an extremely dense content were infrequently found in the gustatory cells of the fungiform papillae.
Following treatment with the amine precursors we observed the appearance of fluorescent cells in the taste buds of the foliate papillae and also the ultrastructural changes of vesicles in the gustatory cells. The results showed that gustatory cells in the foliate papillae of the mouse were capable of taking up amine precursors as previously observed in the circumvallate papillae (TAKEDA, 1977; TAKEDA and KITAO, 1980). NADA and HIRATA (1975, 1976) have also observed fluorescent cells in the taste buds of the foliate and vallate papillae in the rabbit. However, they found no fluorescence in the fungiform papillae after administrations of 5-HTP, 5-HT or 5, 6-DHT. In the mouse, our results confirmed the appearance of fluorescent cells in the taste buds of the fungiform papillae after administrations of 5-HTP or L-DOPA, although the intensity of their fluorescence tended to be weaker than that in the foliate regions. In addition, we observed ultrastructurally the appearance of small dense-cored vesicles in the gustatory cells of the fungiform papillae after administration of 5-HTP. The above results suggest that not only in the circumvallate papillae but also in both the foliate and fungiform papillae, biogenic monoamines are involved in the neurotransmission from the gustatory cells to the sensory nerves.

This study indicated that the taste buds in the fungiform papillae differed in their apical structures from those in the foliate and circumvallate papillae. Furthermore,
they were shown to be poorer in ability to take up amine precursors than the taste buds in the other two papillae. Taste buds in the fungiform papillae are located on a more exposed surface of the papilla, rather than being hidden in the lateral grooves of the papilla. It has been indicated that the taste buds of the fungiform papillae are innervated by the chorda tympani and those of the foliate and circumvallate papillae by the glossopharyngeal nerve. It has been widely accepted that different modalities of taste are perceived in specific anatomical areas of the tongue (Henkin and Christiansen, 1967). Oakley (1967) has shown that responses of the nerves supplying the taste buds have depended upon the nature of the lingual tissue rather than that of the nerves. Therefore, it seems not unreasonable to postulate that responses of the nerves supplying different papillae may reflect both the difference in the apical ultrastructure of the taste buds and also the ability of gustatory cells to take up amine precursors.
REFERENCES


