The Ultrastructure of Encapsulated Sensory Corpuscles in the Fungiform Papillae of Monkeys

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Summary. Both simple and coiled simple encapsulated sensory corpuscles in the fungiform papillae of primate tongues were examined by light and electron microscopy. These were found to be composed of discoid axon terminals, with cytoplasmic lamellae of lamellar cells surrounding them. The axon terminals were characterized by the presence of distinct finger-like projections extending beyond the corpuscular basal lamina to make contact with collagen fibers, as well as numerous mitochondria, clear vesicles and a few dense-core vesicles in the axoplasm. The cytoplasmic lamellae of lamellar cells showed a number of caveolae on the plasma membrane. Further, desmosome-like contacts were found between adjacent lamellae and between the axon and the innermost lamella.

Mechanoreceptors have been described by a number of investigators in the mammalian oral mucosa (for a review, see HOLLAND, 1984). These have included Merkel-neurite complexes in the epithelium, and various sensory corpuscles in the subepithelial connective tissue. Although Merkel-neurite complexes have been studied extensively, only in recent years has the attention of researchers been paid to the ultrastructure of the corpuscular nerve endings in the oral mucosa (SPASSOVA, 1971;1974; WATANABE and YAMADA, 1983; ZAHM and MUNGER, 1985; WATANABE and IDE, 1987; TACHIBANA et al., 1987a, b).

It is well known that the mammalian fungiform papilla is a densely innervated organ sensitive both to chemical and mechanical stimuli (for a review, see ZAHM and MUNGER, 1985). We have recently described the occurrence and fine structure of Merkel-neurite complexes, slowly adapting mechanoreceptors, in the primate fungiform papillae (TOYOSHIMA et al., 1987). In the present study, we further examined encapsulated sensory corpuscles, which have been established to be rapidly adapting mechanoreceptors, concentrating our efforts on the fungiform papillae of two monkey species by means of light and electron microscopy.

MATERIALS AND METHODS

Tongues used in the present study were collected during the autopsy of four Japanese monkeys (Macaca fuscata) and three Cynomolgus monkeys (M. fascicularis). The anterior part of the tongue was dissected free, cut into small pieces and immediately
fixed for 3 hr by immersion in a trialdehyde-DMSO mixture (KALT and TANDLER, 1971) buffered with phosphate. After washing in the phosphate buffer, the specimens were postfixed for 2 hr in phosphate-buffered 2% osmium tetroxide and then dehydrated in a graded series of ethanol, passed through propylene oxide, and embedded in epoxy resin. One-micron sections were stained with toluidine blue. Following light microscopic identification of encapsulated nerve endings, adjacent ultrathin sections were cut, stained with uranyl acetate followed by lead citrate, and examined in a JEOL-100C electron microscope.

Some of the tissues were fixed in 10% neutral buffered formalin. The tissues were then embedded in paraffin and 8 µm serial sections were cut to be stained with the ammoniacal silver technique by SEVIER and MUNGER (1965).

RESULTS

The anterior part of the dorsal surface of the tongue contained a number of fungiform papillae. These papillae had a mushroom-like appearance, 300–400 µm in height and 200–400 µm in diameter. Each papilla was composed of a connective tissue core covered with stratified squamous epithelium.

After silver impregnation, abundant nerve fibers appeared in the connective tissue of the fungiform papilla (Fig. 1). Some of these nerves formed organized endings: corpuscular receptors of both simple and complicated glomerular types in the connective tissue papillae. The complicated glomerular type of nerve endings was similar in morphology to Krause’s end-bulbs (Fig. 1).
Fig. 2. Electron micrograph of a vertical section of the fungiform papilla showing two encapsulated sensory corpuscles of a simple type located beneath the epithelium (EP). AT axon terminals of corpuscles. ×3,000
Ultrastructurally, simple and complicated glomerular endings corresponded to the simple and coiled simple corpuscles designated by Halata and Munger (1983), respectively (Fig. 2, 3). The corpuscle was composed of an axon terminal with lamellated capsule surrounding it.

The axon terminal was discoid in shape and contained numerous closely packed mitochondria. At the periphery, the axon terminal was devoid of mitochondria and filled with clear vesicles, a small number of dense-core vesicles and occasional multivesicular bodies (Fig. 4, 5). At higher magnification and in favorable sections, the axon occasionally showed finger-like projections extending beyond the corpuscular basal

**Fig. 3.** Electron micrograph of a coiled simple sensory corpuscle. Axon terminals surrounded by lamellae of lamellar cells are filled with numerous mitochondria. Note ladder-shaped bundles of fibers (arrow). ×7,100
Fig. 4. High-magnification electron micrograph of the axon terminal (AT). The axon extends a finger-like projection (arrow) towards collagen fibers investing the corpuscle. ×33,500. Inset. Note the presence of clear and dense-core vesicles (arrow) near the base of the projection. ×30,000
lamina to contact the collagen fibers (Fig. 4). These projections contained a parallel pattern of numerous filaments.

The axon terminals were surrounded by 10–15 layers of flattened lamellae of the lamellar cells, 0.5–1 μm in thickness. The most characteristic feature of the lamellar cells was the presence of a large number of caveolae along the plasma membranes (Fig. 5). These caveolae were somewhat more numerous in the inner area of the capsule. A number of cytoplasmic filaments disposed randomly throughout the cytoplasm and a few mitochondria were also components of the cytoplasmic lamellae. The interlamellar spaces were usually occupied by collagenous materials which were continuous with

Fig. 5. Electron micrograph showing a number of caveolae on the plasma membrane of lamellar cells. Note desmosome-like contacts between adjacent lamellae (large arrow) and between the axon (AT) and the innermost lamella (small arrow). × 27,500
the basal lamina investing the encapsulated sensory corpuscles. At the innermost portion of the corpuscle, the cytoplasmic lamellae became apposed to the axon terminal by a gap of about 20 nm in width, and no collagenous material was found in that gap. Adjacent lamellae were often closed to each other; desmosome-like contacts were found frequently along these areas (Fig. 5). These special contacts were also found between the cytoplasmic lamellae and axon terminals.

DISCUSSION

The present study has revealed the fine structural details of simple and coiled simple encapsulated sensory corpuscles in the fungiform papillae of two species of monkeys. The sensory corpuscles were composed of discoid axon terminals with lamellated capsules surrounding them. The ultrastructure of the encapsulated sensory corpuscles examined in the present study was essentially similar to those previously described in various portions of the oral mucosa (SPASSOVA, 1971, 1974; WATANABE and YAMADA, 1983; WATANABE and IDE, 1987; TACHIBANA et al., 1987a, b) and the skin (for reviews, see HALATA, 1975; CHOUCHKOV, 1978).

A noteworthy feature of the corpuscles we observed was the presence of distinct finger-like projections of the axon terminals extending beyond the basal lamina to contact the collagen fibers investing the corpuscles. These projections contained organized filaments and appeared rigid. Similar axonal projections have been demonstrated for other dermal nerve terminals with or without capsules (ANDRES, 1969; SPENCER and SCHAUMBURG, 1973; GOTTSCALDT et al., 1982; BYERS and YEH, 1984; WATANABE and YAMADA, 1983, 1984). The digitate projections in contact with the collagen fibers investing the corpuscles permit the axon terminal to react to the deformation of fungiform papillae, which may provide advantageous information regarding the position and shape of food in the oral cavity during mastication. The Merkel-neurite complexes in the epithelium of fungiform papillae (TOYOSHIMA et al., 1987) may also contribute to these possible functions.

Another interesting feature of the encapsulated sensory corpuscles was the presence of a large number of caveolae on the plasma membrane of the lamellar cells. In regard to the functional significance of these caveolae, MUNGER (1975) speculated that they might be important for regulating the ionic milieu which affects electrical events around the axon terminals. On the other hand, IDE and SAIITO (1980) suggested in their study of the mouse digital corpuscles that the caveolae might be involved in the release of nonspecific cholinesterase presumably synthesized in the lamellar cells. Nonspecific cholinesterase activity has also been recently demonstrated in the encapsulated sensory corpuscles of the rat lip (WATANABE and IDE, 1987; TACHIBANA et al., 1987b) and dog oral mucosa (TACHIBANA et al., 1987a).

Yet another point of interest is the occurrence of desmosome-like contacts between adjacent lamellae and between the axon and the innermost lamella. The morphology of these junctions is similar to those between the axon and the Merkel cell. Although there are several descriptions concerning these junctions in addition to the simple adhesive function, their significance is still entirely speculative.

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