Fine Structure of the Herbst Corpuscles in the Lingual Mucosa of the Finch, *Lonchura striata* *

Kuniaki TOYOSHIMA, Yuji SETA and Akitatsu SHIMAMURA

Department of Oral Anatomy, Kyushu Dental College, Kitakyushu, Japan

Received June 8, 1992

Summary. The ultrastructure of Herbst corpuscles in the lingual mucosa of the finch, *Lonchura striata* var. *domestica*, was examined by light and electron microscopy. Numerous Herbst corpuscles were found at the top of connective tissue papillae just beneath the dorsal epithelium. The Herbst corpuscle was composed of an outer capsule, inner core and central axon. The central axon was discoid in shape and immunoreactive for NSE-antiserum. The central axon was surrounded by compactly stacked layers of thin lamellae of lamellar cell processes. Since these lamellae did not completely encircle the axon as seen in cross sections, they displayed a symmetrical longitudinal cleft dividing the inner core into bilateral halves. Numerous axonal spines were seen to extend from the Y-axis of the axolemma into the cleft and occasionally into the cytoplasmic invagination of the lamellar cell body in the inner core. A number of clear and dense-cored vesicles were seen in the axoplasm near the base of axonal spines. Further, the Ω-shaped coated invaginations were occasionally found on the axolemma near those places. These findings suggest that the area nearby the axonal spine in the central axon of the Herbst corpuscle is a site active both metabolically and functionally.

It is well known that the morphology of mechano-receptors varies with sites in the body and may substantially influence its physiology (IGGO, 1976; IGGO and OGAWA, 1977). However, Herbst corpuscles have been studied in beak skin (ANDRES, 1969; SAXOD, 1970, 1973; HALATA, 1971; MUNGER, 1971) and articular capsules (HALATA and MUNGER, 1980); only a few reports have been made on the oral mucosa (ANDERSEN and NAFSTAD, 1968; BERKHOUDT, 1980; WATANABE et al., 1985).

Recently, we have reported that the lingual mucosa of the finch contained numerous Herbst corpuscles as well as Merkel corpuscles in the subepithelial connective tissue (TOYOSHIMA, 1989; TOYOSHIMA and SHIMAMURA, 1991 a, b). The present study is to describe the fine structure of Herbst corpuscles in the lingual mucosa of this bird.

MATERIALS AND METHODS

Lingual mucosa of the finch, *Lonchura striata* var. *domestica*, was used for the present study. Five adult finches of both sexes were deeply anesthetized by intraperitoneal injection of sodium pentobarbital (0.05 mg/g body weight) and the tongues were dissected free and immediately fixed for 3 h by immersion in a trialdehyde-DMSO mixture (KALT and TANDLER, 1971) consisting of 2.5% glutaraldehyde, 2% paraformaldehyde, 1% acrolein and 2.5% dimethyl sulfoxide in 0.1 M phosphate buffer at pH 7.2. Specimens were then postfixed for 2 h in 2% osmium tetroxide in the same buffer. After a brief washing, the specimens were dehydrated through a graded series of...
ethanol and embedded in Epon-Maraglas (Tandler and Walter, 1977). Sections 1 μm thick were stained with toluidine blue and sites were chosen for thin sections. Thin sections were cut on an Ultracut-E ultramicrotome, stained with uranyl acetate followed by triple-lead stain (Sato, 1968) and observed in a JEM-1200EX electron microscope. 

The specimens prepared for light microscopy were fixed in Bouin’s fixative for 2 days and processed in paraffin. Sections 6 μm thick were impregnated with silver according to Sevier and Munger (1965).

The specimens prepared for immunohistochemistry were fixed for 2 h in Bouin’s fixative containing no acetic acid and embedded in paraffin. Dewaxed 5 μm thick sections were incubated in the rabbit polyclonal antiserum against cow neuron-specific enolase (NSE) (Dako Co.) at a dilution of 1:300 and subjected to the avidin-biotin complex (ABC) method using an ABC kit from Vector (California, USA). Control sections were treated with non-immunized rabbit antiserum prior to incubation with the first antiserum.

**RESULTS**

The antero-dorsal surface of the finch tongue is relatively flat and covered with keratinized squamous epithelium. At the anterior tip of the tongue, a characteristic hairy seedcup is found (Fig. 1). In its frontal section, the tongue consists of a keratinized squamous epithelium which is well-organized into epithelial rete ridges and connective tissue papillae. Numerous Herbst corpuscles appear at the top of the connective tissue papillae just beneath the dorsal epithelium (Fig. 2).

The Herbst corpuscle is usually ellipsoidal in shape and composed of an outer capsule, inner core and central axon. Each corpuscle is supplied by a single myelinated nerve fiber. The myelinated nerve fiber loses its myelin sheath just before entering the corpuscle and the axon extends through the center of the inner core and terminates in a knob-like expansion without branching (Fig. 3). These fibers are immuno-

---

**Fig. 1.** Scanning electron micrograph showing the antero-dorsal surface of the finch tongue. Hairy seedcup (asterisk) is seen at the lingual tip. ×100

**Fig. 2.** Semithin section of the antero-dorsal mucosa of the tongue. Numerous Herbst corpuscles (H) are present at the top of the connective tissue papillae. M Merkel corpuscle. ×880
reactive for NSE-antiserum (Fig. 4).

By electron microscopy, the inner core surrounding the central axon is seen to complete separate from the outer capsule within a corpuscle (Figs. 5, 6). In cross sections, the axon terminal is discoid in shape and surrounded by compactly-stacked layers of thin lamellae of lamellar cell processes (Fig. 7). The lamellar cells are located bilaterally on a production of the Y-axis (MUNGER and IDE, 1987), and straddle the axon with numerous cytoplasmic lamellae extending from the lamellar cell body. The thin cytoplasmic processes extending from one cell body interdigitate in a corresponding array extending from the opposite cell body, leaving only narrow spaces between neighboring lamellar cell processes. The spaces between these lamellae become narrower toward the axon (Figs. 7, 8). Since these lamellae do not completely encircle the axon, they display a symmetrical longitudinal cleft dividing the inner core into bilateral halves (Fig. 7). The plane of bilateral symmetry, i.e., the cleft, is usually a plane transecting the cell bodies of the lamellar cells, a production of the Y-axis.

When the section is cut longitudinally, the axon terminal is observed to end in a bulbous enlargement in an inner core (Fig. 6). At the extreme tip (IDE et al., 1988) of the axon terminal, the axon is covered partially with or without lamellae of lamellar cells (Fig. 9).

The cytoplasmic lamellae contain a feltwork of thin filaments, occasional mitochondria and vesicles. The lamellae are separated from one another by a space about 20–40 nm in width (Fig. 8). Where the lamellae are apposed to the axon terminals, i.e., the X-axis of the axon, a gap of about 20 nm in width is seen and no filamentous substance is found in that gap. Adjacent lamellae are often close to each other and desmosome-like junctional specializations are found along these areas (Figs. 7, 8). These intimate appositions are also established occasionally between the axon and the apposed lamellae (Figs. 10, 11).

The axoplasm contains numerous neurofilaments

---

**Fig. 3.** Light micrograph showing innervation of Herbst corpuscles impregnated with silver according to SEVIER and MUNGER. Central axons can be seen in cross (small arrows) and longitudinally (large arrow) sectioned Herbst corpuscles. ×380

**Fig. 4.** Central axon of the Herbst corpuscle is immunoreactive for NSE-antiserum. ×680
Fig. 5. Electron micrograph showing a perfect cross section of a Herbst corpuscle. The Herbst corpuscle is composed of an outer capsule (OC), inner core (IC) and central axon (A). The inner core is completely separated from the outer capsule. L lamellar cell. ×5,000
Fig. 6. Electron micrograph showing a perfect longitudinal section of a Herbst corpuscle. Central axon (A) is encircled by two parallel rows of lamellar cells (L) and ends in a knob-like expansion. Arrows axonal spines. ×5,000
and microtubules, scattered mitochondria and occasional lysosomes and multivesicular bodies (Fig. 9). In the trunk region of axon terminal, mitochondria are clustered just below the axolemma. At the extreme tip of the axon terminal, numerous mitochondria are distributed throughout the axoplasm.

The most characteristic feature of the axon terminal is the presence of numerous axonal spines projecting from the Y-axis into the cleft of the inner core (Figs. 10, 11). Since the cleft of the inner core is usually related to the cell bodies, i.e., the nuclear portions of the lamellar cells as described above, axonal apines sometimes extend deeply into cytoplasmic invaginations of the lamellar cells. The axonal spines contain abundant filaments reaching down to the superficial axoplasm. Numerous clear and dense-cored vesicles are found to accumulate in the axoplasm near the base of the axonal spines, and Ω-
shaped coated invaginations are observed on the axolemma near those regions (Fig. 11).

DISCUSSION

The occurrence and fine structure of avian sensory corpuscles have been described in detail by Malinovsky and Pac (1982) in various species of birds. According to their study, considerable variability exists in the morphology of sensory corpuscles among the species, as is the case with mammals.

Avian sensory corpuscles are usually classified into two distinct types, i.e., Merkel or Grandry corpuscles and Herbst corpuscles (Munger, 1971; Malinovsky and Pac, 1982; Malinovsky, 1986). The Merkel corpuscle is a characteristic neuro-paraneuronal complex in nonaquatic birds, and the Grandry corpuscle is characteristic in aquatic birds.

It has been believed that the Herbst corpuscle is a typical avian mechanoreceptor equivalent to the Pacinian corpuscle in mammals (Munger, 1971; Halata, 1971; Malinovsky, 1986) and characterized by rapid adaptation (Doward et al., 1971; Gregory, 1973; Gottschaldt, 1974). As in the case of the Herbst corpuscle, the central axon of the Pacinian corpuscle is also immunoreactive for NSE (Iwanaga et al., 1982). However, slight differences in morphology and physiology have been noted between Herbst and Pacinian corpuscles.

As was described previously by Munger (1971), the Herbst corpuscle is much smaller in size than the Pacinian corpuscle. Further, the Herbst corpuscle lacks cellular lamellae between the outer capsule and inner core. Physiologically, Doward et al. (1971) found the frequency response and adaptive characteristics of Herbst and Pacinian corpuscles to be approximately equivalent. The significant difference between the two receptors is that the Herbst corpuscle responds to a somewhat lower frequency (also see Munger, 1971).

In their study on the ultrastructure of pigeon articular capsules, Halata and Munger (1980) found two types of Herbst corpuscles, large and small ones. They further subdivided the large type of Herbst corpuscles into typical corpuscles with an unbranched inner core, and those with a branched inner core. Halata and Munger (1980) suggested that this variability in the structure of Herbst corpuscles might be reflected in an equivalent variability in physiologic parameters, i.e., rapid adapting function. The occurrence of the branched inner core also has
been reported in Pacinian corpuscles of mammals (MALINOVSKÝ, 1986; IDE et al., 1987).

In the present study, in contrast, we recognized no branching of the axon in the inner core of the lingual Herbst corpuscles of the finch. This may reflect the fact that the mechanosensation of the lingual mucosa is not so complex as that of avian articular capsules.

The axon terminals of the Herbst corpuscle in the present study are characterized by the presence of numerous spines. According to MUNGER et al. (1988), axonal spines are a common feature of all mechano-receptors. As far as we are aware, however, the present paper is the first to report the occurrence of axonal spines in the Herbst corpuscles, a representative mechanoreceptor in birds. As with the cases of Pacinian corpuscles in mammals, axonal spines usually project from the Y-axis of the axon into the cleft of the inner core. The terms "X-axis" and "Y-axis" have been applied by MUNGER and IDE (1987) to a short axis and a definite long axis of the elliptical cross section of the central axon of Pacinian corpuscles, respectively. Thus, the X-axis always faces the lamellae and the Y-axis always abuts the cleft in the inner core lamellae.

Axonal spines of the Herbst corpuscle sometimes extended deeply into cytoplasmic invaginations of the lamellar cells. These structures are reminiscent of Merkel cells. As noted by many investigators, it is conceivable that the axonal spines of the mechanosensory axon may act as "tentacles" receiving mechanical deformation.

Numerous clear and dense-cored vesicles were found in the axon terminal of the Herbst corpuscle. These vesicles tended to accumulate near the base of the axonal spines. Further, we found Ω-shaped coated invaginations on the axolemma near the base of the

![Electron micrograph showing a portion of the extreme tip of the axon. Numerous mitochondria, lysosomes, multivesicular bodies and neurofilaments are seen throughout the axoplasm (A). L lamellar cell, Arrow axonal spine. ×11,000](image-url)
Fig. 10. Electron micrograph showing an axonal spine (asterisk) projecting into the cleft in the inner core. Desmosome-like junctional specializations (arrows) are seen between the axon (A) and the apposed lamellae. ×20,000

Fig. 11. An axonal spine (asterisk) extending into the cytoplasmic invagination of the lamellar cell body (L). Note the presence of numerous clear and dense-cored vesicles in the axoplasm (A) near the base of the axonal spine. ×33,000. Inset. Coated invagination is seen on the axolemma facing the cleft (arrow). ×24,000
axonal spines. The occurrence of such vesicles near the axonal spines also has been reported in the axon terminals of Pacinian corpuscles (MALINOVSKÝ et al., 1982; IDE et al., 1987, 1988), Meissner corpuscles (IDE, 1976), simple corpuscles (BYERS and YEH, 1984; TOYOSHIMA et al., 1987) and free nerve endings (WATANABE and YAMADA, 1984). As was also suggested by IDE (1976), the accumulation of clear and dense-cored vesicles nearby the axonal spines might reflect metabolic as well as functional activities in these regions. However, the physiological role of these vesicles is unknown at the present.

HALATA and MUNGER (1980), in their study of pigeon Herbst corpuscles, noted the morphological resemblance between the cleft of the inner core of Herbst corpuscles and the node of Ranvier of myelinated axons. Recently, MUNGER and IDE (1987) and IDE et al. (1988) have proposed that the axonal spines at the cleft and extreme tip of Pacinian corpuscles may be the site of restricted current flow and of mechano-electric transduction, just as the stereocilia of the hair cells of the cochlea have been thought to be the site of transduction (HUDSPETH, 1985; HOLTON and HUDSPETH, 1986).

REFERENCES


Dr. Kuniaki TOYOSHIMA
Department of Oral Anatomy
Kyushu Dental College
Kokurakita-ku, Kitakyushu
803 Japan

豊島 邦昭
803 北九州市小倉北区真鶴2丁目6-1
九州歯科大学
口腔解剖学第二講座