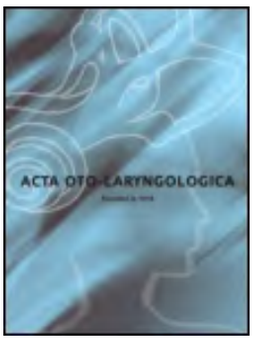

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THE CONSISTENT OCCURRENCE OF A STRIATED ORGANELLE (FRIEDMANN BODY) IN THE INNER HAIR CELLS OF THE NORMAL CHINCHILLA

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Abstract. Striated organelles have consistently been observed in electron micrographs of serial sections from the inner hair cells of normal chinchilla cochleas. The striated organelle is located in the infracuticular plate region. It lines the cuticular plate, and the direction, pattern and periodicity of the striations vary along its length. The striated organelle is seen in close association with the cell membrane, smooth endoplasmic reticulum, microtubules and mitochondria. The striated organelle may play an active role in inner hair cell function, and its proliferation under pathological conditions, as observed by others, may be accompanied by alterations in sensitivity of the inner hair cell to stimuli.

The Friedmann body is a laminated cytoplasmic inclusion, or striated organelle. These organelles have often been observed in vestibular hair cells in humans, associated with Meniere's Disease (Friedmann et al., 1963), eighth nerve tumors (Hilding & House, 1964), Conn's Syndrome (Friedmann et al., 1965), and in animals in cases of drug intoxication (Friedmann et al., 1966; Jahnke, 1969; Spoendlin, 1970). They have occasionally been reported in normal vestibular hair cells (Engström et al., 1962; Lowenstein & Osborne, 1964; Engström et al., 1972; Hoshino, 1975), and in humans their presence has been correlated with old age (Rosenhall & Engström, 1974). The striated bodies were found near or within the cuticular plate, and in pathologic specimens they have been observed in contact with the rootlets of the stereocilia (Spoendlin, 1970). They were originally believed to be either crystalline inclusion bodies resulting from the overproduction of phospholipids (Friedmann et al., 1965), or pathologic alterations in protein metabolism (Jahnke, 1969; Spoendlin, 1970).

Striated bodies have also been described in cochlear hair cells of the adult deaf white mink in association with degenerative changes occurring in the organ of Corti (Hilding et al., 1967). In the inner hair cells of the normal squirrel monkey (Engström et al., 1972) and cat (Kimura, 1966; Spoendlin, 1966) the striated bodies were found in the infracuticular plate region.

We report here the consistent occurrence of the striated bodies in the inner hair cells of normal chinchillas. Other investigators have observed striated organelles in cochlear and vestibular hair cells and many attributed their presence to pathologic changes. However, the occurrence of the striated organelle in the inner hair cells of yet another species provides additional evidence that they are a normal structural component of the inner hair cell and that they may play a role in inner hair cell function.

MATERIAL AND METHODS

Both cochleas from 10 normal chincillas one year to seven years old were perfused with 2% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2, containing 0–10 mM $MgCl_2$. Specimens were fixed at room temperature and stored overnight in fixative at 4°C. They were then washed in phosphate buffer, post fixed 1 hr in 1% osmium tetroxide in phosphate buffer, and

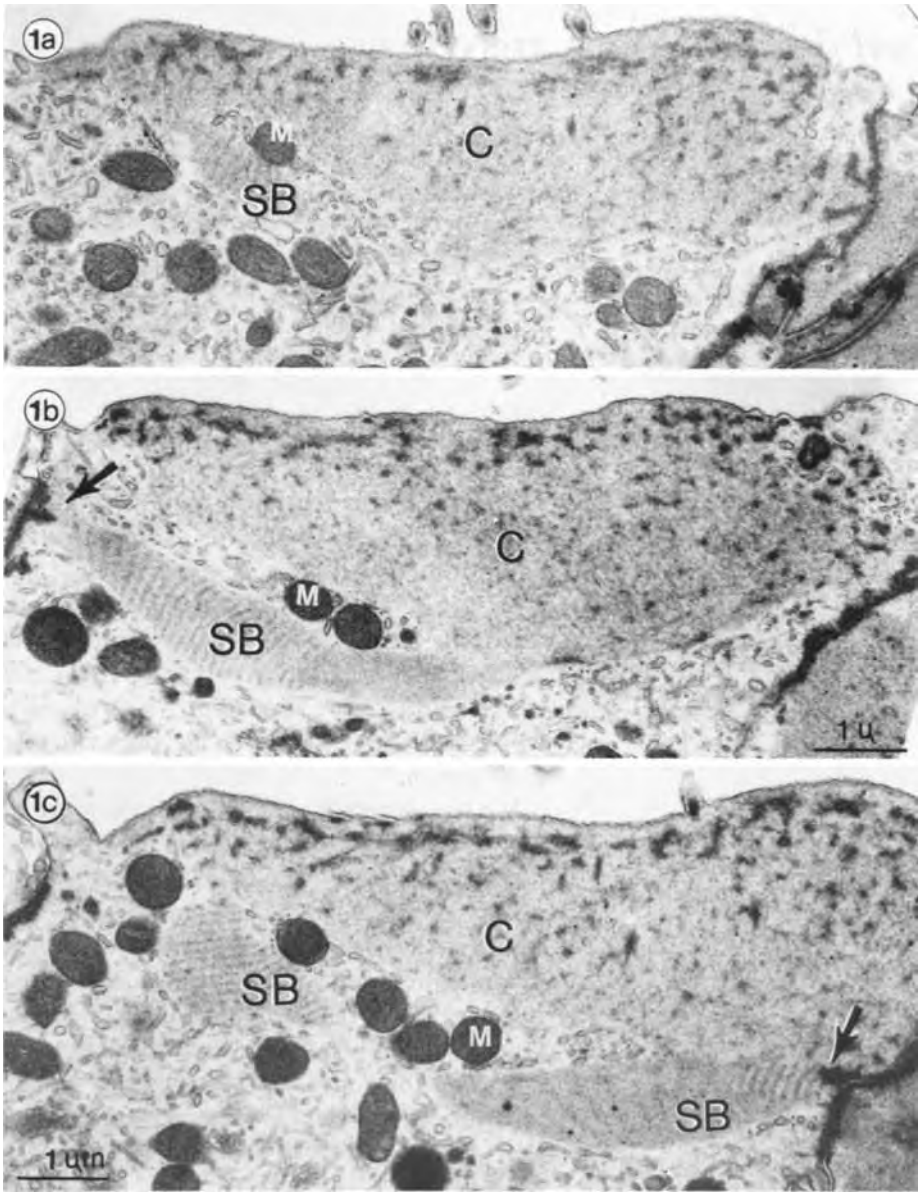

Fig. 1. Radial sections through three inner hair cells. The striated body (*SB*) is present below the cuticular plate (*C*). It is attached to the cell membrane (*arrows*, 1*b*, *c*) in the region of the junctional complex, and the dark staining material of the junctional complex merges with the dense bands (1*c*). The striated body is in close association with mitochondria (*M*).

washed 30 min in phosphate buffer. Cochleas were dehydrated through ethanol and propylene oxide, embedded in Aradite (Bohne, 1972), and the organ of Corti dissected. Thin sections were cut on a Porter Blum 2B microtome, mounted on Formvar-coated single slot grids, stained for 1 hr in 1% uranyl acetate in 50% ethanol, and 10 min in 0.3% lead citrate. Serial sections were examined in a Siemens 1 A electron microscope.

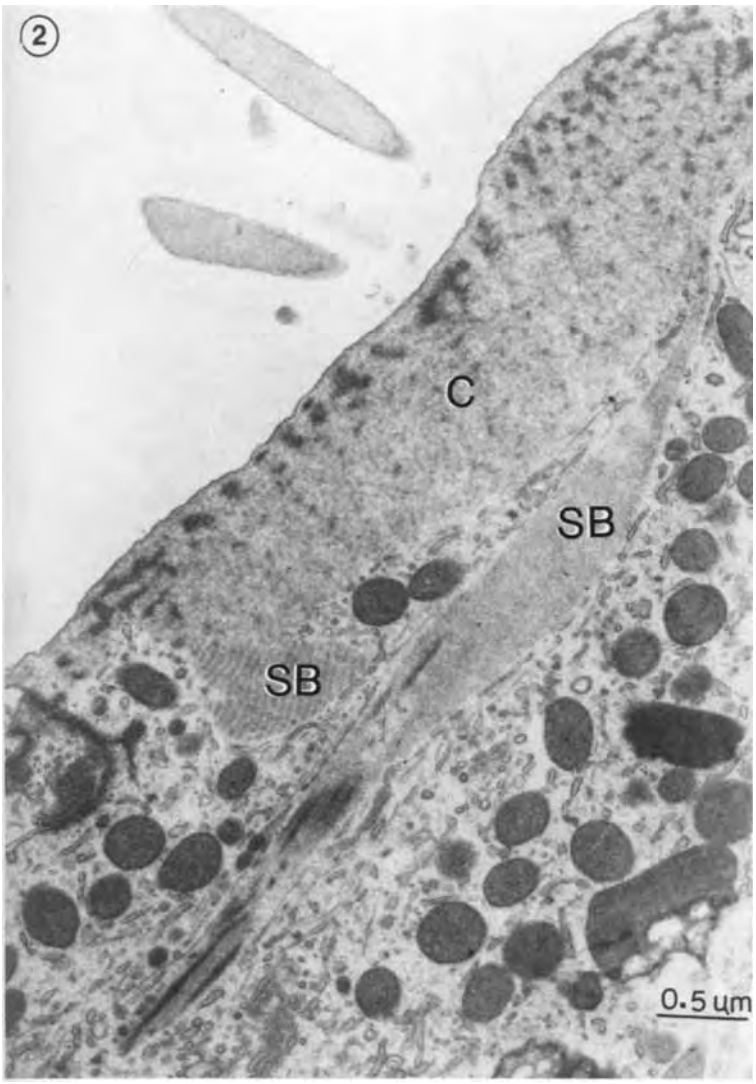

Fig. 2. A radial section through an inner hair cell. The striated body (*SB*) lines the cuticular plate (*C*) and projects down toward the centrally located nucleus.

RESULTS

We examined sections from both cochleas from the normal animals. In all cases, when serial sections were observed we found striated bodies in every inner hair cell (over 70 inner hair cells sectioned). Striated bodies were not observed in outer hair cells of these animals although three times as many outer hair cells were examined.

When the organ of Corti is sectioned in a radial plane parallel with the long axis of the hair cells, the striated bodies are found below the cuticular plate (Fig. 1). The striated body appears fusiform in shape, lines the cuticular plate and curves to follow its contours. In the radial plane, the striated body is composed of electron-dense bands (20–30 nm), separated by spaces of less electron-dense material (30–40 nm). The dense bands repeat with a periodicity of 50–60 nm. The striated body is at times separated from the cuticular plate, and it may be surrounded on both top and bottom surfaces by cytoplasm and endoplasmic reticulum. It is associated with mitochondria present in

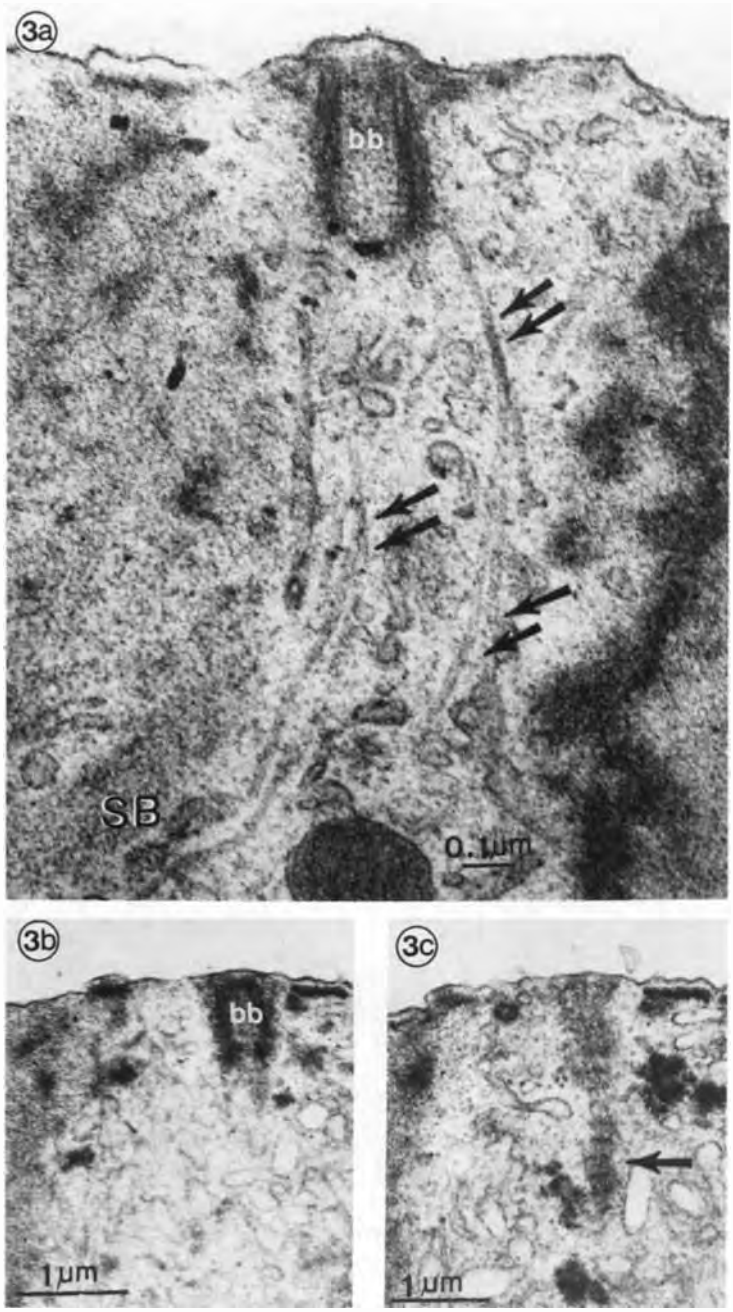

Fig. 3. Radial sections through inner hair cells. In a section from the same inner hair cell in Fig. 2 (3*a*) the striated body (*SB*), sectioned oblique to the striations, is seen close to the basal body (*bb*) and its associated microtubules (*double arrows*). Serial sections through a basal body (3*b*, *c*) show the cross striated ciliary rootlet (*single arrow*) projecting down into the cytoplasm from the basal body.

this area, and in some instances they appear to be in contact (Fig. 1*a*). In each hair cell examined, the striated body appears to be attached to the cell membrane in at least one location. It has been observed attached to the side of the cell toward the modiolus (Fig. 1*b*) and attached to the side of the cell toward the inner pillar cells (Fig. 1*c*). The point of attachment is always near the surface of the reticular lamina where the inner hair cell is in contact with the supporting cells and where tight junctions, intermediate junctions and desmosomes are

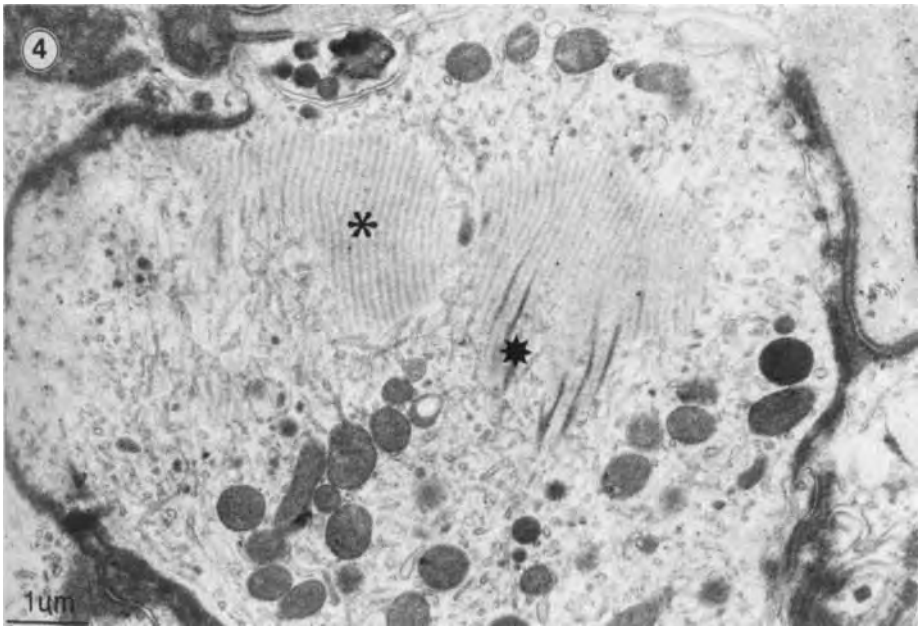

Fig. 4. A section parallel to the reticular lamina through an inner hair cell. The asterisk indicates a portion of the striated body where the banding pattern is similar to that seen in Fig. 1. The star indicates the alternate banding pattern.

known to occur (Gulley, 1976; Iurato et al., 1976). The striated body appears to merge with the darkly staining electron-dense material that extends out from the junctional complex (Fig. 1*c*).

The striated body has a complex ultrastructure. In the region of the cuticular plate just below the stereocilia, it is observed sectioned oblique to the striations (Figs. 1*b*, *c*, 2). In some inner hair cells, the striated body projects into the cytoplasm of the inner hair cell toward the centrally placed nucleus (Fig. 2). The striated body can be seen close to the basal body (Fig. 3*a*), and may lie adjacent to the striated rootlet (Fig. 3*b*, *c*) and microtubules (Fig. 3*a*) associated with the basal body.

When the organ of Corti is sectioned in a plane parallel with the reticular lamina, perpendicular to the long axis of the hair cells, the striated body can be seen in many cells at one time. The body again appears to line the cuticular plate just as it comes in contact with the cytoplasm (Fig. 4). However, when the striated organelle is sectioned in this plane, the direction and pattern of the striations differ from the direction and pattern observed in radial sections. The most frequent orientation of the striations is in a radial direction from the area close to the inner pillar cells, toward the modiolus. In some places the pattern of striations is the same as that seen in Fig. 1; it is composed of dense bands of equal width with a periodicity of 50–60 nm. In other areas, the body assumes a different banding pattern (Figs. 4, 5) with thick dense bands (30–40 nm) alternating with thinner dense bands (20–30 nm). The bands are separated one from the other by a less electron-dense space (30–40 nm). When the striations are observed in this alternate banding pattern, the periodicity of the striations increases to 70–80 nm, and the body has the more characteristic appearance of Friedmann bodies as described by other investigators.

The orientation of the banding pattern is variable, and at times the striations are per-

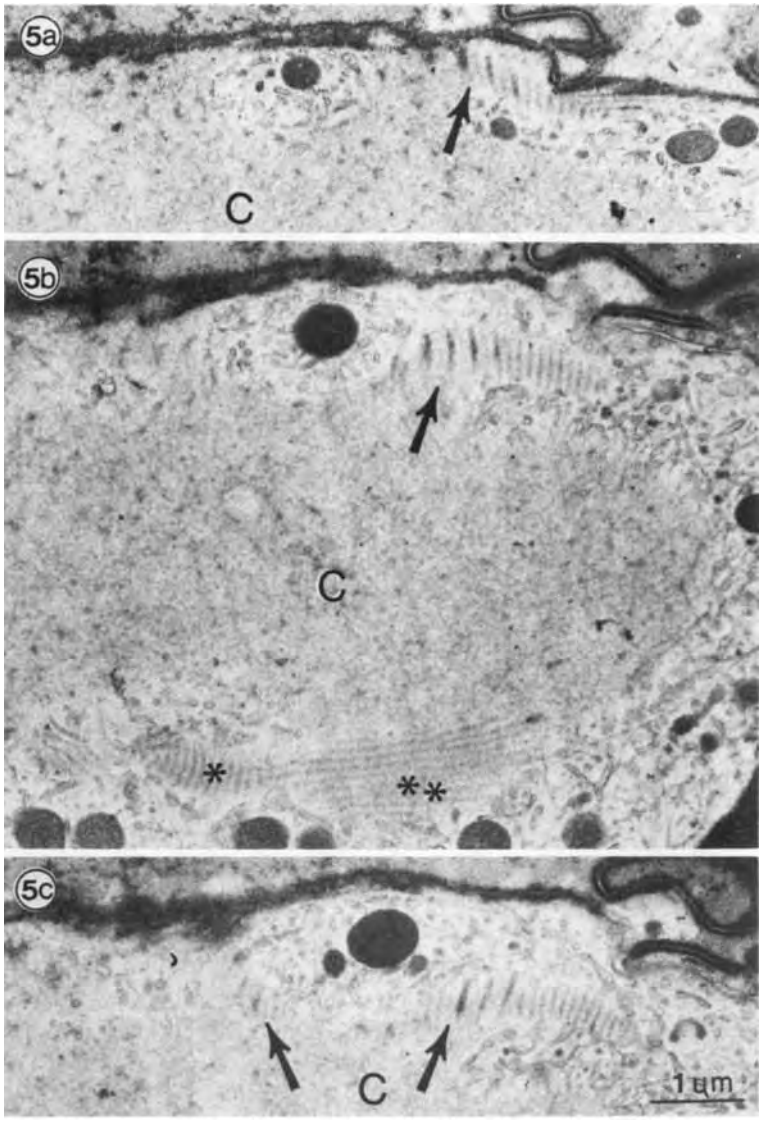

Fig. 5. Sections parallel to the reticular lamina through one inner hair cell. The striated body (*arrows*) can be seen along the periphery of the cuticular plate (*C*). The striated body is associated with the electron-dense junctional material (5*a*) and continues around the cuticle free region of the cell (5*b*, *c*) where the basal body and mitochondria are usually found. At times the striations (*asterisks*) are perpendicular to each other (5*b*).

pendicular to each other (Fig. 5*b*). When the cells are sectioned in this plane, the striated body is seen associated with the dark-staining material of the junctional complex along the circumference of the cell (Fig. 5*a*). It surrounds the cuticle-free region where one normally finds the basal body (Fig. 5*b*, *c*). The striated body appears in close association with microtubules projecting into the cytoplasm (Fig. 6*a*). The electron-dense bands of the body may be continuous with elaborations of the smooth endoplasmic reticulum (Fig. 6*b*).

DISCUSSION

We have described the occurrence of striated bodies in the inner hair cells of normal chinchillas. These chinchillas are supplied to us from breeders in the area. Their environment is controlled, and they have never been exposed to any drugs or intentional trauma. We consider their auditory systems normal, and physiological data from other chincillas in this laboratory appear normal. The striated bodies have been observed consistently in every

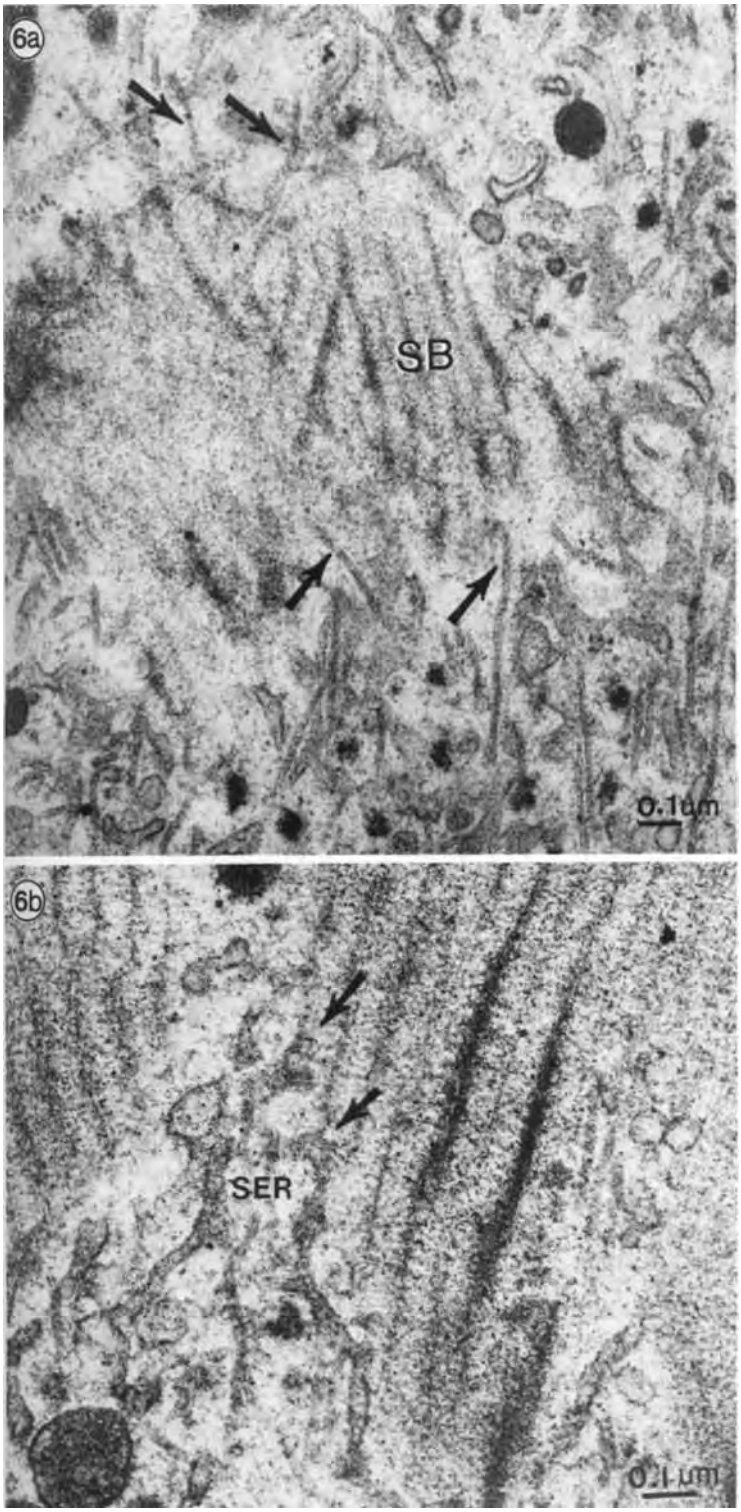

Fig. 6. Sections parallel to the reticular lamina through two inner hair cells. The striated body (*SB*) is associated with microtubules (*arrows*, 6*a*) projecting into the cytoplasm just under the cuticular plate. The striated body is also seen associated with the smooth endoplasmic reticulum (*SER*) and elaborations of the SER appear to merge with the electron-dense band (*arrows*, 6*b*).

inner hair cell serially sectioned, but they have never been observed in outer hair cells of these animals.

The presence of the striated body in every inner hair cell examined in normal chinchillas, and in squirrel monkeys and cats, indicates that they are a normal structural component of these cells. They are not an indication of cell injury or metabolic change resulting from trauma, disease, drug intoxication or old age. Striated bodies have not been previously reported in the chinchilla hair cells probably because their detection requires the observation of serial sections. When it exists as a thin band lining the cuticular plate it is very difficult to detect. It is most easily seen when the inner hair cell is sectioned parallel to the reticular lamina. When scanning radial sections or tangential sections at low magnification, it appears only as dense spots or dense bands. Such dense spots and dense bands may be found in micrographs of inner hair cells from animals of various species and in some cases their presence has been noted (Flock, 1965).

The role that the striated organelle plays in the inner hair cell is not known. However, since mechanical stimulation of the stereocilia appears to be the first step in the transduction process (Davis, 1965; Hudspeth & Jacobs, 1979), the presence of the striated organelle in the infracuticular plate region, just below the area of insertion of the rootlets of the stereocilia into the cuticular plate, may be of some significance. The striated organelle could play a passive role in maintaining the cytoarchitecture of the inner hair cell. It might also play an active role by controlling the interaction of contractile proteins, by actually contracting or by spatially organizing contractile proteins so that the resulting contraction occurs in a specific direction. Analysis of the morphology and characteristic location of the striated organelle within the cuticular plate, as well as comparison of the striated organelle with similar striated structures that have been observed in other systems may reveal its function.

The location of the striated organelle below the area of insertion of the stereocilia suggests that the striated organelle could anchor the rootlets of the stereocilia in the cuticular plate. Its association with the electron-dense material at the periphery of the cell suggests that it could attach the cuticular plate to the cell membrane. In this manner, the striated organelle would aid in maintaining the integrity of the reticular lamina.

However, the association of the striated organelle with microtubules, mitochondria and smooth endoplasmic reticulum suggests it may play an active role. The appearance of the striated organelle and its association with a membrane system thought to release and sequester calcium (Henkert et al., 1978) is reminiscent of the contractile apparatus in striated muscle, although in the striated body the organization of the components is less complex. Striated structures have also been seen in other systems: leptomeric organelles in striated muscle attached to the Z-line material of the sarcomeres (Karlsson et al., 1968), cross striated ciliary rootlets (Matsusake, 1971) and rhizoplasts (Salisbury & Floyd, 1978), and striated microfilament bundles in smooth muscle (Ashton et al., 1975) and non-muscle (Goldman et al., 1979) cells. These are attached to the cell membrane and some contain muscle-like contractile proteins. They are thought to play an active role in contraction especially of the cell periphery since they are in a position to deform the cell membrane.

In the inner hair cell, the presence of the striated organelle may indicate that there is an area in the apical region of the cell where the randomly oriented cuticular plate filaments are organized. This may be similar to the terminal web region in brush border cells of the intestine where cytoplasmic filaments located below the microvilli display a high degree of structural organization (Hull & Staehelin, 1979). The sensory cells of the ear are morphologically similar to these cells. Like the brush border cells which have actin filaments in the microvilli and terminal web, the sensory cells

of the inner ear have stereocilia containing actin (Flock & Cheung, 1977), and actin filaments projecting from the cell membrane across the apical end of the cell (Flock, 1979). The polarities of the actin filaments in the hair cells are the same as those in the microvilli and terminal web (Flock & Cheung, 1977; Flock, 1979).

In the terminal web, peripheral and microvillar membrane associated actin filaments interact with myosin monomers and two types of contraction have been experimentally induced: a shortening of the microvilli (Mooseker, 1976), and a circumferential pinching in of the apical part of the cell (Rodewald et al., 1976). Anatomical evidence has shown that a similar circumferential contraction may occur at the level of the cuticular plate in the inner hair cells of the chinchilla cochlea (Slepecky et al., 1980), causing the apical surface of the inner hair cell to bulge into scala media and the stereocilia to fan out into the endolymph. Since this phenomenon and the striated organelle have been observed only in the inner hair cells, perhaps they are related. It may be significant that in the region immediately below the stereocilia, the most consistent orientation of the dense bands creating the cross striations is in the radial direction. If the dense bands are analogous to Z-lines and the actin filaments in the infracuticular plate region are oriented perpendicular to them and antiparallel in a manner similar to the organization of contractile proteins in striated microfilament bundles (Ashton et al., 1975; Begg et al., 1978) and myofibrils, then contraction would occur in a longitudinal direction.

The occurrence of the striated organelle in inner hair cells may be one indication of a functional difference between inner and outer hair cells. Its proliferation and change in location under pathological conditions, as noted by other investigators, should probably be accompanied by alterations in sensitivity to stimuli. Further analysis of the striated organelle under normal and pathological conditions may help us to define its role.

ZUSAMMENFASSUNG

Quergestreifte Organellen, „striated organelles" wurden regelmäßig in elektronenmikroskopischen Aufnahmen von Serienquerschnitten der inneren Haarzellen von normalen Chinchillacochleae beobachtet. Die quergestreifte Organelle befindet sich in der infrakutikulären Plattenzone. Sie bedeckt die kutikulären Platte und Richtung, Muster and Periodizität der Querstreifen ändern sich über deren Länge. Die quergestreifte Organelle wird in enger Verbindung mit der Plasmamembrane, dem endoplasmiatischen Reticulum, den Mikrotubuli und Mitochondrien beobachtet. Die quergestreifte Organelle spielt möglicherweise eine aktive Rolle in der Funktion der inneren Haarzelle und ihre Wucherung unter pathologischen Bedingungen kann, wie von anderer Seite beobachtet wurde, von Veränderungen in der Sensitivität der inneren Haarzelle gegenüber Anreizen begleitet sein.

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