A freeze-fracture study of the skate electroreceptor

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Summary

The sensory epithelium lining the ampulla of Lorenzini in the skate was examined by the freeze-fracture technique. Anastomosing tight junctions (zonula occludens) completely encircle the apex of each receptor cell joining it to neighbouring support cells. The tight junctions separate two distinctly different regions of the receptor-cell surface. The apical P-face has numerous large particles while just below the tight junctions of the lateral surface have many smaller particles. On its basal surface each receptor cell makes several evaginating ribbon synapses with an afferent nerve. Three regions of the synaptic evagination can be distinguished on the basis of membrane specializations: 1. At the tip of the evagination a regular array of large particles is found on the P-face of the receptor cell directly opposite a similar regular array of large particles on the P-face of the afferent nerve; 2. just above the tip at a narrow constriction, below which vesicles are not found, a population of large particles on the P-face of the receptor cell opposes a well-defined strip of large particles that cleaves with the E-face of the nerve fibre; 3. at the arch of the synaptic evagination randomly occurring dimples are found on the P-face and protrusions on the E-face of the receptor cell. The density of these protrusions increased in skates that were electrically stimulated. We suggest that the co-extensive arrays of particles at the tip of the ribbon synapse is an intercellular junction; that the active zone of the synapse is at or above the constriction; and that membrane retrieval occurs in the synaptic arch region.

Introduction

In 1678 Lorenzini first described the long jelly-filled canals that open on the surface of sharks, rays and skates, and terminate in ampullae. It has only recently become clear that the ampullae of Lorenzini endow elasmobranchs with an acute sensitivity for ambient electric fields; for example, skates respond to field gradients as low as 10 nV/cm

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(Kalmijn, 1966, 1974; Bullock, 1982). The sensory receptors in the ampullae that are responsible for electroreception are specialized neuroepithelial hair cells, similar in origin to mechanoreceptors in the vertebrate lateral line organ, vestibular apparatus and cochlea, and to the photoreceptors in the vertebrate retina (Szabo, 1974). Among these sensory organs, the ampullae of Lorenzini have perhaps the simplest anatomical organization.

Ampullae are grouped together within capsules of connective tissue just under the skin. Each ampulla consists of a cluster of 5–10 pouches or alveoli, the walls of which are lined by an epithelium of interdigitating receptor cells and supporting cells. The apical surface of each receptor cell, which faces the lumen of the canal, bears a single kinocilium and is specialized for sensory transduction; the basal surface makes several synapses on an afferent fibre of cranial nerve VIII. A typical ampulla may contain around 10 000 receptor cells and receive innervation from about 10 nerve fibres.

The afferent synapses of electroreceptors contain ribbons of fuzzy material. Ribbon synapses are also found in vertebrate photoreceptors and collections of dense presynaptic material are associated with synaptic vesicles in a variety of acoustico-lateralis receptor cells (Osborne, 1977; Saito, 1980). The morphological similarities among these synapses suggest that they rely on similar synaptic mechanisms.

Electroreceptor cells have been extensively studied in a variety of species with light and electron microscopy (Dotterweich, 1931; Barets & Szabo, 1962; Waltman, 1966; Derbin, 1970; Szabo, 1972). This is the first study of an electroreceptor using the freeze-fracture technique; a preliminary report was presented previously (Sejnowski & Yodlowski, 1978). (See also Akert *et al*., 1980.)

Materials and methods

Nine skates (*Raja erinacea* and *Raja oscillata*) with fin spans of 20–30 cm were caught off the shore of Woods Hole, Massachusetts during the summer and kept briefly in an aquarium with circulating seawater at room temperature. Each animal was pithed before being transcardially perfused with fixative consisting of 2% paraformaldehyde and 3% glutaraldehyde in elasmobranch Ringer (200 mM urea, 200 mM NaCl, 200 mM sucrose, 20 mM $NaHCO_3$, 5 mM KCl, 8 mM $CaCl_2$, 0.5 mM $MgCl_2$, buffered with 30 mM NaHEPES at pH 7.3). One animal was anaesthetized with MS-222 before pithing. After 2–3 h of fixation the hyoid capsules were removed from the skate and individual ampullae were dissected from the capsules.

To prepare the tissue for freeze-fracturing, ampullae were soaked in elasmobranch Ringer containing 30% glycerol for 1–2 h, cut with a tissue chopper into 200 μm slices, mounted on gold discs and frozen in Freon 22 slush. The tissue was fractured with either a knife or in a complementary replica holder, and replicated at $-120°$ C on a Balzers 360M apparatus fitted with an electron beam gun for platinum shadowing and a quartz crystal monitor for standardizing the replica thickness. The replicas were cleaned in Purex bleach for 1h, rinsed in dilute acetic acid, mounted on grids coated with Formvar and carbon, and examined in an AEI 6B electron microscope or a JEOL 100-S electron microscope. The negatives were photographically reversed before being printed so that the platinum deposits appear white and the shadows are black.

To prepare tissue for thin-sectioning, fixed ampullae were thoroughly rinsed in elasmobranch

Ringer, postfixed with 2% OsO_4 in sodium barbital buffer, washed in sodium acetate buffer, stained with 0.5% uranyl acetate in sodium acetate buffer for 12 h, dehydrated in a graded series of methanol, and embedded in Araldite. Thin sections were cut, mounted on grids, stained with lead citrate for 2 min, and examined with an AEI 6B electron microscope.

Four skates were electrically stimulated following pithing. A Grass stimulator was used to deliver 0.5 V square pulses at 5 Hz for 5 min between the head and the tail while the animal was in a shallow pool of seawater. In one experiment the nerve from a hyoid capsule was monitored with a hook electrode and a Grass P-16 amplifier to verify the effectiveness of the stimulation. Control skates were prepared under identical conditions but left for 5–30 min without stimulation before fixation.

Results

Apical surface

Only the very apex of the receptor cell faces the lumen of the canal (Fig. 1). When exposed by freeze fracture the lumenal surface shows the supporting cells arranged in a polygonal pattern. The apical surface of each receptor cell protrudes, like an island, near the edge of a single supporting cell (Fig. 2). The supporting cell wraps around the receptor cell and forms a short border with itself between the receptor cell and the lateral boundary of an adjacent supporting cell. A kinocilium, seen in thin section (Fig. 1) and cross fracture (Fig. 4), arises from each receptor cell. Each supporting cell has a protruding rosette on its P-face, which could be the basal body of a cross-fractured cilium. In addition, the borders of the supporting cells are lined with numerous cross-fractured microvilli.

When the supporting cell is fractured away from the receptor cell, anastamosing tight junctions are seen to completely encircle the receptor cell near its apical surface (Fig. 3). The P-face of the receptor-cell apical plasmalemma, which faces the lumen, has fewer but larger particles, approximately 10 nm in diameter, than the lateral plasmalemma below the tight junctions (Fig. 3). The P-face of the receptor cell within and immediately around the tight junctions is free of particles.

Basal surface

Each receptor cell makes several synapses with an afferent nerve fibre; each synapse has a synaptic ribbon which forms the core of a flat process evaginating the postsynaptic nerve fibre (Fig. 5). The ribbon is covered with synaptic vesicles up to a constriction just above the tip of the synaptic evagination. When freeze fractured, the ribbon material can be identified as a double row of large particles adjoining vesicles that appear with either their convex E-faces or concave P-faces (Figs. 6, 11).

Flat processes, like interposing fingers, extend out from the supporting cells to separate the presynaptic and postsynaptic cells at the insertion of the synaptic evagination (Fig. 5). Dimples are commonly seen on the P-face of the receptor cell in the region overlying the supporting cell, which we call the synaptic arch (Figs. 7, 10). Protrusions are often found on the E-face of the synaptic arch that are complementary to

the dimples seen in the corresponding P-face (Fig. 11). The P-face of the receptor cell in this region has a high concentration of small particles similar to those found below the tight junctions (Fig. 3) while the E-face is relatively free of particles (Fig. 11).

Receptor cells of the electrically stimulated skates usually contained more protrusions and dimples at the synaptic arches compared with the receptor cells of unstimulated control skates. Protrusions were counted on the E-faces of synaptic arches, such as that shown in Fig. 11, and were normalized by the longitudinal distance along the synaptic ribbon. Only 2–5 protrusions/μm were found on the synaptic arches of control animals, whereas the arches of stimulated animals had 10–15 protrusions/μm.

The receptor cell membrane at the tip of the evagination has a rectilinear array of large particles that cleave almost exclusively with the P-face (Figs. 7, 8) and leave complementary imprints on the E-face (Fig. 9). Both the imprints and particles are spaced about 10 nm apart and the rows are tilted at 45° to the axis along the tip. Just above this highly organized tip region is a second type of particle array composed of somewhat larger particles that are less concentrated and less ordered than at the tip. These particles cleave more often with the P-face (Fig. 8).


Fig. 1. Thin section through the apical surface of a receptor cell (rc). A cilium (c) protrudes into the lumen of the canal, which is filled with mucous and extracellular material. A band of tight junctions (cut transversely here between the arrows) connects the receptor cells to surrounding supporting cells (sc). × 56 000.

Fig. 2. Freeze-fracture plane through the lumenal aspect of an ampulla revealing the P-faces of receptor cells (arrows) surrounded by supporting cells. Cross-fractured microvilli protrude from the borders of the supporting cells. A single protuberance arises from each supporting cell (circles) which may correspond with the basal body of a cilium. × 12 000.

Fig. 3. Freeze-fractured P-face of a receptor cell. Anastomosing tight junctions encircle the protruding apical surface (a) separating it from the basal surface (b) of the cell. A small portion of the supporting cell E-face remains adhering to the tight junction network (between arrows). The prominent strand of the double tight junction at the right is presumably where the supporting cell joins itself after encircling the receptor cell. × 76 000.

Fig. 4. The apical P-face of a receptor cell (rc) at high magnification. The kinocilium (c) on the receptor cell has been cross-fractured. Compare the large particles on the P-face of the receptor cell with the relatively fewer and smaller particles on the P-face of the neighbouring supporting cell (sc). A piece of the receptor cell has been fractured away (arrow) revealing a few strands of tight junction on the supporting cell. × 100 000.

Fig. 5. Thin section through a ribbon synapse between a receptor cell (rc) and the primary afferent nerve fibre (nf). Fingers from the supporting cells (sc) are inserted between the receptor cell and the nerve fibre beneath the synaptic arch. Coated vesicles and pits are found at the top of the synaptic arch (arrowhead). The ribbon is covered with synaptic vesicles except near the tip. In this vesicle-free region aggregates of dense material line the presynaptic membrane (black arrows). Postsynaptic dense material is found inside the nerve fibre lining the invagination and is particularly dense around the constriction above the tip (white arrows). × 167 000.
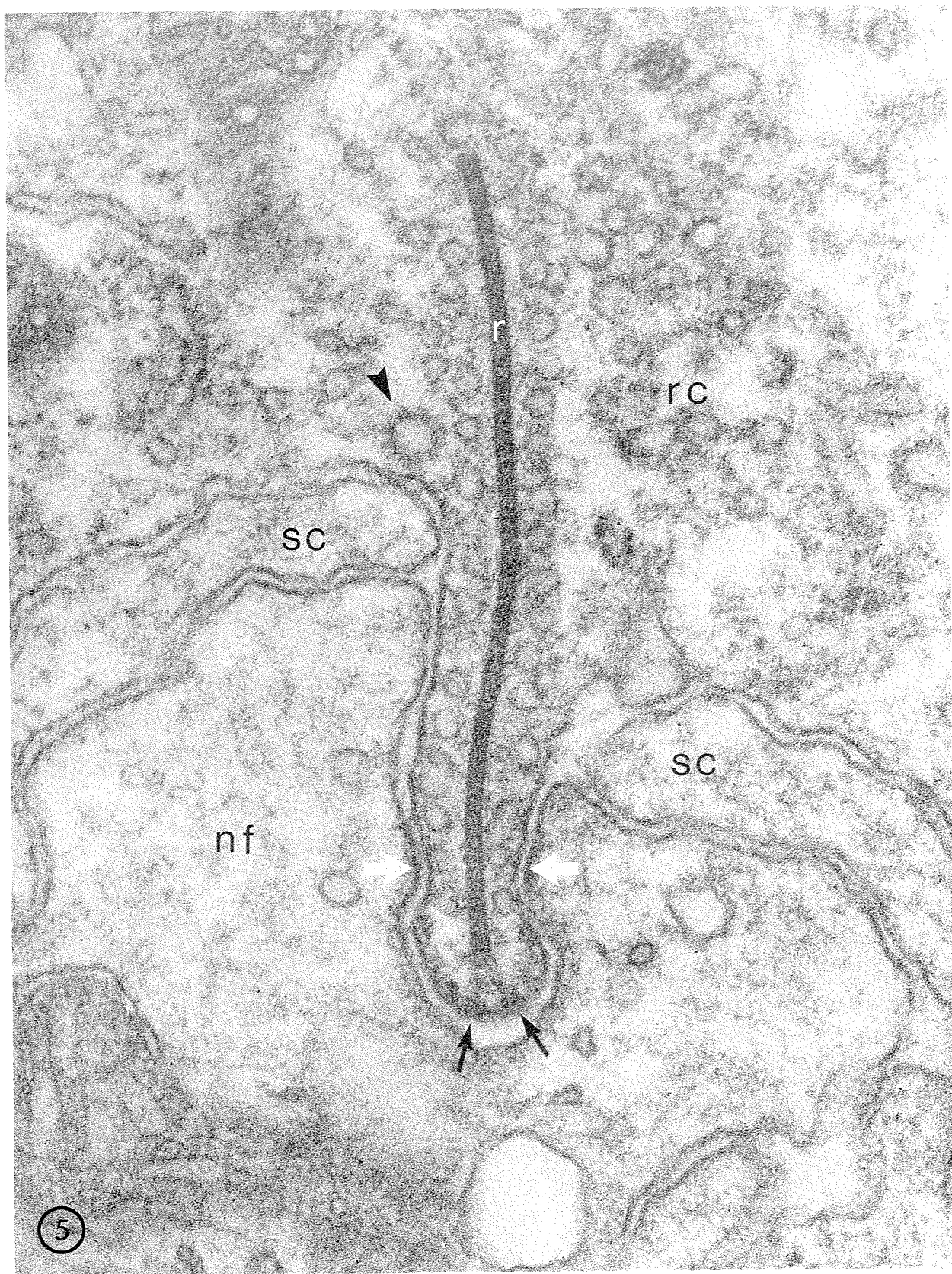
③

a

b

④

c

rc

sc

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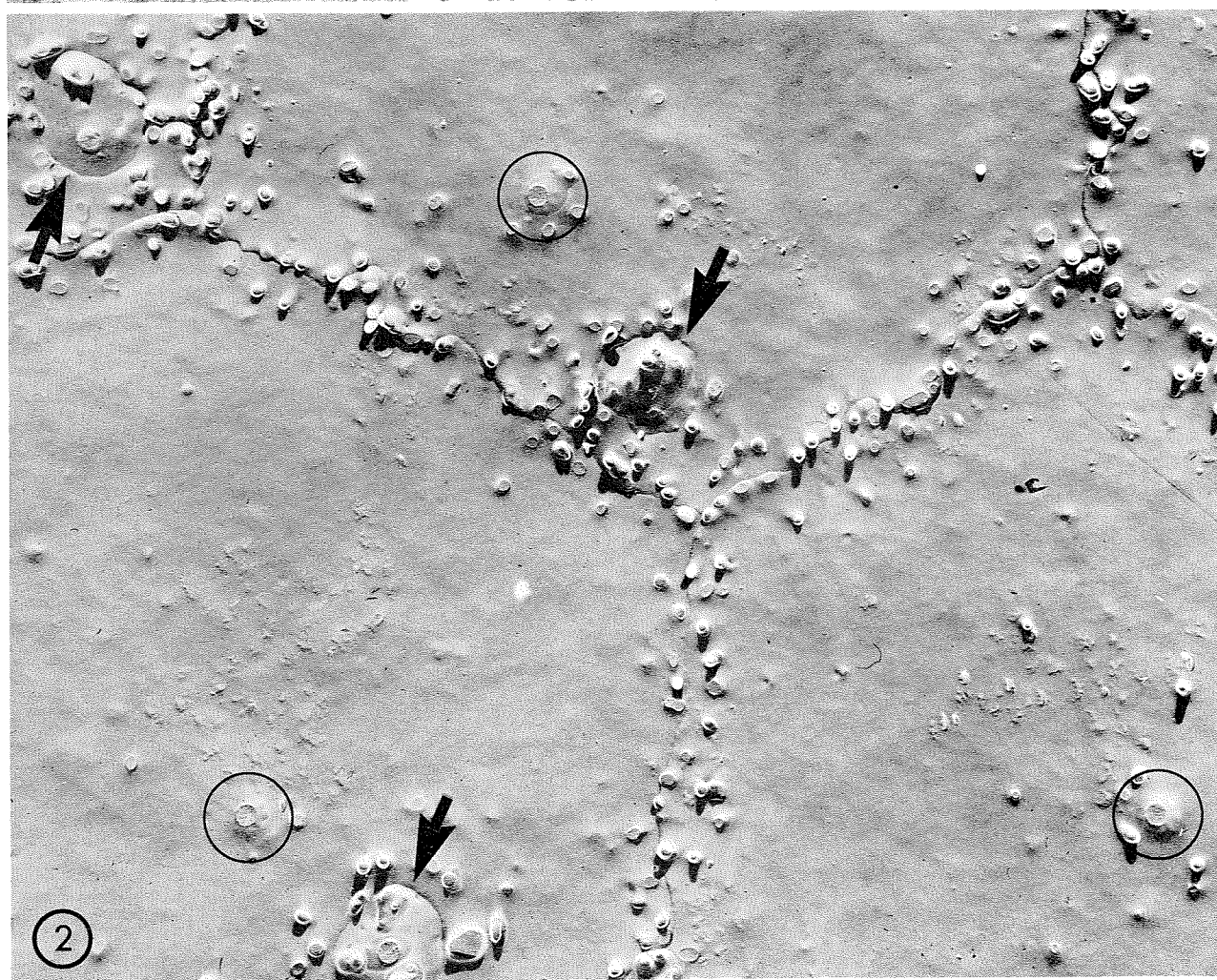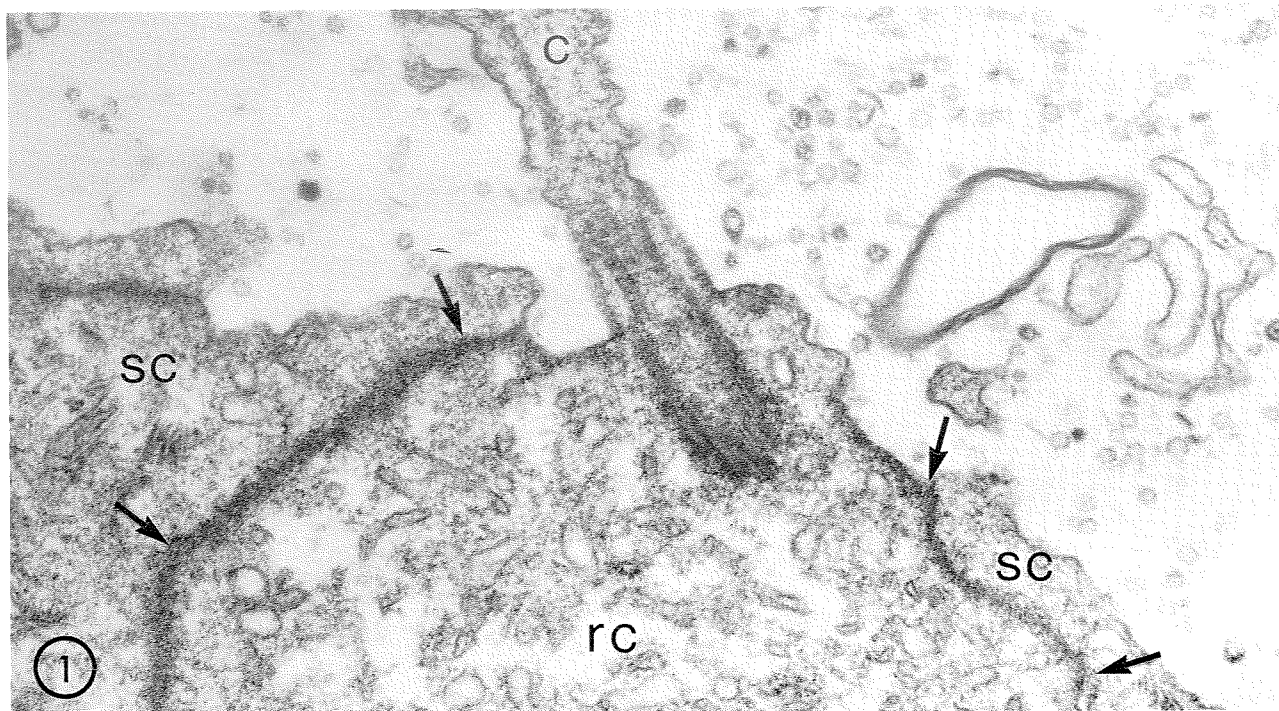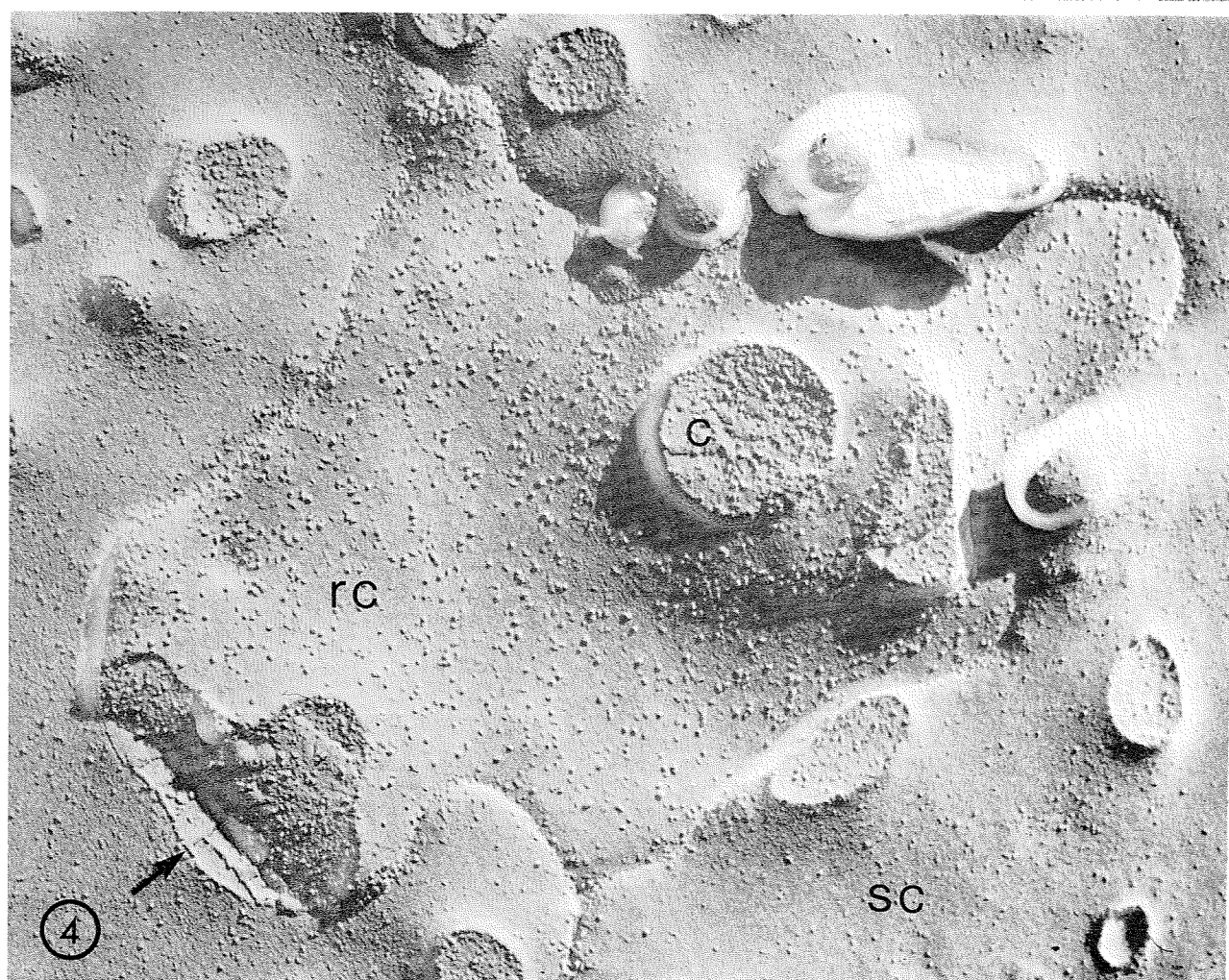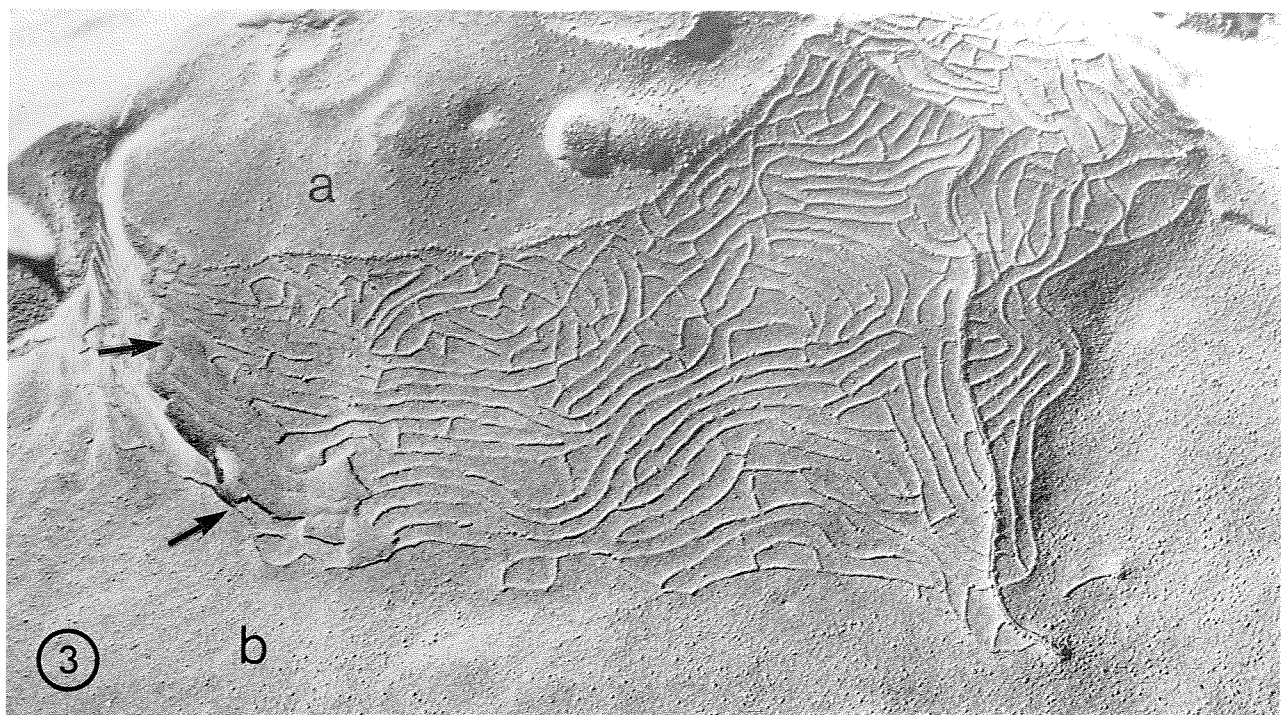
Fig. 6. Freeze-fracture through a ribbon synapse. Much of the receptor cell has been fractured away, exposing the evaginating process containing the ribbon (r) and synaptic vesicles and the E-face of the receptor cell membrane (EF). The postsynaptic nerve fibre (nf) is cross-fractured. A portion of P-leaflet of the nerve in the area opposed to the tip of the receptor evagination contains large particles packed in a regular array (arrows). × 133 000.

Fig. 7. Freeze-fracture of a synaptic evagination exposing the P-face (PF) of the receptor cell. The ribbon (r) within the invagination has been cross-fractured. Numerous large particles are packed in a regular array along the tip (arrow). The membrane at the top of the synaptic arch, like that of the rest of the basal and lateral receptor-cell surface, is characterized by many small particles and several dimples (arrowheads). × 83 000.

Fig. 8. Higher magnification of the P-face (PF) of a receptor cell at the tip of an evaginating process. Large particles are packed into a tight rectilinear array (arrows). Moving laterally from the tip the large particles become progressively less numerous and less ordered. × 150 000.

Fig. 9. High magnification of the presynaptic region showing the E-face (EF) of the receptor cell at the tip of the evagination. Very few particles are visible but particle imprints and striations mark the tip of the evagination. This view includes a very short segment of cross-fractured cytoplasm in the evaginating process. × 150 000.
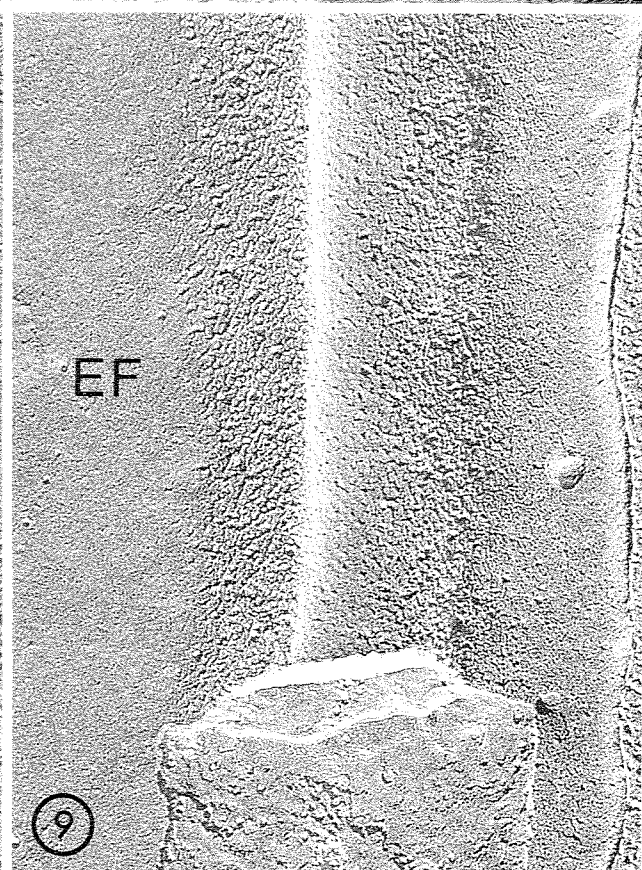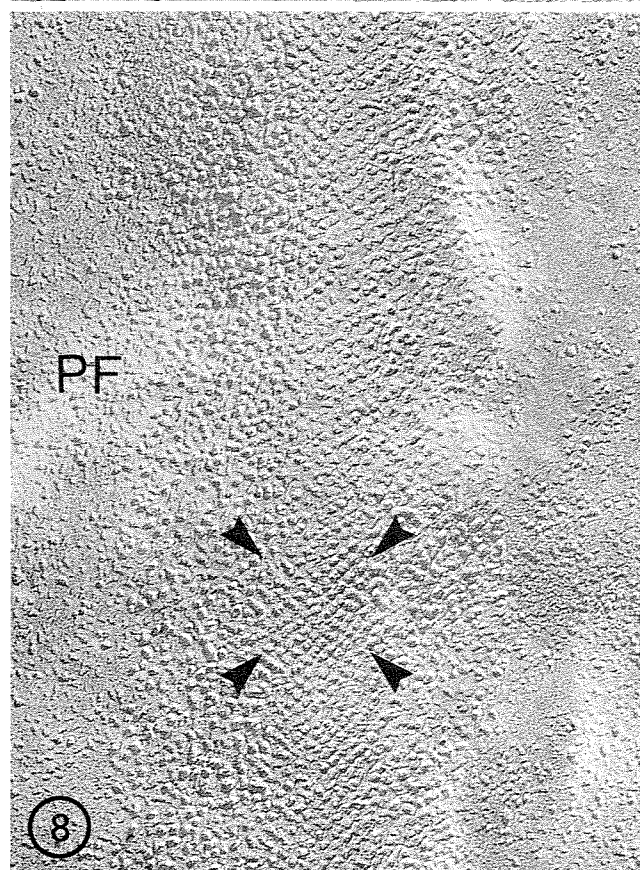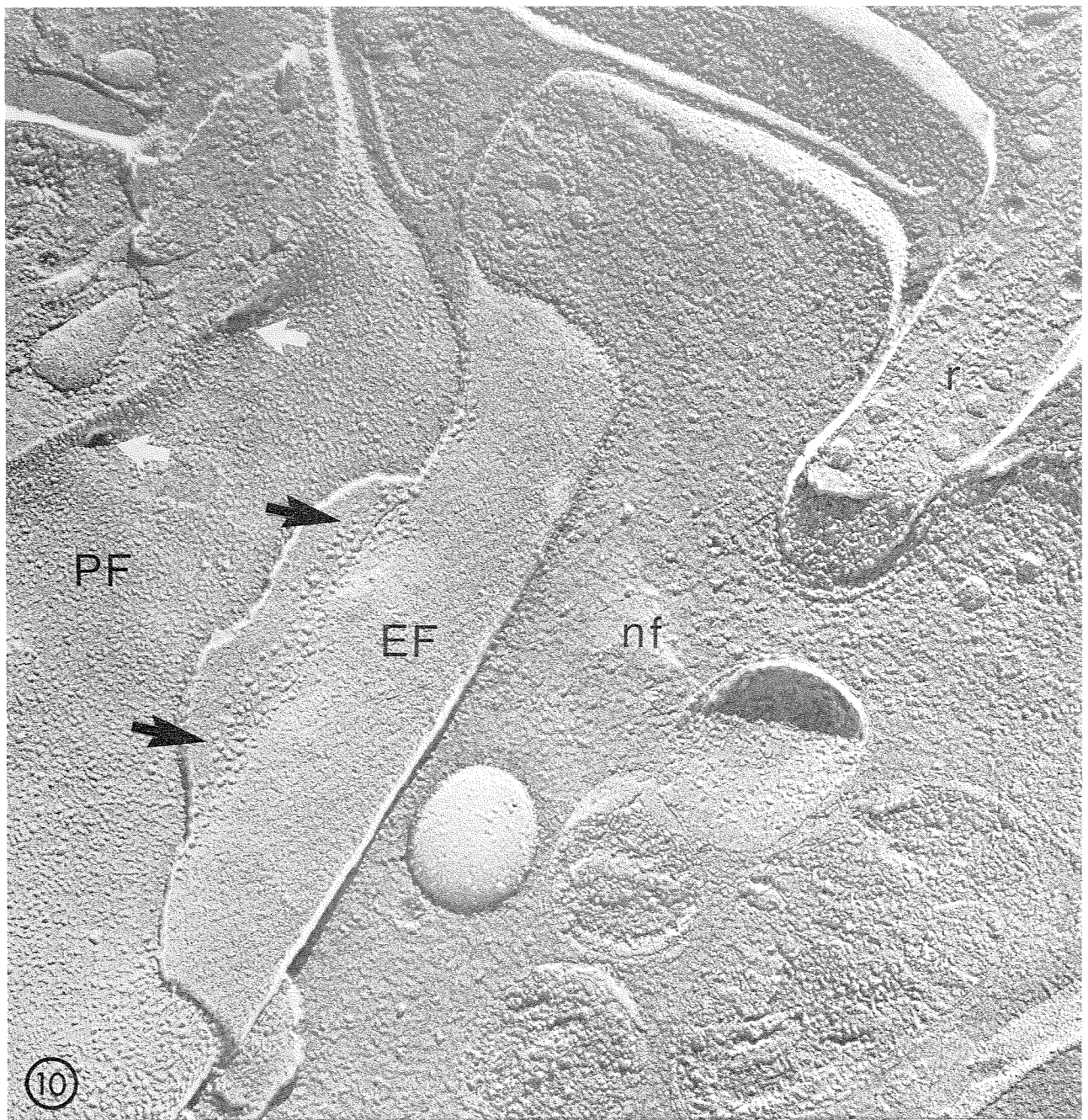
Fig. 10. Two ribbon synapses arising from the same receptor cell innervating the same cross-fractured nerve fibre (nf). The ribbon on the right (r) lies inside a cross-fractured evagination. A fragment of the E-face (EF) of the postsynaptic nerve fibre remains attached to the other synapse to the left. A strip of large particles appears along the constriction above the tip of the invagination (black arrows) and striations are visible below the constriction. Note also the dimples (white arrows) on the P-face (PF) of the receptor cell. Photograph provided by Dr John Heuser. × 133 000.
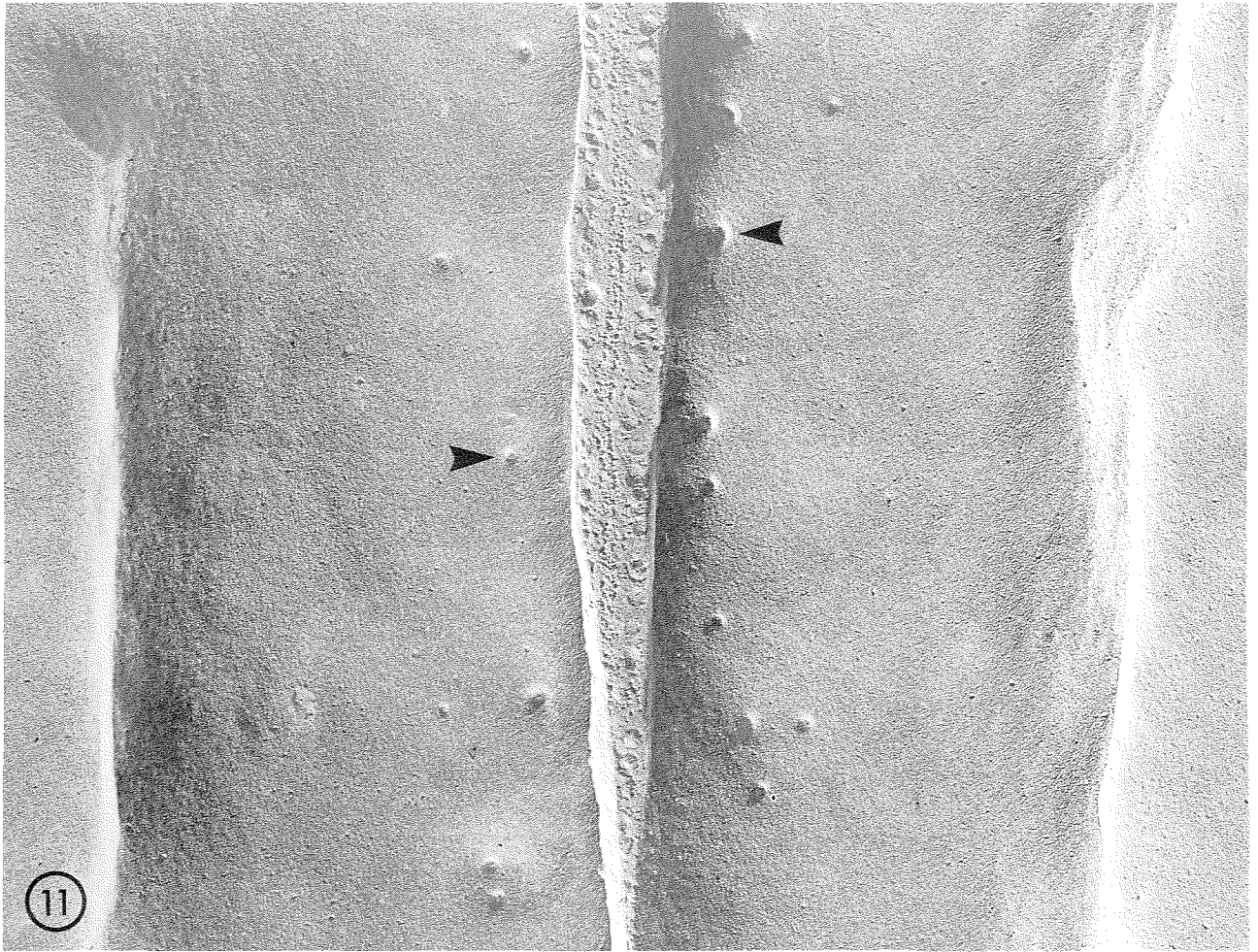
Fig. 11. Cross-fractured ribbon and E-face of a receptor cell at the top of the synaptic arch after electrically stimulating the skate. Numerous protrusions (arrow heads) lie along the synaptic arch; these may correspond to necks of vesicle openings. × 83 000.

Afferent nerve

The postsynaptic nerve fibre at the bottom of the invagination has a tight rectilinear array of large particles on its P-face (Fig. 6) similar to that found on the opposing P-face at the tip of the receptor cell (Fig. 7). The corresponding E-face of the nerve fibre at the tip has a complementary striated texture and few particles (Fig. 10). The rows of particles and the striations are about 10 nm apart and tilted at 45° to the axis along the tip. A narrow, well-defined strip of irregularly-spaced particles 8–10 nm in diameter is found on the E-face of the nerve fibre adjacent to the constricted neck of the evaginating receptor cell (Fig. 10).

Discussion

In order for an ampulla to detect microvolt signals at the opening of a long canal many centimetres away, the walls of the canal and the surface of the sensory epithelium must have a very high electrical resistance. Electrical isolation is provided by an extensive system of tight junctions between epithelial cells of the canal and between supporting and receptor cells of the ampulla (Waltman, 1966). The freeze-fracture view of receptor cells confirms the evidence from thin sections that the network of tight junctions is continuous and therefore completely encircles the apical surface (Fig. 3). Complete anastomotic networks of tight junctions are also found between other epithelial cells (Staehelin, 1974), including hair cells in the organ of Corti (Gulley & Reese, 1976).

It has been suggested from physiological experiments on skate ampullae that voltage-sensitive channels on the apical surface of the receptor cell contribute to its high electrical sensitivity (Obara & Bennett, 1972; Clusin *et al.*, 1975; Clusin & Bennett, 1977a,b, 1979a,b; Bennett & Clusin, 1979). The tight junctions which electrically isolate the apical from the basal surface of the electroreceptor also separate two regions of membrane with distinctive particle organization. The relatively homogeneous population of large particles found on the apical surface of the receptor may represent the channels that carry the currents observed physiologically, and the tight junctions may contribute to confining these channels to the apical surface; this is regarded as an important function of tight junctions in many epithelial cells (Dragsten *et al.*, 1981).

The intramembrane particles that are found in freeze-fractured ribbon synapses of receptor cells in the skate ampulla of Lorenzini are summarized in Fig. 12. Large particles in regular arrays are co-extensive on the P-faces of both the receptor cell and the nerve fibre at the tip of the evagination. Similar arrays of particles are found at the tips of ribbon synapses in vertebrate photoreceptors (Raviola & Gilula, 1975). The synapses in unstimulated receptor cells of both the retina and the ampulla of Lorenzini are tonically active; for example, some nerve fibres from ampullae have resting firing rates of 20–50/sec (Murray, 1962). In cone cell endings of the turtle retina the surface area of the presynaptic membrane is considerably decreased in the light-adapted state when the ribbon synapses are less active (Schaeffer &Raviola, 1978). The symmetry of the particle specializations at the tip of a ribbon synapse suggests that they are junctions between the receptor and the nerve, perhaps serving to anchor the presynaptic and postsynaptic membranes.

Two other types of intramembrane specializations oppose each other across the synaptic cleft immediately lateral to the tip. The large particles that cleave mainly with the presynaptic P-face are similar to the presynaptic P-face particles that are believed to mediate Ca^{2+} entry at other synapses (Pumplin *et al.*, 1981). In a highly restricted region opposite the narrow constriction of the presynaptic cell, ordered aggregates of large particles are found on the E-face of postsynaptic nerve fibres. Neurotransmitter receptor molecules at excitatory synapses often cleave with the E-face of the postsynaptic membrane (Landis *et al.*, 1974; Landis & Reese, 1974; Franzini-Armstrong, 1976; Rheuben & Reese, 1978). The locations of the particle specializations in the presynaptic and postsynaptic membranes together with the observation that synaptic vesicles are
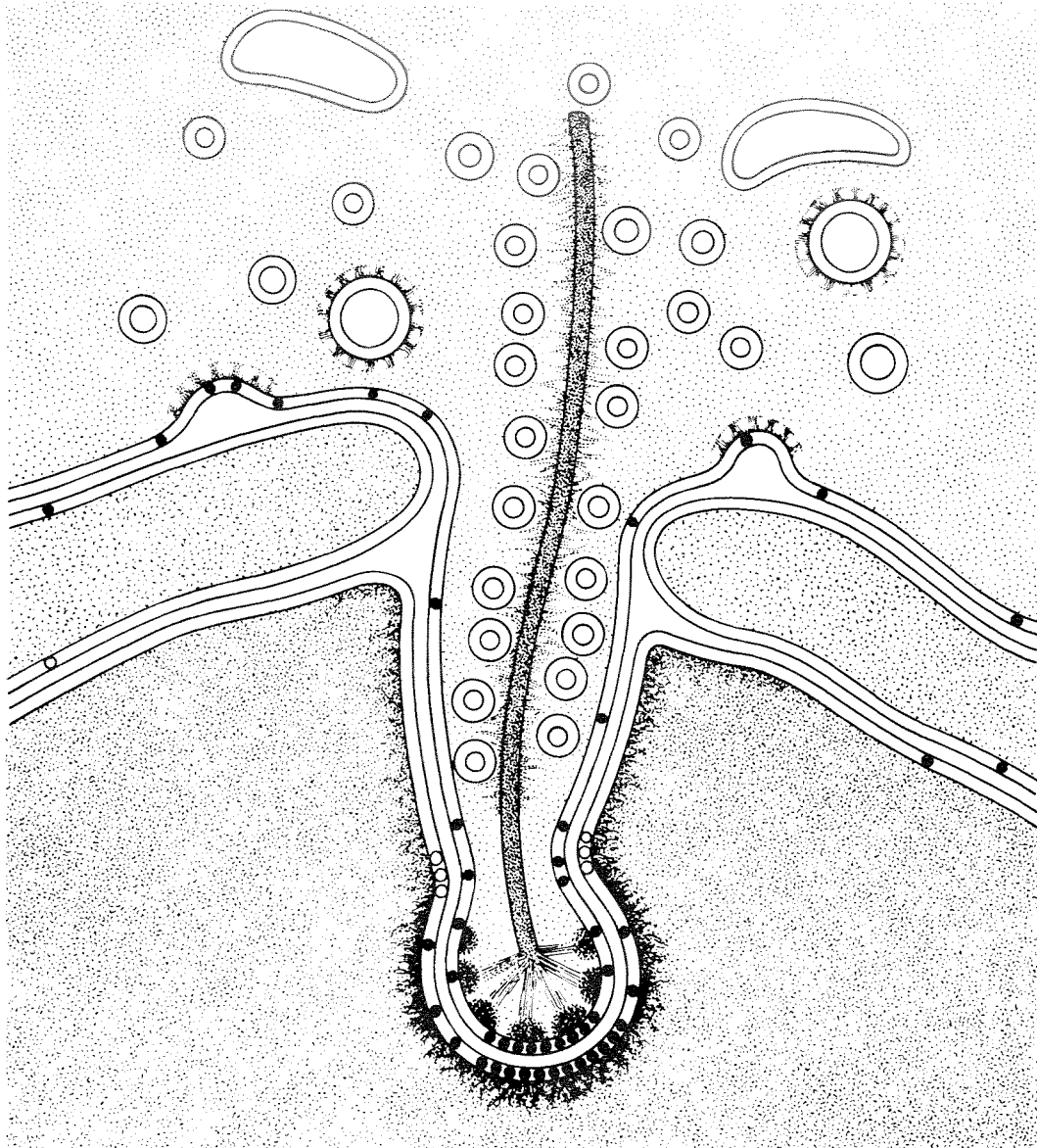
Fig. 12. Summary of principal features and intramembrane particle specializations at a skate electroreceptor ribbon synapse. Particles appearing on the P-face of a membrane are shown as solid circles and E-face particles as open circles.

found above the constriction but not below indicate that the active zone of the synapse is probably at or above the constricted region.

The large dimples in the P-face and protrusions on the E-face of the receptor cell commonly found near the top of the synaptic arch probably represent sites where vesicles are joined to the membrane. This part of the synapse is unlikely to be part of the

active zone since transmitter molecules released at these sites would be prevented by interposing supporting cells from quickly reaching the postsynaptic nerve fibre. Coated vesicles are commonly found at many synapses where membrane retrieval occurs (Heuser & Reese, 1977); the association of coated vesicles with the top of the arch in thin sections suggests that the dimples and protrusions represent sites of membrane budding rather than vesicle fusion.

Evidence from freeze-fractured ribbon synapses in skate electroreceptors suggest three specialized regions: an intercellular junction at the tip of the evagination, an active zone lateral to the tip, and membrane retrieval at the synaptic arch. The same sequence has recently been proposed for ribbon synapses in the turtle retina (Schaeffer *et al.*, 1982). One difference between the freeze-fracture images of the two ribbon synapses is the E-face protrusions found along the active zones of cone pedicles, which were interpreted as images of exocytosis of synaptic vesicles. We have not found images of vesicle exocytosis at ribbon synapses in skate electroreceptors and have not made measurements to see if there is an increase in the number of large particles following stimulation (Heuser & Reese, 1979, 1981). Our identification of the active zone is therefore provisional. The study of membrane dynamics at sensory synapses is at a relatively early stage; the homogeneity and high frequency of synapses in the ampulla of Lorenzini make it an attractive preparation for further investigation.

Acknowledgements

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