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Unusual Retinal Cells in the Dolphin Eye

Abstract. *By comparison to the cellular constituents of the retinas of certain other diving mammals, the elements of the dolphin retina include an unusually large number of specialized cells. Both cone and rod receptors may be identified. An unusual amacrine cell may be seen which produces a process that spans the cells between the inner plexiform and outer plexiform layers. Most unusual is a layer of giant ganglion cells which appears to serve most of the central retina. The giant ganglion cells support giant dendrites and optic nerve fibers which range up to 8 micrometers in diameter.*

Specialization of the auditory system of the bottlenose dolphin (*Tursiops truncatus*) has been established by research of the last two decades (*1*). But the visual system is not well described. Opinions on generalized cetacean visual capabilities are diverse. Rochon-Duvigneaud surveyed the eye anatomy of several species and concluded that function must be very limited (*2*). In contradiction, Mann has reported cone receptors (indicative of color vision and high resolution) in the whale (*Balaenoptera*) and proposed a mechanism that would correct for the optical problems which confront eyes used in both air and water (*3*). A recent evaluation of visual acuity of the Pacific dolphin (*Lagenorhynchus*) which showed thresholds of about 6 minutes of arc does not necessarily confirm the presence of a duplex (rod and cone) retina (*4*).

Similar acuity thresholds have been reported in the California sea lion (*5*), in whose retina we were able to find only rod receptors (*6*). Recently we have examined a limited supply of well-preserved eyes from Atlantic bottlenose dolphins, where retinas are structurally similar to those of terrestrial mammals such as dogs and cats (*7*), except that cones were found to be more plentiful and highly specialized. Amacrine and ganglion cells were numerous.

Eight eyes were quickly removed from dolphins killed for humane reasons by intracardial injection of pentobarbital. The eyes were opened, fixed in 4 percent buffered glutaraldehyde, and stained by the method of Golgi (*8*), hematoxylin and eosin, or silver techniques. Figure 1 shows a section of dolphin retina stained by Golgi technique. In the upper center is a typical cone outer segment, ellipsoid and cell body. Lateral to the cone outer segment are unstained, long filamentous structures that are probably rod outer segments, which we have seen stain occasionally by Golgi process. On the extreme right, in the receptor layer, are other bulbous structures which may be unstained cone outer segments. To the left is a large matrix of Müller cell fibers which have been stained heavily and obscure parts of several other receptors. In Fig. 2 are cells in the inner plexiform layer with characteristic lateral processes of amacrine cells. However, these cells also have processes that penetrate through the bipolar cell layer and terminate in the outer plexiform layer. In some thick sections, we have been able to follow these apical processes for 60 to 100 μm in the outer plexiform layer. Most frequently, the apical process terminates (as in Fig. 2) in a densely stained area. Therefore it is not possible to state that all such cells in the dolphin retina have extensive ramifications in the outer plexiform layer. Considering the general infrequency of staining of specific cell types by the Golgi technique, it is probable that this cell is common in the dolphin's eye since several such cells have been seen in each eye we processed.

In Fig. 3 is a transverse section of retina, pigment epithelium, and scleral tissue photographed through the interference contrast microscope (*8*). Although the tissue is unstained, all layers of the retina may be identified. This low magnification photograph shows several of the giant cells in the ganglion cell layer. The size and frequency of giant ganglion cells is the major difference between this and retinas of other mammals. The giant cell bodies range up to 150 μm in diameter and appear to predominate in the central 40° of retina. Most giant ganglion cells give rise to large dendritic processes and large optic nerve fibers. Both dendrites and axons may be seen in Fig. 3. The giant axon diameters range up to 8 μm and form a very thick nerve fiber layer. Even in thick sections, interference microscopy allows visualization of the cell body details including the nucleus and the nucleolus, which is seen as a central depression in the cells in Fig. 3. Less spectacular ganglion cells range down to cell body diameters in the 6 to 12 μm range. Occasionally, these cells stain by the Golgi technique. However, we have never seen a "giant cell" which had been silver stained. The smaller ganglion cells appear infrequently, interspersed below the giant cells which lie one against another forming a tightly packed pad of cells which is seen as the focal plane of the interference microscope varied throughout the 75 μm sections. Unusually large cells were seen occasionally in the inner plexiform layer. Their diameters were around 20 μm.

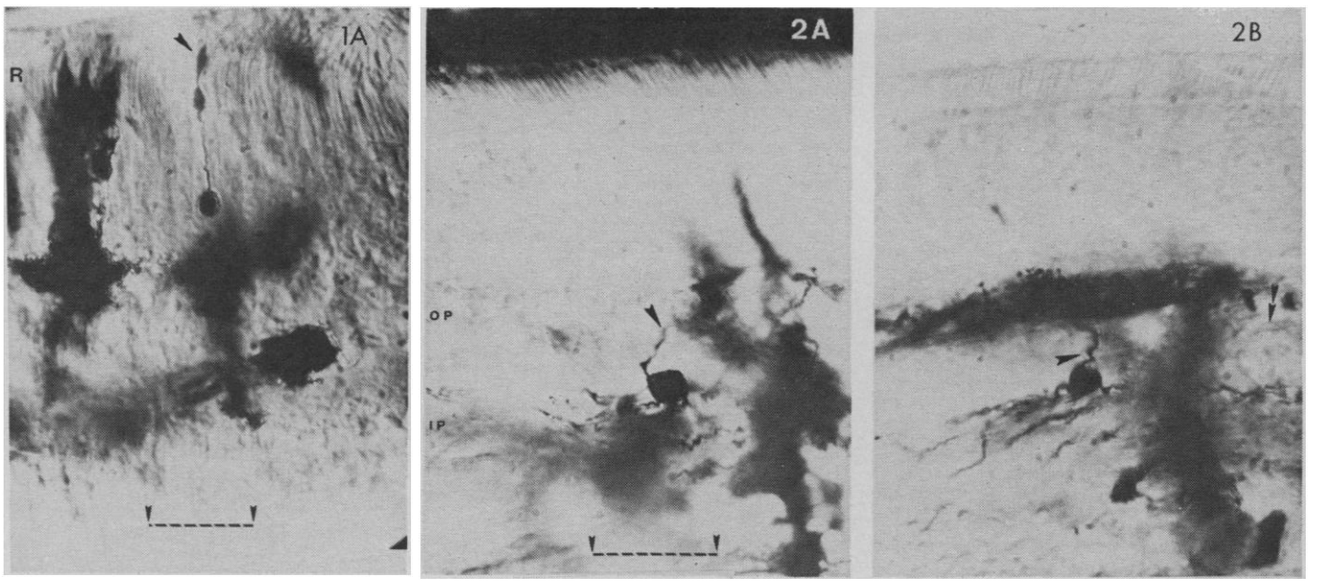

Fig. 1. Cone outer segment (marked by arrow) ellipsoid and cell body surrounded by stained Müller's fibers. Unstained rod outer segments may be seen in the receptor layer (*R*). Irregularities in the receptor layer (far right) are unstained cone outer segments among rods. Other indications of receptor duplexity were seen in Golgi material as diffuse and compressed receptor cell terminals; Golgi-Kopsch method; interference-contrast (scale, 50 μm). Fig. 2. Interplexiform cells. Receptor outer segments are at top. Outer plexiform layer (*OP*) and inner plexiform layer (*IP*) lie above and below the interplexiform cells. These cells are from different sections of the same retina. (A) Outer process (marked by arrows) ended in a reticulum of stained Müller's fibers. (B) To the right of cell B (double arrow) is a displaced unstained giant cell; Golgi-Kopsch method; interference-contrast (scale, 50 μm).

An outline of one of these may be seen in Fig. 2B at the extreme right edge of the inner plexiform layer. We have not been able to view the terminals of these cells. Perhaps they are analogous to the displaced ganglion cells which have been described by Polyak (*9*).

The general comparative anatomy of the eyes of marine mammals has been summarized on several occasions. Much of this information has been clouded by the poor state of the tissue which was obtained from animals slaughtered for commercial purposes. The presence of cone visual receptors has been both denied and confirmed in cetaceans (*2, 3*). We have seen them regularly, in both Golgi stained tissue and hematoxylin and eosin stained tissue, and also as gross irregularities in the outer segment layer of unstained tissue viewed by interference contrast microscopy. Amacrine cells with processes spanning the bipolar cell layer have been reported infrequently (*9*), but only in terrestrial mammals. Recent sightings in cats and primates have been described by Gallego and Laties (*10*). These cells have been classified into two types. In the first type, the apical process expands only slightly in the outer plexiform layer as distinct to the "interplexiform" amacrine cells which have been named by Gallego (*10*). One common facet of reports on these cell types is the extreme rarity with which they are seen in Golgi stained material. According to Gallego, Cajal only reported a few such cells in hundreds of eyes. Therefore, our numerous observations on eight dolphin eyes suggest that this cell is relatively common. It is not possible to say whether all such amacrine cells in the bottlenose dolphin eye are of Cajal's "special" type without diffuse terminations in the outer plexiform layer of Gallego's "interplexiform" type, where several hundred micrometers may be spanned in this layer. Usually, the cells that we have seen terminate as in Fig. 2, A and B. On occasion, we have been able to trace dendrites along the outer plexiform layer for some distances, suggesting that some are of the interplexiform type. However, we have not been able to confirm the presence of the less diffusely expanded cell type.

Morphologically, the apparatus appears available to provide color vision for the dolphin. However, even enlightened speculation on the function associated with the specialized amacrine cells requires much electrophysiological and behavioral research. It is interesting that the specialized amacrine cells that we have seen frequently in dolphins have been found only in terrestrial mammals which have both cone and rod receptors. Gallego has made the observation that these amacrine cells may provide for feedback around the bipolar cell

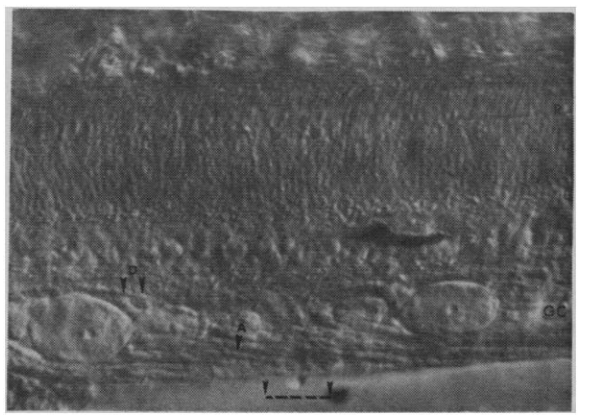

Fig. 3. Retina and epithelium. Receptor (*R*) and ganglion cell layer (*GC*) are marked. Giant cell, far left, is 80 μm long at its equator. Giant cell outlines are visible between cells in the focal plane. Multiple dendrites (*D*) arise from some cells. Axons (*A*) of ganglion cells form the nerve fiber layer. The retina was prepared by the Golgi-Kopsch method; this area did not stain. Interference-contrast (scale, 100 μm).

layer, perhaps even from the inner plexiform layer to the receptors and horizontal cells. The meaning of such a hypothetical feedback system cannot be defined at this time. In any case, their presence in the dolphin as well as terrestrial mammals suggests that they may be a general feature of the mammalian retina.

The most unusual structures we have seen in the dolphin retina are the giant ganglion cells and their giant appendages. Although a few giant cells may be found in other mammals, such as dog and cat, they comprise only a small percentage of the ganglion cell population. Furthermore, there is no data to show that the axons produced by them attain the diameters which we have found in the dolphin retina. In the central 30° to 40°, the giant cells occupy a large percentage of the space between the inner nuclear layer and the inner limiting membrane. Functionally, such large dimensions must lead to rapid communication between the retina and the brain. Since very large ganglion cells have been reported in other cetaceans (*2*, *3*), it is possible that they play some role in the maintenance of function when conversion to anaerobic metabolism is required by long periods under water.

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Mitochondrion of Yeast: Ultrastructural Evidence for One Giant, Branched Organelle per Cell

Abstract. *Three-dimensional models constructed from 80 to 150 consecutive serial sections of entire yeast cells showed that all the separate mitochondrial profiles were cross sections through a single, branching, tubular structure about 50 to 60 micrometers in length and 200 to 600 nanometers in diameter. The data are contrary to conventional notions of mitochondrial size, form, and number per cell and should lead to a reassessment of mitochondrial genetics and biogenesis.*

Mitochondria are energy-producing organelles in eukaryotic cells. Except for the unicellular alga *Micromonas*, which is reported to contain a single mitochondrion (*1*), all eukaryotic species have been presumed to carry numerous mitochondria per cell. This presumption is based on observations of whole cells and sections by various microscopic methods, and on data from centrifugation experiments (*2*). We now propose a different model of the mitochondrion. Serial sections of entire cells revealed only one huge, branched, cristate mitochondrion per cell in yeast, regardless of the physiological state of the aerobic culture at the time of collection and processing. This folded, branched organelle occupied a substantial portion of the extranuclear space but was not closely appressed to the cell membrane. Data from budding cells in synchronous cultures further revealed that the single mitochondrion was continuous between mother and bud portions through 80 to 90 percent of the cell cycle and remained thus until the new cell wall was completed.

Cells of the diploid strain iso-N of *Saccharomyces cerevisiae* were grown synchronously and asynchronously in liquid nutrient which included glucose or ethanol as energy sources (*3*). Samples of cell suspensions were fixed in 3 percent glutaraldehyde and then were sedimented and resuspended in fresh fixative solution containing 5 percent glutaraldehyde and 8 percent formaldehyde in neutral cacodylate buffer (*4*). Subsequent treatment included either postfixation with 5 percent sodium permanganate or digestion of the cell wall

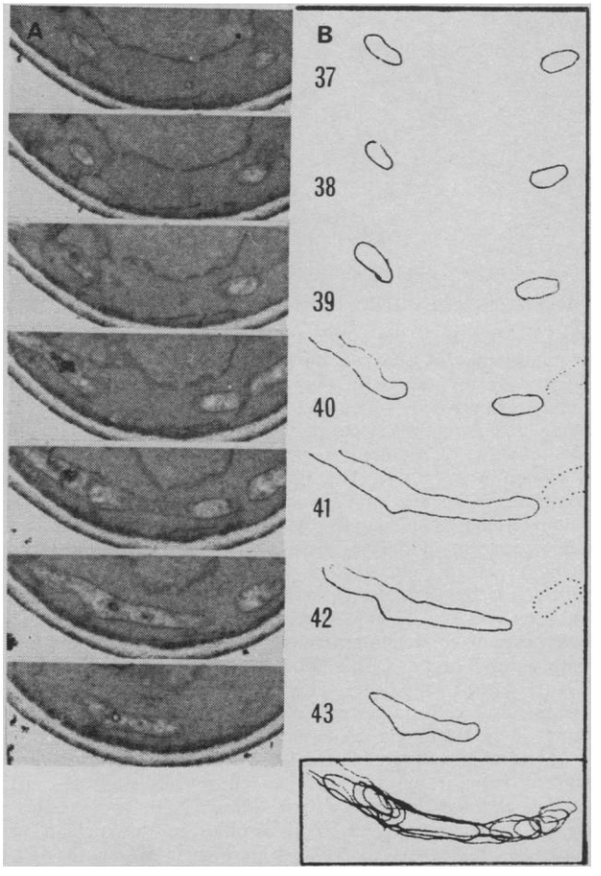

Fig. 1. (A) Electron micrographs of thin sections of a consecutive series through a budding yeast cell are shown in part. The separate mitochondrial profiles in sections 37 to 40 are connected to one another in sections 41 to 43. This single entity in turn was connected to the rest of the giant, complex mitochondrion in this cell. (B) A cumulative view of the superimposed tracings of the mitochondrial profiles aids in showing the continuity (× 12,000).