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Growth of the teleost eye: novel solutions to complex constraints

Russell D. Fernald
Institute of Neuroscience, University of Oregon, Eugene, OR 97403, U.S.A.

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Synopsis

The cichlid fish, *Haplochromis burtoni,* is highly dependent on vision for survival in its natural habitat. As is true of most teleost fishes, the eyes continue to grow throughout life without any obvious changes in visual capability. In *H. burtoni,* for example, retinal area may increase by 27× in just 6 months. During growth, there is no obvious change in the visual sensitivity, visual acuity or lens quality which must all be appropriate for the enlarging eye. This requires that during growth competing constraints be met. For example, to maintain visual acuity, the number of ganglion cells per visual angle subtended on the retina must remain the same as must the convergence ratio of the cones onto those ganglion cells. In contrast, to maintain visual sensitivity, the number of rod photoreceptors per unit retinal area must remain the same. These requirements are in conflict since a larger eye may preserve acuity with fewer cells per unit area in a larger retina. In addition, the lens properties must remain the same as the animal increases in size so that the image available is of similar quality throughout life. Experiments have been performed to reveal the adaptations during growth which allow the fish to preserve its image of the world throughout life.

Introduction

The African cichlid fish, *Haplochromis burtoni,* relies primarily on visual recognition of particular chromatic and spatial patterns to mediate important social interactions. In its natural habitat, the shore pools of Lake Tanganyika, males defend territories from which they court females (Fernald & Hirata 1977a, b). A female, after spawning in a male's territory, broods the developing young in her mouth for approximately 12–14 days, well away from the territory. The overall area of the territorial arena is limited by suitable substratum, and the total number of territories is determined by male-male competition (Fernald & Hirata 1977b).

Adult males have distinctive color patterns which are important both for the maintenance of territories and for reproductive behavior. These patterns are: black forehead stripes, black opercular spot and eye-bar, blue or yellow body color, yellow-orange egg spots on the anal fin, black pelvic fins, orange humeral scales and blue lips (Fig. 1). Non-territorial males remain in a school together outside the territorial arena with females and juveniles. The animals live in turbid shore pools in which measurements of transmissivity revealed that light in the blue and orange regions of the spectrum are transmitted significantly better than at other wavelengths (Fernald & Hirata 1977a). These color regions are well matched to the chromatic patterns used for social signalling (Fernald 1977).

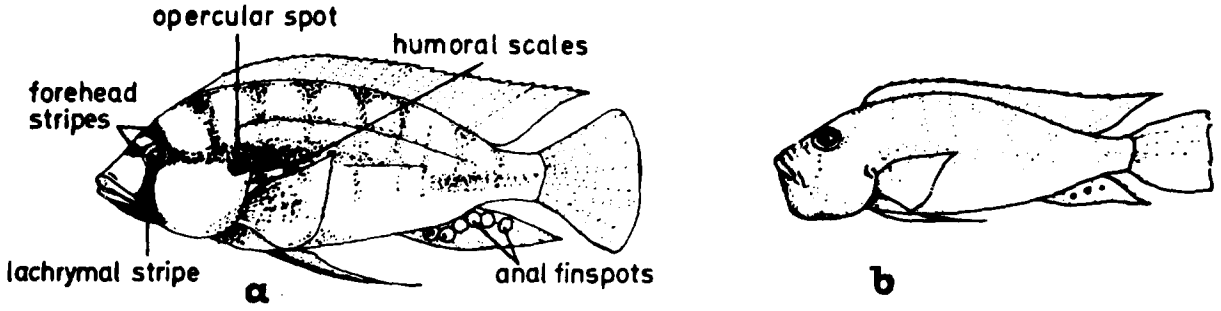

Fig. 1. Schematic illustration of the coloration patterns of a territorial adult male (a) and an adult female (b) *Haplochromis burtoni.* The lachrymal stripe (eye to mouth bar), forehead stripes and opercular spot of adult males are black. The humoral scales are orange-red and the 5 to 9 anal fin spots are yellow-orange. The dorsal and caudal fins have rows of small reddish spots between the rays; pectoral fins are transparent and the pelvic fins have a black lower edge. The female is shown with young in her buccal cavity. Females are cryptically sandy colored except for a few small anal fins spots which are pale yellow-orange.

Since vision is so important for behavior in this species, it is not surprising to realize that the eye enlarges enormously as the animal grows. Since most teleosts continue to grow throughout life, the relative rate of eye growth generally depends on the overall rate of growth and on the allometric relationship between body size and eye size. In other cases studied (goldfish, Johns 1977, guppy, Müller 1952), the size changes significantly more slowly than in *H. burtoni,* where the radius of the eye may triple during the first two months of life. The growth and developmental rate are strongly influenced by the social situation (Fernald & Hirata 1980, Fraley & Fernald 1982). Specifically, males which grow up defending territories grow and mature much faster than do broodmates which grow up without territories (Fraley & Fernald 1982). This slowing of the growth and maturation is reflected in the time onset of coloration patterns, the onset of behavior patterns, rate of whole body growth and rate of testicular development. From analysis of these measures, it is clear that non-territorial males are not prevented from maturing, but that both the rate and phenotypic expression of maturation are inhibited in these males. Although those studies were done within groups of broodmates, our more recent observations suggest that these effects are even more pronounced if there is a size difference between territorial and non-territorial animals (Muske & Fernald, unpublished). Such regulation of development may be adaptive in a social system where territorial space is limited.

In the shore pools where *H. burtoni* live, only about 10% of the adult males are able to breed (Fernald & Hirata 1977b). These breeding males are brightly colored, highly visible and much more likely to be preyed upon. When one such territorial animal is removed by a predator, the non-territorial males quickly congregate and fight over the space, with the winner acquiring not only the territory, but the concomitant territorial coloration and behavioral patterns. Despite the fact the siblings may have eyes differing in size by a factor of two in a period of just four months, there is no obvious difference in their visual abilities.

To preserve visual function during this growth, three critical features of the functioning eye must be conserved: (1) the photopic visual acuity; (2) the scotopic visual sensitivity; and (3) the optimal quality of the lens. Maintaining these essential properties of the eye imposes apparently conflicting constraints on the growth of the eye. Here I will first describe the retinal structure in *H. burtoni,* then the process of retinal growth and finally, I will outline our current understanding of the novel solutions to each of the problems posed by such postnatal growth.

Retinal structure and growth

Teleosts have a retinal structure characteristic of all vertebrates with well defined, alternating layers of neuropil and cell bodies arranged in a transparent

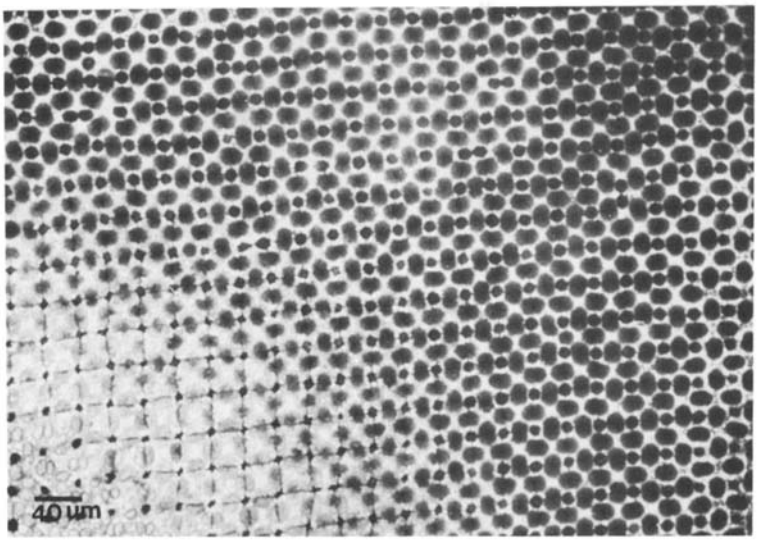

Fig. 2. Tangential 3μ section through the retina of a mature male *Haplochromis burtoni*. Plane of section slightly oblique through inner segments. Toluidine blue, Bar = 40μm.

thin gelatinous layer at the back of the eye. The cone photoreceptors are arranged in a highly ordered spatial array, which, in *H. burtoni,* consists of a single cone centered in a square of four twin cones (Fig. 2). The rod photoreceptors are distributed throughout this array with 8 to 18 rods per cone array, depending upon the retinal region (Fernald & Liebman 1980). This difference in rods per cone array reflects the fact that rod density is constant across the retina and the cone density is greater at the temporal pole of the retina (Fig. 4). The crystal-like cone arrangement, which is common to most visually active teleosts, is possibly a result of selection for high acuity in an eye with a very short focal length lens (Fernald 1981a).

We have measured the absorbance characteristics of the retinal photopigments microspectrophotometrically and found three different cone pigments and one pigment in the rods (Fernald & Liebman 1980). The central, single cone, which is physically shorter than the twin cones, contains a photopigment sensitive at 454 nm and each member of the twin cones contains a different photopigment, with one maximally sensitive at 523 nm the other at 562 nm. The rod photopigment absorbs maximally at 500 nm, and all the photopigments are based on vitamin A_1 (Fernald & Leibman 1980). To discover how the pigments in the twin cones are arranged across the retina I have used a histochemical technique in which particular cone types are selectively stimulated with monochromatic light and the activated mitochondria subsequently stained (Fernald 1981a). The twin cone photopigments have an alternating symmetry about each central single cone, so that considering the single cone as the center, the twin cones are positioned as 'square-dance couples' would be, alternating 523 nm and 562 nm photopigments (Fig. 3). This particular symmetry most closely packs dissimilar pigment types into each unit area of retina so that chromatic patterns can, in principle, be resolved equally well over the entire retinal surface (Fernald 1981a).

This high degree of retinal order persists as the fish grows, even though a newly hatched young fish could swim in a tight circle within the eyeball of a one-year-old fish! To discover how visual function is maintained in the face of such extreme growth, we must first describe generally how the retina grows.

Vertebrate eyes continue to grow postembryonically, although this growth is normally attributed to stretching of the existing neural tissue, rather than to neurogenesis (Walls 1967, Mann

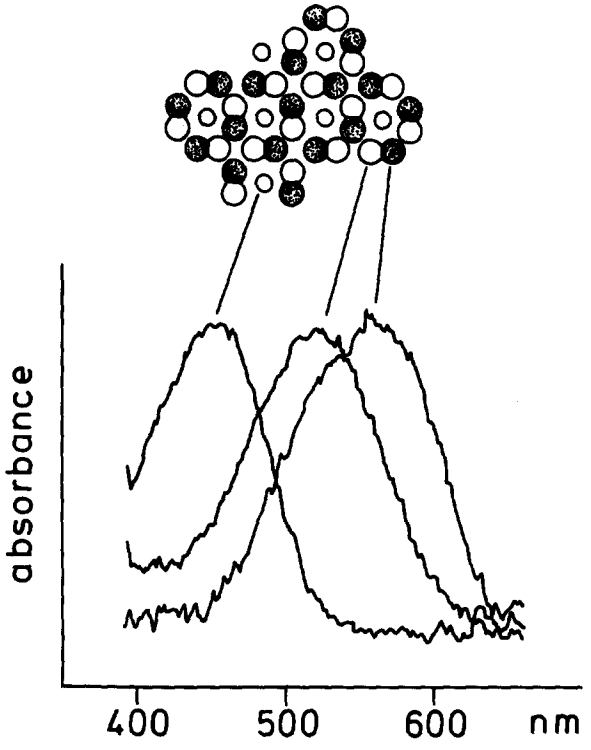

Fig. 3. Schematic illustration of the distribution of cone pigment types across the retina as related to the absorbance of photopigment contained in the cone outer segment measured microspectrophotometrically. The four-fold rotational symmetry shown diagramatically packs each unit area of the retina so as to minimize the distance between cones containing different pigment types.

1950). In teleosts and amphibians, however, studies have shown that the number of retinal cells does increase with eye size in adult animals (Müller 1952, Lyall 1957, Blaxter & Jones 1967, Hollyfield 1972, Wagner 1974, Scholes 1976, Johns 1977, Meyer 1978, Sandy & Blaxter 1980). In all species examined, cell addition occurs in a germinal zone located at the retinal margin. In this germinal zone, cell division results in fully differentiated retina being formed, following the general sequence of cell production proposed for embryonic retinal neurogenesis (e.g. Scholes 1976). To understand this growth process in *H. burtoni,* we have analyzed the retinal cell density as a function of age (size) of the animal.

Eyes from fish of various sizes were fixed in Bouins fixative and embedded in epon (Fernald 1983). Following sectioning at 3-micron intervals, the tissue was sampled as shown schematically in Figure 4. Photomicrographs were taken at high power (≃400×) and all the retinal cell types were counted from the photographs. After conventional corrections (Abercrombie 1946), the number of cells of all types were compared for small (Fig. 4) and large (Fig. 5) eyes. Three main conclusions can be drawn from this evidence.

First, the absolute densities of all cell types except for rod photoreceptors are significantly smaller in the large eye than in the small eye. This means that the convergence of cones onto second order cells remains about the same as the animal grows. Second, the density of all non-rod cells is greater in the temporal region near the margin in both large and small eyes. Third, the rod density is constant throughout the retina and approximately constant between the small and large eyes. It is important to note that although the rod density remains constant, the ratio of rods to ganglion cells increases dramatically from small to large fish. We will discuss the functional significance of this observation below. Since the absolute density of all cell types except for rod photoreceptors decreases with eye size, stretching of existing neural retina as well as cell addition, must accompany the enlargement of the eye (Müller 1952).

Preservation of visual function during growth: results and discussion

Now we can consider the questions posed above about the preservation of visual function during this growth. First, what would be required to maintain the photopic visual acuity during growth? Photopic visual acuity is dependent on the cone photoreceptor spacing across the retina, and on the convergence of the cones onto higher order processing cells, since in normal bright light viewing, only the cones participate in phototransduction. As the fish grows, and the eye enlarges, the fish eye receives light from the same solid visual angle in space, which is about 181.1° in *H. burtoni* (Fernald 1981b). This volume of space projects onto a larger retinal surface as the eye grows, so that any object has a larger image in a larger eye. If we assume, for

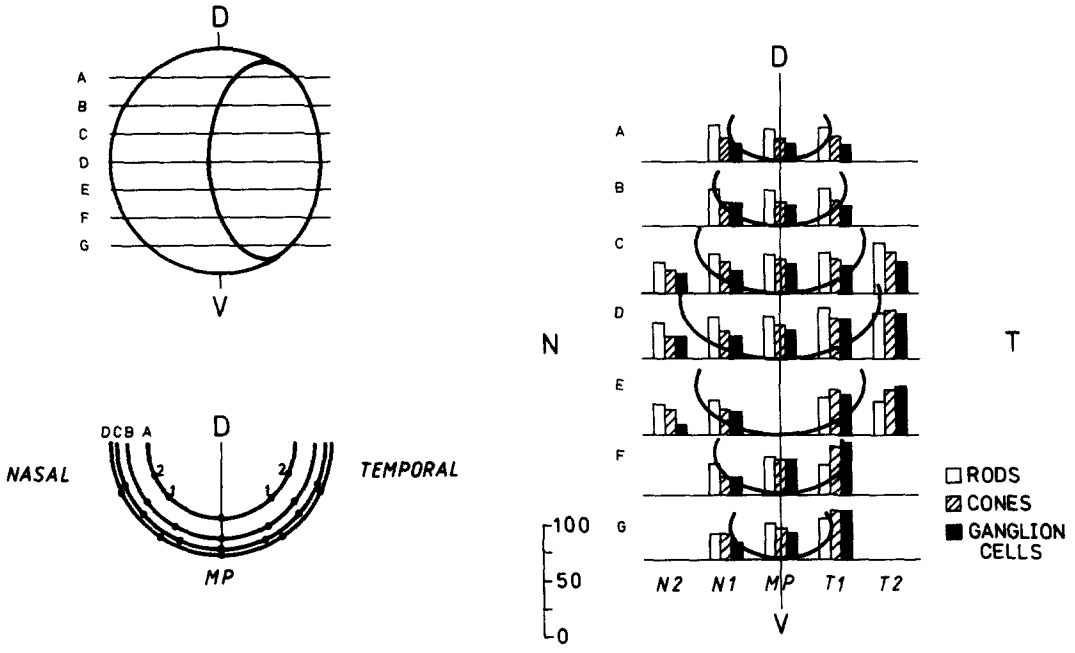

Fig. 4. Left: Schematic illustration of sectioning and sampling procedures. In each horizontal section (A–G), nasal (N), temporal (T) and mid-point (MP) cell densities were counted. Right: Corrected cell density counts are illustrated for an eye of radius 0.85 mm. Rods, cones and ganglion cells are illustrated to indicate the location of the sample point within the eye.

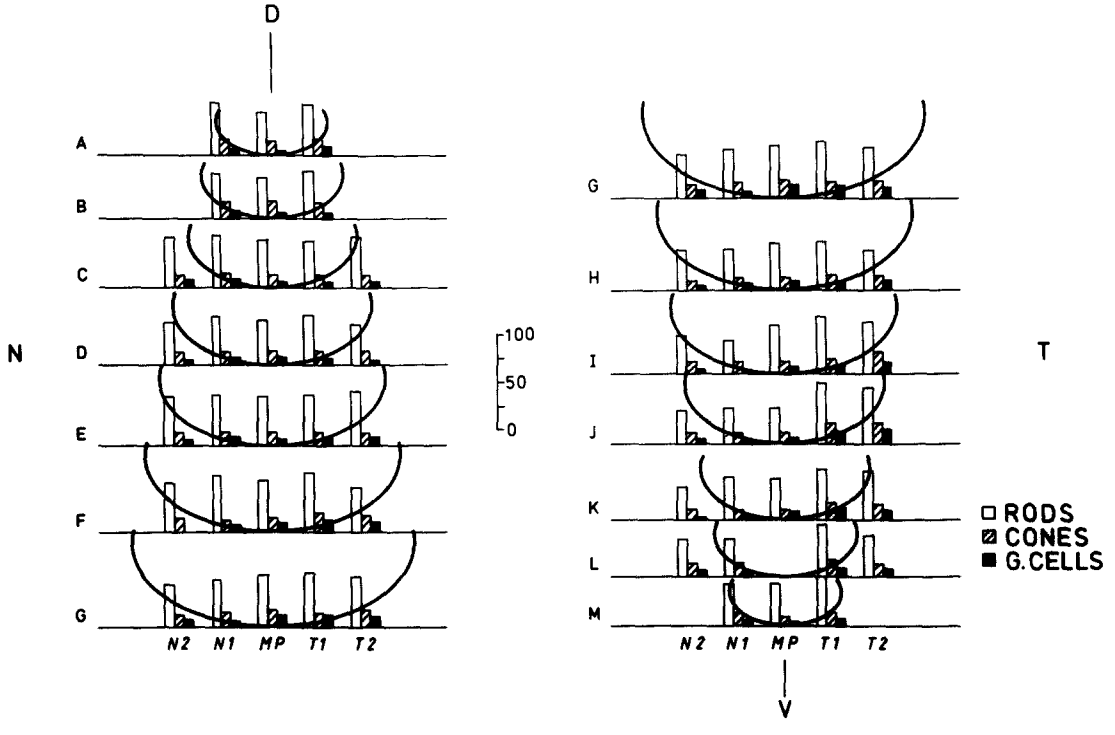

Fig. 5. The retinal cell densities for an eye of radius 2.4 mm where the samples are laid out to illustrate their relative position in the intact eye. Dorsal pole is top left and ventral pole, bottom right. Compare cell densities with Figure 4 right.

this discussion that the larger lens produces an image of comparable quality in the larger eye, then we can see that the larger eye can have cone photoreceptors at greater absolute spacing without loss of acuity. Stated another way, for the photopic visual acuity to remain constant, the density of cone photoreceptors per degree of visual angle must remain the same, and the ration of cones to higher order cells (ganglion cells) must remain the same. For the sample eyes shown in Figures 4 and 5, the radius of the eyes differs by a factor of about 3 (r = 0.85 versus r = 2.4) whereas the cone density per unit area decreases only by a factor of about 0.62 when comparing the most cone dense areas in each eye. The actual cone density in the temporal region per angle of arc is 6.9 cones per degree in the small eye as compared to 14.8 cones per degree in the large eye, meaning that the best theoretically achievable acuity actually improves significantly as the eye grows. This improvement is due to the addition of new cone photoreceptors at the margin of the eye as growth occurs. Recent behavioral studies have confirmed the improvement in visual acuity with fish eye size in the sunfish (Hairston et al. 1983).

We can now address the second constraint on visual function during growth of the eye, the maintenance of scotopic sensitivity as the eye grows. We have used an operant conditioning paradigm to measure the scotopic visual threshold in *H. burtoni* (Allen & Fernald 1981). The behaviorally measured scotopic visual threshold is constant over a wide range of fish sizes, and thus appears to remain nearly unchanged as the fish grows. The scotopic sensitivity is dependent upon rod photoreceptors which are active at low light levels. Although the number of rods per unit area remains constant as the animal grows (see Fig. 4, 5), the convergence of rods onto higher order cells increases dramatically. As noted above, the number of ganglion cells per visual angle increases just slightly as the animal grows, so the portion of visual space represented by each ganglion cell is nearly the same. These ganglion cells receive an increasingly large number of rod photoreceptors however, and how they might preserve their integration properties during growth remains unknown. Müller (1952) was the first to notice that rod density was maintained during growth in his study of the guppy (*Lebistes reticulatus*). Since Müller observed mitotic figures associated with cell division at the retinal margin, he suggested that the rod photoreceptor density was maintained by migration of rods from this marginal site of generation into the retina. The rod photoreceptor consists of a long outer segment ($\sim 50\mu$) connected by an ellipsoid to a cell body with processes extending vitread and ending in rod spherules where bipolar cell connections occur. One might imagine that lateral migration of these structures could cause some disruption in retinal function. Johns & Easter (1977) however, presented data obtained from ^{3}H-thymidine labelled goldfish in support of this hypothesis, suggesting that the retinal layers shear past one another during growth. This method of growth seemed highly unlikely in a rapidly growing fish, such as *H. burtoni,* which depended so critically upon vision. Therefore, we have repeated some experiments and performed new ones to test this hypothesis of rod density maintenance in the retina.

Ideally, one would like to measure cell densities of a single eye at two different ages. This being impossible, we instead compared different sized eyes within the same animal by using the experimental paradigm illustrated in Figure 6. Fish are injected intraperitoneally with ^{3}H-thymidine, a metabolic precursor of DNA which is incorporated exclusively into nuclei of proliferating cells. This label, when made visible in the tissue by autoradiographic processing of the histological sections, marks the cells which were produced during the time that the radioactive precursor was available in the locus of cell division. Since the retinal growth zone at the margin of the eye is producing new cells almost continuously (Müller 1952), the injected precursor should result in a heavily labelled ring of cells around the margin of the eyes. Were extra rods being produced at the margin to be moved centralwards, they would be visible in the form of extra labelled rods.

Experimentally, we take animals from a brood of known parentage, and inject them with ^{3}H-thymidine (30 uCi per gbw). Twenty-four hours after injection, we anesthetize the fish and surgically

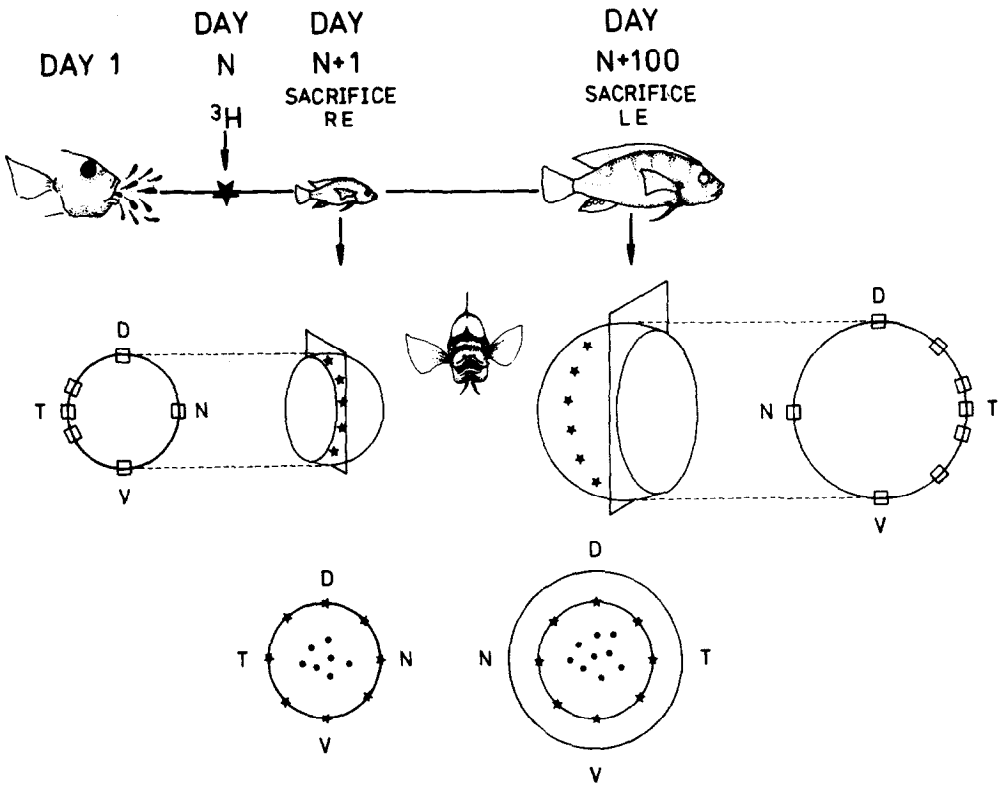

Fig. 6. Experimental paradigm for measuring growth using the radioactively labelled DNA precursor ^{3}H-thymidine. N days after hatching (Day 1), the fish are injected intraperitoneally and one eye prepared for histological sectioning 24 h later. After the chosen growth period, the second eye is prepared identically to the first. The middle panel shows schematically the sample points and the locus of radioactive label (*).

remove one eye. After the desired period of growth, the second eye is similarly removed, both eyes are fixed, embedded, sectioned and prepared for autoradiography by standard procedures (Hendrickson & Edwards 1978).

As expected, the margins of the retinae from fish treated with ^{3}H-thymidine are heavily labelled in all layers, consistent with earlier results based on mitotic figures and autoradiography (Müller 1952, Scholes 1976). Using this annular ring label, we could compute the contribution of new cell addition and retinal stretching to the enlargement of the eye by comparison of two eyes which have been allowed to grow to different final sizes. In *H. burtoni,* new cell addition accounts for about 40% of the enlargement of the retinal area and stretching for the remainder. Were extra rods being produced at the margin prior to their lateral motion into the retinal center, they should have been visible as large amounts of labelled rod nuclei in the marginal label. No excessive number of rods could be seen at the retinal margin.

We did find, however, significant amounts of labelling in the layer of rod nuclei across the entire extent of the retina (Fig. 7) (Fernald & Johns 1980). These we interpret to be newly generated rods produced by cell division within the retina proper. The stem cells which give rise to the new rods have not yet been located. Repeating the experiments using goldfish has confirmed that new rods are indeed produced throughout the extent of the retina in this teleost as well (Johns & Fernald 1981). The failure to find this result in earlier experiments may have been due to the significantly slower growth rate of the goldfish, although labelled rods are visible in autoradiographs (e.g. Scholes 1976). Retinal autoradiographs from goldfish examined after 24 h survival time showed significant amounts

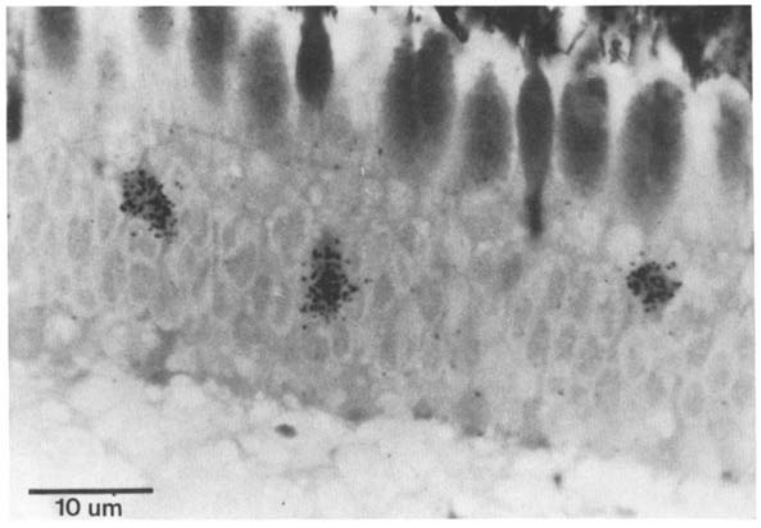

Fig. 7. Autoradiograph of the retina (sclera upwards) of an adult *Haplochromis burtoni* injected 24 h previously with ^{3}H-thymidine, showing three labelled nuclei in the outer nuclear layer. Labelled nuclei are found only in the outer nuclear layer and these nuclei are cytologically indistinquishable from the surrounding nuclei of rods.

of other labels in addition to the new rods making the earlier interpretation of the results difficult (Johns 1977). At longer survival times, however, tissue turnover diluted the label of all but the new rods.

Thus, in the teleost retina, as tissue is being added at the margin and existing retina is stretching, the absolute density of all cells except rods is decreasing. New rod photoreceptors are being generated throughout the retina and being integrated into the existing retinal circuitry. This resolves two of the three constraints on retinal structure necessary to account for the maintenance of visual function during growth. Both these constraints, however have implicit in them that the image available to the retina is of comparable quality throughout life. This may be the most difficult of the limits on growth because of the unique optics of the fish eye.

The dioptric power of the teleost fish eye is vested entirely in the spherical lens, since water, the cornea and the intraocular vitreous humour have almost identical refractive indices (Hogben & Landgrebe 1938). The spherical lens is incompressible, and accommodation is achieved through movement of the lens within the globe. As the lens grows, the dioptric power decreases and the extent of movement during accommodation increases so that the maximum accommodative amplitude does not change significantly (Fernald & Wright, unpublished). Eye movements allow the fish to 'aim' this axis of accommodation at any target of interest (Fernald 1981b).

Vertebrate lenses grow throughout life by the division of cells at the lens surface. The fiber cells produced there are gradually covered by newer tissue giving the lens a layered structure. Thus the fish must produce an ever larger lens with proper refractile properties from new cells added at its surface. Spherical lenses of uniform refractive index produce poor images because rays entering at different distances from the optic axis are focussed at different distances from the lens (Fig. 8a). Teleosts do not suffer from this imperfection (Fig. 8b) and it has long been presumed that this is because the refractive index is highest in the center of the lens and decreases continuously and symmetrically with respect to radius in all directions (Maxwell 1854, Matthiessen 1880). How this could be achieved has remained a mystery. We have recently demonstrated that there is a refractive index gradient by direct measurement, although we postulate that its form is significantly different from that pre-

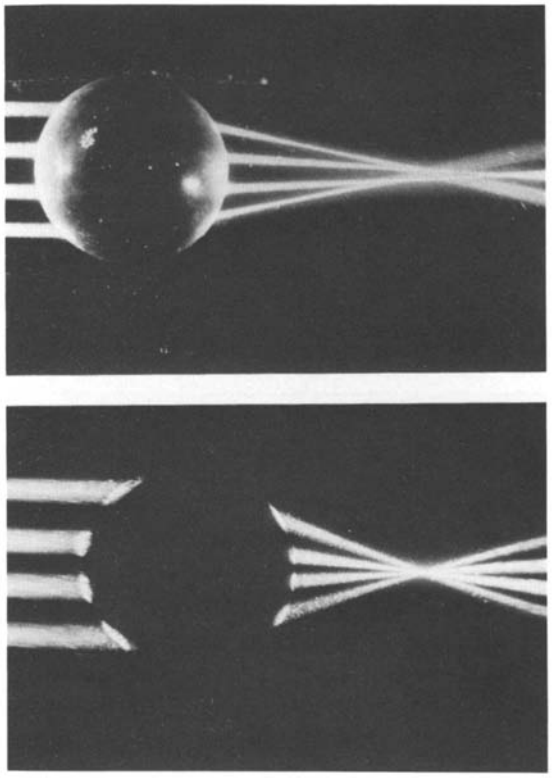

Fig. 8. a – glass sphere of uniform refractive index (n≈1.53) illustrating longitudinal spherical aberration. Laser beam is from an argon source (Coherent Radiation 800, λ = 494nm); *b* – freshly excised *H. burtoni* lens suspended by its ligament in oxygenated fish Ringer's solution and illuminated by laser beams. The finely focused cone of light is typical of illuminated fresh fish lenses.

viously hypothesized (Fernald & Wright 1983).

We measured the optical properties of the lens which are dependent on the refractive index, since direct measurement of refractive index is difficult in a lens known to have a refractive index gradient. Using a laser beam, we were able to measure the paraxial focal length of the whole lens (Sivak & Kruezer 1982) and then of the more central portions of the lens produced by surgical reduction (Fernald & Wright 1983). The lens consists of two physically distinct zones: the outer cortex and the inner core. The outer cortex layers of the lens are held in a spherical shape by the lens capsule which extends around the entire lens. These gelatinous layers deteriorate quickly when the capsule is removed. Their orderly, layered organization is evident only in freshly excised eyes or in well fixed preparations. In contrast, the lens core is a hard, nearly imcompressible sphere of dense protein. In *H. burtoni,* the lens core radius is 0.674 of the whole lens radius (s.d. = 0.051, N = 40) in all sizes of fish, a strikingly regular relationship (see Fig. 2, Fernald & Wright 1983).

Freshly excised lenses, regardless of size, showed a finely focused cone of light, terminating in a single point (Fig. 8b). In contrast, when we surgically removed the cortex, the lens core focused light significantly differently. To assure ourselves that this difference was due to the optical characteristics of the core and not the procedure we performed several control experiments (see Fernald & Wright 1983 for details). With the lens core there is no well defined focal point, but rather the emerging light rays assume a shape characteristic of a spherically aberrant lens with a uniform refractive index. Moreover, the ratio of the paraxial focal length (f) to the radius (r) is significantly different from that of the intact lens. For the intact lens, the ratio is f/r = 2,252 (s.d. = 0.046, N = 12, λ = 494 nm) whereas for the core of the lens, the ratio is f/r = 2.952 (s.d. 0.256, N = 10). To assess the optical homogeneity of the core, we systematically removed additonal layers from the lens core and repeated the measurements. This surgical 'peeling' of the lens was done with fine forceps under a dissecting microscope. The well delineated lamina of the lens made it possible to produce spherical lens cores with each 'peeling' by removing naturally occurring layers. We found for all deeper layers that f/r, and hence the refractive index, remained the same.

Thus, for lenses of all sizes, the lens center has a nearly uniform refractive index, and not a gradient as originally predicted (Luneberg 1944). Instead, a steep refractive index gradient appears only to exist between the outside of the lens core (0.67 R) and the newly added cells at the outer edge of the lens (1.0 R). These new cells produce tissue with a refractive index of about 1.38 (Hogben & Landgrebe 1938), whereas the older, original cells nearer the lens center have a refractive index close to 1.56 (Matthiessen 1880). This suggests that the maintenance of a nearly aplanatic lens during growth is achieved through the increasing thickness

of the lens cortex which acts as a corrective coating on the spherically aberrant lens core.

Conclusions

Based on these measurements, we propose that the optical integrity of the fish lens is maintained during the growth of the fish as follows: Newly added tissue at the lens surface has a low refractive index (n = 1.38) primarily because of the low protein concentration (≃20%, Philipson 1969). New layers slowly lose their water content and are compacted, joining the highly protein-concentrated (≃60%) core of the lens. With the loss of water, the refractive index increases to its maximum (n = 1.56) and no further increase in refractive index occurs. This accumulation of tissue in the center of the lens may account for a core of nearly uniform refractive index.

As the teleost lens grows, the increasing thickness of the cortical shell must have the proper refractive index gradient to correct the increasingly large spherically aberrant core. Regulation of both the overall lens size and the protein concentration gradient across the cortex are important for the continued optical integrity of the lens and hence the eye during growth.

In summary, the photopic visual acuity is preserved during growth by virtue of the fact that the larger eye has larger images and hence the cone photoreceptors can be moved apart and still subtend the same visual angle. The scotopic visual sensitivity is preserved by maintaining the absolute density of rod photoreceptors constant by generation of new rods in situ through cell division all across the retina. The optical quality of the lens is preserved by having a 'corrective' shell, the lens cortex, around the lens increase in thickness as the lens grows, allowing 'correction' of the ever larger lens.

Understanding the resolution of these problems, however, reveals another layer of ignorance about questions such as: What controls the eye's growth as a function of the social situation? How does the retina come to be positioned appropriately for the image produced by the lens? How do the output fibers from newly formed retina join those from older retina in the brain to give the animal an understandable image of the world as growth occurs? How do the new rods connect into the old retina to allow detection of photons at low light levels? These are just a few of the many questions which arise and their answers will surely bring new insights about general principles of organization and development of the nervous system applicable throughout the animal kingdom.

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