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GROWTH OF THE ADULT GOLDFISH EYE—I: OPTICS

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Abstract—We have measured the optical and retinal fields of goldfish eyes; the animals ranged from 6 to 20 cm in body length. Both fields are spherically symmetric, invariant with the size of the eye, and equal (retinal field = 185.3° ± 4.1°, optical field = 183.6° ± 2.7°, means ± S.D.). They are tilted with respect to one another by a few (<10) degrees. We have also measured the retinal magnification factor, the number of μm per degree on the retinal surface. It is 20.5 × lens diameter, where lens diameter is expressed in mm.

Key Words—goldfish; optical field; retinal field; growth; retinal magnification factor.
Animal Classification—*Carassius auratus* (Euteleostei, Ostariophysi, Cypriniformes).

INTRODUCTION

The eye of a goldfish grows throughout the animal's life, even into adulthood (Johns and Easter, 1975). The retinal growth results from both hypertrophy and hyperplasia, but particularly the latter. For example, animals 6 cm long have approx 80,000 ganglion cells, while 20 cm fish have about 350,000, which means that there are many more optic fibers reporting to the brain from the large retinas than from the small ones. In this study, we have sought to learn if the visual fields subtended by these growing retinas also change.

We have addressed this question by comparing goldfish of different sizes. Implicit to our approach is the assumption that the larger animals are older versions of the smaller ones, an assumption which we have checked and confirmed. We used two approaches to measure the visual field. In the one, we determined the acceptance angle of the pupils of freshly killed animals [the optical field (Hughes, 1976)]. In the other, we made frozen sections of freshly removed eyes from fish in the same range of sizes, and measured the angular subtense of the retina [the retinal field (Hughes, 1976)]. Both angles were measured with respect to the center of the spherical lens, which is coincident with the anterior nodal point (Charman and Tucker, 1973), therefore, together they yielded the information we were after.

We found that both optical and retinal fields measure 183–186°, independent of the size of the animal.

METHODS

Goldfish (*Carassius auratus*), 6–20 cm long tip-to-tip, were obtained commercially from Ozark Fisheries, Stoutland, Mo., and were maintained in standard aerated aquaria. They were anesthetized by immersion in 0.02% aqueous tricaine methanesulfonate, and all procedures were carried out on anesthetized or freshly killed fish. Body lengths were measured just after anesthetization. Nine animals were used in the determination of the optical fields, ten for the retinal fields.

Optical field

The acceptance angles of 12 meridians, separated by intervals of 15°, were measured for each eye, using the instrument shown in Fig. 1. Each meridional scan passed through the optic disk, located by shining a bright light on the animal's rather translucent head. The pigmented retinal epithelium prevents this intracranial light from entering the eye except at the disk, which appears luminous. By adjusting ψ, the tilt of the animal about its longitudinal axis, and θ, the animal's orientation in the horizontal plane, it was a simple matter to find the position at which the lens brightened maximally when viewed along a horizontal ray perpendicular to the vertical faces of the water-filled aquarium. This was taken as the setting of (ψ, θ) at which the center of the disk lay along the sighting line through the pupil. This interpretation was confirmed ophthalmoscopically. This value of ψ was then fixed until we had completed our measurements on that animal.

Horizontal sightings perpendicular to the vertical faces of the aquarium were assured by having grids on both faces. The observer sighted along a ray connecting corresponding points on the two grids. Every tenth line on the grids was thickened, which allowed maintenance of constant angle of regard when the fish obstructed the view of the corresponding point on the other grid.

To measure the acceptance angle of the pupil, we used the fact that the aperture appears black when viewed along a ray which enters it. Accordingly, the animals were rotated through the angle, θ, until the observer could no longer see into the pupil along a horizontal line perpendicular to the vertical faces of the aquarium. Then the animal was rotated in the opposite sense until the pupil disappeared again. Each scan through θ was characterized by the three values corresponding to the optic disc center and the two extreme sighting angles. Monitoring the location of the disk in each scan provided a check on eye movements, but they proved to be absent, or at least too small to detect. Next the animal was rotated about its transverse axis, through an angle $\phi = 15°$, and θ was

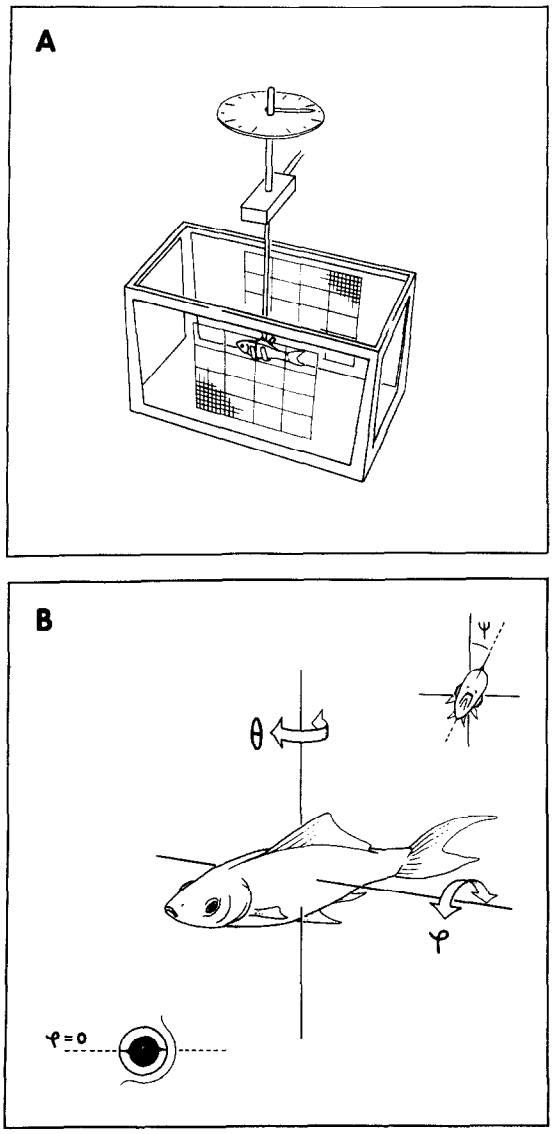

Fig. 1. A: A schematic view of the instrument used to measure the optical field. The animal was suspended in a water-filled aquarium, rotated about the vertical axis, and viewed along horizontal rays perpendicular to the walls of the aquarium. The graticules aided in selection of the sighting line. B: A close view of the suspended fish and the angles θ, ϕ, and, in the upper right drawing, ψ. The sketch of the eye on the lower left shows the pattern of pigmentation in the iris for $\phi = 0°$ or 180°.

varied again. Duplicate readings were taken at each value of ϕ.

Even though the cornea is optically inactive underwater (Charman and Tucker, 1973), the acceptance angle of the planar pupil may exceed 180° since the lens protrudes through it. When the aperture is viewed from the extreme tangential line of sight, the ray into the pupil passes through the external part of the lens, and this introduces an error, since we claim to be measuring all our angles with respect to its center. The error is only about 0.2° in our instrument, owing to the long sighting distance into the pupil, and we have therefore ignored it.

We adopted the convention that $\phi = 0°$, 90°, 180°, 270° were the temporal, dorsal, nasal, and ventral directions, respectively. The eye was horizontal when the intersections of the iris lines with the pupil lay horizontally (see Fig. 1, lower inset).

Retinal field

A different group of animals was used for the intraocular measurements. One eye was carefully removed from the anesthetized animal and quickly immersed in an acetone dry ice mixture. It was held there with forceps by a strand of conjunctiva until the bubbling stopped, indicating that the eye had assumed the temperature of the solution, and was therefore frozen. This took less than 10 sec even for the largest eyes. The frozen eye was lowered onto the horizontal stage of a sliding microtome, into a drop of liquid resin (Tissue Tek II: OCT Compound) and moved until the iris–sclera junction, a circle concentric with the pupil, was vertical to the face of the microtome stage. This assured that the plane of section would be parallel to, and eventually include the retinal axis, the line connecting the centers of lens and retina. We estimate the maximum uncertainty of orientation at $\pm 5°$. The resin was then quickly frozen and, after the eye was firmly attached to the stage, more resin was poured around and over the eye to provide a strong mechanical support. The 16 eyes were cut in one of the three planes: dorsoventral (4), nasotemporal (5), and oblique, parallel to a line from the dorsonasal to the ventrotemporal quadrant (7). This last plane was intended to include the optic disk and the retinal axis. After the first eye was removed, the fish was wrapped in a moist cloth. This environment and the maintenance of the ocular circulation were intended to keep the morphology of the second eye normal during the interval of about 30 min before it was frozen and sectioned. There was no systematic difference between first and second eyes, so both were included in the data. In four cases, only one eye was used, the other going for other purposes.

After the resin was frozen, sections were cut at 100 μm intervals. The sections themselves were discarded, and the block face (including a calibration scale) was photographed at a magnification of 1.11–1.29. When the plane of section was far from the center of the eye, photographs were made only occasionally, but as the center of the eye approached, a photograph was taken after each advance of 100 μm. When the plane of section had obviously passed the center, the block was discarded.

The film (Kodak Plus X Pan) was developed (Kodak Microdol) and projected by a microfiche viewer (Dagmar Universal III) for detailed examination and drawing. The collection of photographic negatives from each eye was examined and the one in which the cross sections of both the lens and the globe were largest was chosen for detailed analysis. All measurements for a given eye were made from the one negative. A positive print of one of them is shown on the right of Fig. 2.

First, the center of the lens was determined by trial and error, with an estimated uncertainty of less than 50 μm. Next, the ora terminalis, the boundary between retina and iris, was located on both sides of the lens with an uncertainty of ± 75 μm or less, depending largely on the sharpness of the negative. (Both of these estimates of error are given in units which refer to the eye, not to the negative or to its projected image.) Three features were used to identify the ora terminalis. The sensory retina, visible in the negative as a narrow black line, becomes thinner at its margin until it vanishes at the ora. The pigmented retinal epithelium behind the sensory retina also becomes thinner and merges into the iris. Finally, pigment in the epithelial cells of the iris is much less dense than in the pigmented retinal epithelium. These characteristics of the ora are seen in the photograph on the left of Fig. 2, a light micrograph of this region.

Lines were drawn connecting the lens to the two orae, and the angle, ρ, the retinal field in one meridian, was

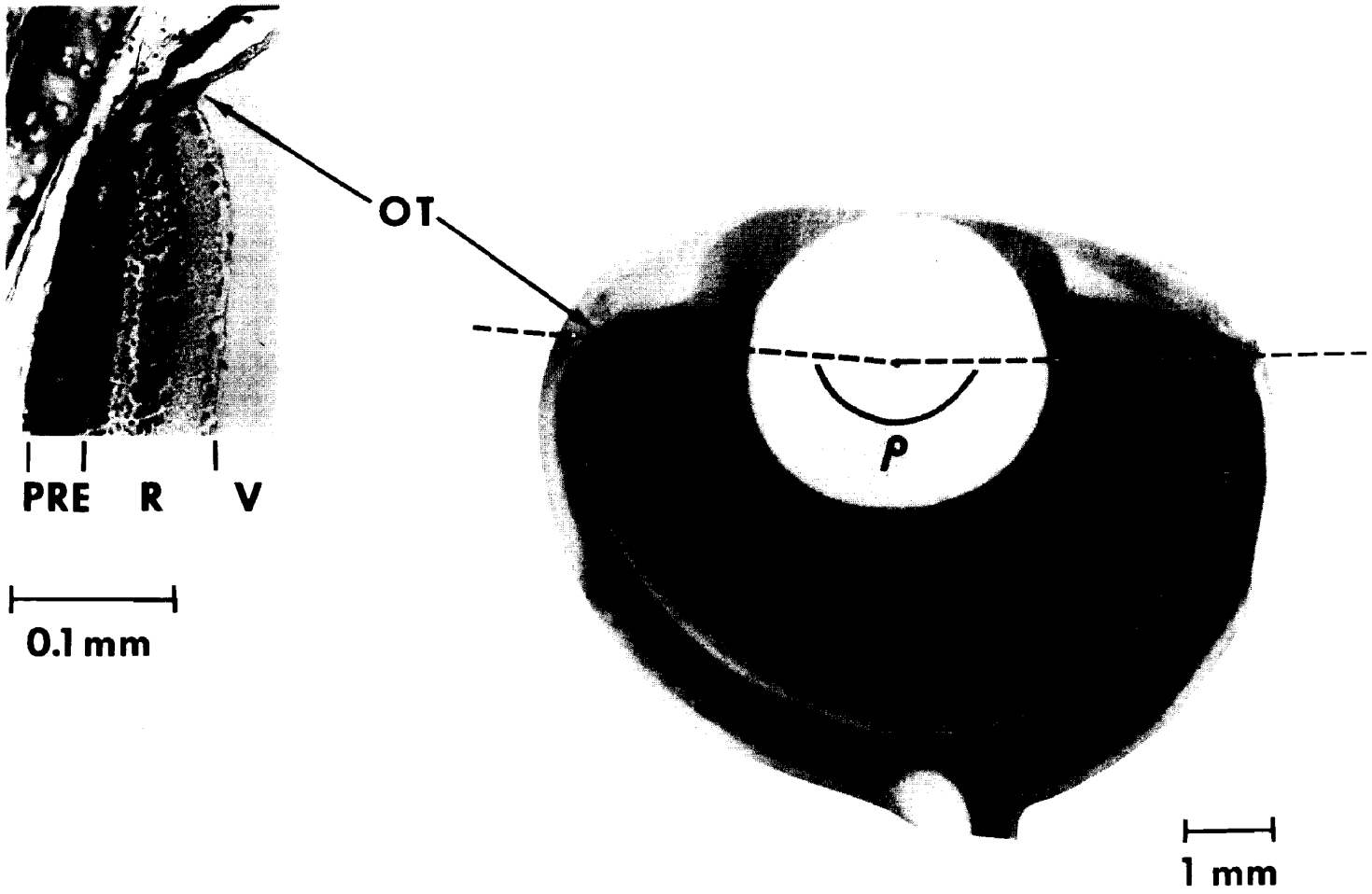

Fig. 2. Right: a print of one of the negatives used in the determination of the retinal field (ρ). Left: a histological cross section through the region of the ora terminalis (OT). Abbreviations: PRE, pigmented retinal epithelium; R, sensory retina; V, vitreous. (Paraffin histology; 5μm section stained with Foot's modification of Masson's trichrome.)

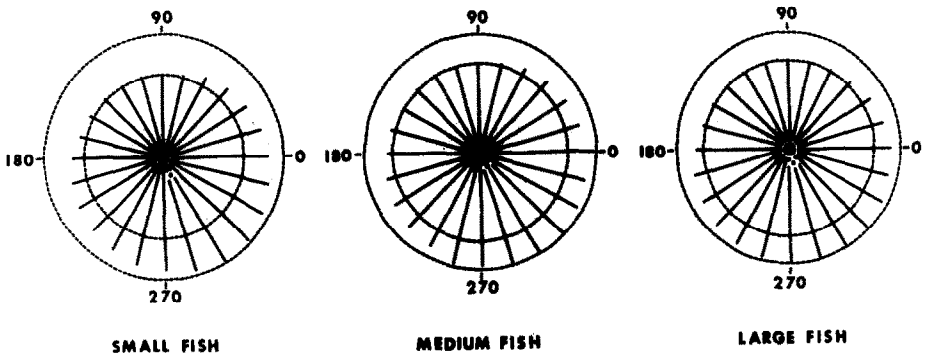

Fig. 3. The uncorrected optical fields of the eyes of three sizes of fish. The spokes pass through the optic disk (×). Their orientations indicate ϕ, and their lengths, θ, the acceptance angle of the pupil in that meridian. The convention is: $\phi = 0°$, 90°, 180°, 270° correspond to temporal, dorsal, nasal, and ventral directions. The small dot in the lower right quadrant shows the computed optic center of the field. The circles show the range of values: 74–111°, 80–107°, and 80–105° for small, medium, and large fish, respectively.

measured with a protractor. Finally, the length of the retina was determined by measuring the extent of the sensory retina/pigmented retinal epithelium (R/PRE) boundary. We measured retinal length at this level because it is very near the outer segments of the cones in a light-adapted eye.

RESULTS

Optical field

The nine fish used for measurement of the acceptance angle of the pupil fell into three groups: small (5.8, 6.3 and 7.1 cm), medium (9.5, 10.0 and 10.2 cm), and large (15.0, 17.0 and 18.8 cm). These sizes correspond to ages of <1, 1–2, and 3–4 respectively (Johns, unpublished results based on an analysis of the growth rings of the scales; Lagler, 1956). The data within each group were pooled, and the polar plots in Fig. 3 illustrate these measurements on the three groups of fish. In this representation the orientations of the spokes give ϕ. The summed lengths of pairs of colinear spokes give the angle, θ, through which the animal was rotated during each scan. The spokes intersect at the optic disk. Their lengths vary systematically and are longest in the lower right quadrant and shortest in the upper left. This indicates that the optic disk did not project to the center of the optical field. In order to make meaningful comparisons between animals of different sizes, it is necessary to transform these data to refer to the optic axis, the center of the optical field, of each group of eyes. A description of the transformation is given below.

The transformation requires a knowledge of the optic axis, which we did not know. We estimated it, by trial and error, beginning by assuming that it intersected the colinear pair of spokes most different in length. In Fig. 3, small fish, this is the pair at $\phi = 120°$ and 300° which are $\theta = 74°$ and 111° in length. We assigned the optic axis to the midpoint of the arc and then computed the subtense of each of the 22 remaining spokes with respect to that point. For this computation, we used the relation for a spherical triangle (Selby, 1954):

$$(\cos a) = (\cos b)(\cos c) + (\sin b)(\sin c)(\cos A)$$

in which a, b, and c are the angles subtended by the sides, with respect to the center of the sphere, and A is the angle on the sphere's surface opposite a. In our case, we used:

a = computed value of spoke relative to estimated optic axis,

c = measured value of spoke relative to optic disk,

b = estimated displacement from optic disk to optic axis,

$A = \text{ABS}(\phi_c - \phi_b)$,

$\phi_c = \phi$ of the spoke, c,

$\phi_b = \phi$ of the spoke, b.

Several values of b and ϕ_b were tried until a roughly symmetric distribution (all values of θ within 3° of the mean) was achieved.

Figure 4 shows the data transformed so that the spokes now originate on the optic axis. In all cases, the optic disk was located in the dorsonasal quadrant of the optical field, displaced from the optic axis 13–17° up a spoke tilted 15–30° from the vertical. The precision with which the disk could be localized is not impressive. This inaccuracy resulted from three sources of error, two experimental (locating the center of the disk and positioning the eye horizontally) and one analytical (the trial and error method of finding the optic axis).

The spokes in Fig. 4 are more nearly equal than in Fig. 3. We conclude that the optical field of the pupil is spherically symmetric, and we emphasize that the transformation could not make it appear symmetric if it were not so.

The data from the three groups are shown more quantitatively in Fig. 5. Here we have plotted the orientation of the spokes in Fig. 4 along the abscissa, and the lengths on the ordinate. Note that the values for all three groups of fish show some scatter, but that the means ± S.D. overlap considerably. We conclude that all three sizes of fish have optical fields which are spherically symmetric and constant in angular subtense. The grand mean of the half acceptance angles is 91.8° ± 1.4°; the total optical field is twice that, or 183.6° ± 2.7° (means ± S.D.).

Retinal field

The lens was very nearly spherical; the ratio of equatorial to axial diameter was 1.04 ± 0.01 (mean ± S.E.M.). Hereafter, when we use the term "lens diameter", it will be the mean of these two. Its

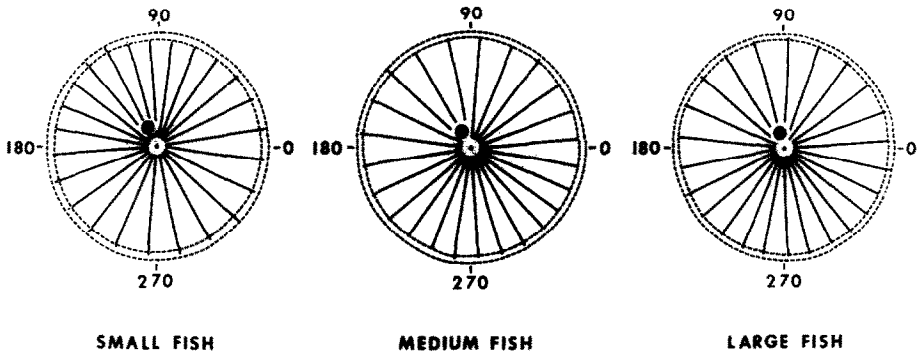

Fig. 4. The data of Fig. 3 transformed to show the optical field in relation to the optic center. The same conventions are used as in Fig. 3. The ranges are: 88–94°, 90–95°, and 90–94° for small, medium, and large fish, respectively.

relation to body length, shown in Fig. 6, is monotonically increasing, is probably not linear, and shows some scatter. This last feature is particularly evident for the two 20 cm fish; the diameters of their lenses ranged from 2.9 to 3.9 mm. In any one fish, however, the right and left lens diameters differed by no more than 11%, and usually by much less. At least some of the scatter in the measured values was due to meridional asymmetry of the lens. The ratio of equatorial to axial diameter was systematically greater in the nasotemporal than in the dorsoventral direction (1.07 ± 0.01 vs 1.02 ± 0.01, means ± S.E.M.)

In the remaining illustrations, we use lens diameter as the independent variable since it covaries more tightly than body length with other measures of ocular geometry. Figure 7A shows retinal length vs lens diameter. The straight line through the data is the least squares linear regression constrained to go through the origin. The good fit leads to the conclusion that retina and lens grew proportionately.

Figure 7B illustrates retinal field vs lens diameter. The striking correlation of Fig. 7A is noticeably absent here; the points scatter over 16°. The slope of the least squares linear regression equation is 2.6°/mm, suggesting that the retinal field increases slightly with growth of the eye. The data scatter so widely, however, that the regression equation has little predictive value (correlation coefficient = 0.40). The variance of the points around the regression line is sufficiently large that a horizontal line through the mean would also fit the data ($F = 2.7$; d.f. = 14; $0.1 < P < 0.2$). The apparent increase in the size of

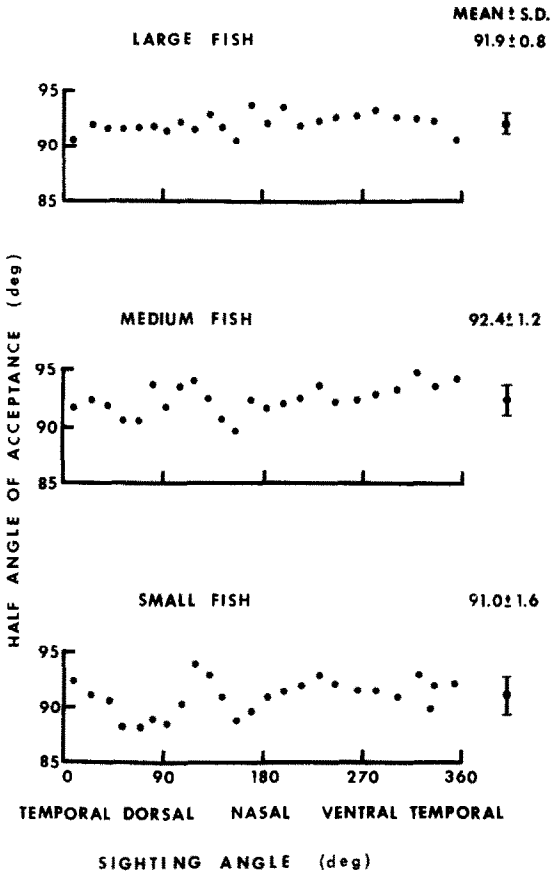

Fig. 5. The data of Fig. 4 plotted to permit a detailed comparison of the lengths of the half-spokes. The abscissa shows spoke angle, relative to optic center; the ordinate, spoke length. The means ± S.D. of each are given on the right.

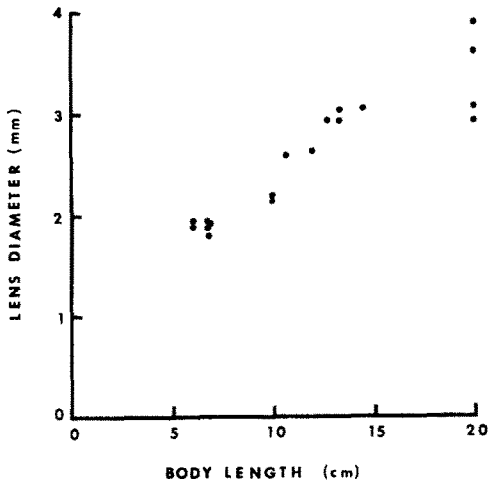

Fig. 6. Lens diameter vs body length. Each point refers to a different single lens.

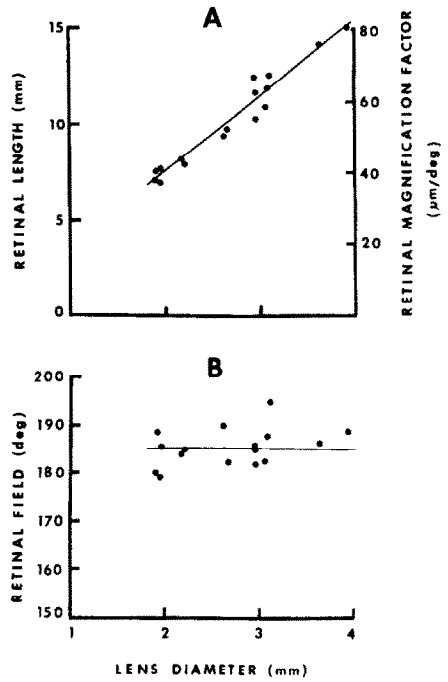

Fig. 7. A: Left ordinate: retinal length vs lens diameter. The line through the data is given by retinal length = 3.8 × lens diameter. Right ordinate: retinal magnification factor vs lens diameter. The retinal magnification factor is computed assuming a retinal field of 185.3° for all eyes. The line through the data is given in these coordinates by: retinal magnification factor = (20.5 × lens diameter) μm/deg mm. B: Retinal field vs lens diameter. The horizontal line shows the mean value (185.3°). In both a and b, each point represents a different eye.

the retinal field is not statistically significant; we conclude that the retinal field is constant at 185.3° ± 4.1° (mean ± S.D.). It is similar in all three planes of section; the means ±S.D. for the three orientations (nasotemporal, dorsoventral, and oblique) are 184.7° ± 2.6°, 186.0° ± 3.8°, and 185.8° ± 5.1°. From this we conclude that the retinal field is spherically symmetric.

Two sources of variability warrant mentioning. First, the uncertainty in locating the ora terminalis and the center of the lens would contribute 2–4° in the largest and smallest eyes, respectively. Second, small displacements of the lens, either artifactual or accommodative, could also play a role. For instance, a displacement of the lens center by only 5% of the lens diameter would alter ρ by 8°; recall that the entire range was 16°.

It is generally believed that accommodation in teleosts, when present, is accomplished through movement of the lens by contraction of the retractor lentis muscle [reviewed by Schwassmann (1975) and Sivak (1975)]. The accommodative state of the animal would therefore influence the size of the retinal field. Whether or not the goldfish accommodates is controversial; Kimura and Tamura (1966) reported that it does not, while Sivak (1973) reported that it does. We do not believe that accommodation accounted for the variability of lens position that we have observed, since all of the fish were deeply anesthetized prior to enucleation and accommodation should therefore have been relaxed (Tamura, 1957). The possibility that lens displacements were produced as an artifact of the freezing process cannot be excluded. We believe that much of the scatter in the values of retinal field stems from such displacements.

In six of the obliquely sectioned eyes, the same photographs included both the retinal axis and the optic disk. The center of the optic disk was displaced 5–11° in the ventrotemporal direction from the center of the retinal filed. This displacement is in the same direction as, but smaller than, the disk's displacement of 13–17° relative to the optic axis, illustrated in Fig. 4. The discrepancy between these two values implies that the retinal and optical fields were not exactly coaxial, but were tilted by a few degrees with respect to one another. Figure 2 illustrates the probable source of the difference; the plane of the pupil is slightly tilted with respect to the line connecting the two orae. The optic axis is almost certainly the line connecting centers of lens and pupil, and would therefore be tilted with respect to the retinal axis.

If we accept that the retinal field is equal to the mean value given above, and assume a spherical lens, then we can compute the retinal magnification factor, the number of μm/deg at the R/PRE boundary. This is given by the ordinate on the right of Fig. 7A. In these coordinates, the slope is 20.5 μm/deg mm.

Retinal sphericity was assessed by measuring the distance from the center of the lens to the R/PRE boundary at seven points: 0°, ±30°, ±60°, and ±90° with respect to the retinal axis. This distance was systematically greater axially, and decreased toward the equator (by 2, 6 and 14%, mean values at 30°, 60° and 90°, respectively).

The ratio: (distance from lens center to the R/PRE boundary)/(lens radius) was 2.46 ± 0.16 (mean ± S.D.) on the retinal axis, and decreased to 2.41, 2.31 and 2.12 at 30°, 60° and 90° respectively. It showed no systematic variation with lens diameter, indicating that small, medium and large eyes were conformal.

DISCUSSION

The main conclusions of this report are, first, that the optical and retinal fields are both spherically symmetric, second, that they do not vary as the animal grows, and third, that they are approximately equal (183–186°). It is important to stress the limits of these conclusions. We have not sampled very small goldfish, so we can not be sure that the field is constant very early in life. Concerning the equality and spherical symmetry of the two fields, we should point out that the optical field was measured in 12 meridians on all eyes, while the retinal field was measured in only one meridian per eye, and in only three meridians total.

Stell and Hárosi (1976) have reported that the goldfish retina is 10% longer nasotemporally than dorsoventrally. This asymmetry might be expected to produce a similar difference in the retinal fields, but we noted none. We have compared the retinal lengths histologically (Johns, unpublished data) and confirmed that the nasotemporal extent exceeds the dorsoventral, but only by 4%. Even so, our measurements should have caught such a difference in field size if it were there. We suggest that the retinal asymmetry

is not reflected in the fields, but instead, probably in slightly different magnification factors in the two meridians.

Hughes (1976) has recently compared the optical and retinal fields in fully dilated eyes of cats, and found that the optical exceeds the retinal by 38° in the horizontal meridian. Most of this excess (26°) is in the nasal field, where the animal's view is blocked by its nose. The remaining 12° in the temporal field are probably diminished by construction of the pupil, suggesting that the two fields may be more nearly equal for most conditions of vision. The goldfish lacks an appreciable pupillary reflex, therefore the optical field will not vary with light level. Another difference is the position of the eyes, frontal in cats and lateral in fish. Hughes (1976) states that in the rabbit, which also has lateral eyes, the two fields are equal. He suggests: "The discrepancy between the optical and retinal fields may thus be greater in animals with frontal than in those with lateral eyes" (p. 153). Our observations support this generalization.

The values which we obtained for the optical and retinal fields in the goldfish differ from those reported previously for fish: 203.5° (Müller, 1952), 195° (Charman and Tucker, 1973), 190° (Trevarthen, 1968), and 180° (Tamura, 1957; Walls, 1963). Tamura, Walls and Trevarthen assert their values of the optical field with no statement of how they measured it. In fact, the exact value was not very important in the contexts of their papers, so we suggest that they were only approximate estimates, and we believe our value of 183.6° to be more carefully derived. Müller worked on the eye of the guppy (*Lebistes reticulatus*), and made all his measurements on unfixed and unfrozen whole eyes. He drew an outline of the eye, assigned a center to the round profile of the sclera, and measured the angular subtense of the sclera about this center, apparently assuming that the sclera and the retina were concentric. Our frozen sections (see Fig. 2) show that the R/PRE boundary is not concentric with the external boundary of the sclera. The latter has a smaller radius, owing to the fact that the retina approaches more closely to the sclera at its margins. Thus, Müller's method of measurement overestimated the retinal field. Its relation to the optical field is unclear. In the recent report of Charman and Tucker (1973), the figure given for the goldfish retinal field is 195°. These workers used methods essentially similar to ours, so we must attempt to account for the difference of 9–12° between their value and ours. We first suspected that the lenses might have assumed different positions in the frozen eyes. If the lenses had moved toward the cornea in our fish or toward the retina in theirs, then the two results would differ in the observed direction. But both groups found that the lens and R/PRE boundary were concentric, which rules out that interpretation. A more likely explanation is that our criteria for locating the ora terminalis were different from theirs. We have stated ours in the Methods, and feel quite confident that they are accurate, since they are supported by the evidence from histological sections.

Such strict attention to quantitative details might be unwarranted were it not for the fact that the relation between the two fields bears on retinal growth. If the optical field were 190° or less, in keeping with the results of Tamura (1957), Trevarthen (1968), and this report; and if the retinal field were 195° as stated by Charman and Tucker (1973); and if the two fields were coaxial; then there would be an annular zone, 2.5–7.5° wide, around the margin of the retina, shadowed from image-forming rays. This is the zone where retinal neurogenesis is believed to occur in both embryonic (Hollyfield, 1972) and adult (Müller, 1952; Johns and Easter, in preparation) fish eyes. In view of the fact that much of the retinal development in other animals goes on in reduced, diffuse light (e.g. *in utero*, *in ovo*, or behind closed lids), it seemed possible that a peripheral dark annulus of functional significance might exist. We are convinced, from our measurements, that this is not the case. Even if the two fields were coaxial, their sizes matched so closely that the entire retina would be exposed to light. Given that the two fields are tilted slightly with respect to one another, it follows that a crescent-shaped portion of the ventrotemporal retina may be shaded but the dorsonasal retinal margin would therefore always be exposed to light entering through the pupil. Since retinal neurogenesis goes on even in that region, reduced light must not be required.

In other respects, our data agree with Charman and Tucker (1973). Specifically, we concur on the near-sphericity of the retina, on the concentricity of the lens and retina, and on the approximate emmetropy of the eye. This latter point stems from our observation that the distance from lens center to the R/PRE boundary was 2.12–2.46 times the lens radius, and from their conclusion that the focal length of the lens was 2.36 times the lens radius. This value differs substantially from Matthiessen's ratio of 2.55 (Matthiessen, 1880), and our fishes' eyes would have been badly hypermetropic with lenses satisfying Matthiessen's ratio. In view of Schwassmann's (1975) finding that goldfish are emmetropic, we favor the value of 2.36 over the older, larger value.

Müller (1952) found that the retina and lens grew proportionately in guppies, and our data on goldfish confirm his results. Both Müller (1952) and Baerends, Bennema and Vogelzang (1960), who studied a cichlid, *Aequidens portalegrensis*, found that the growth of the lens was positively allometric with respect to the growth of the eye as a whole. This means that the proportion of the eye occupied by both the lens and the retina is greater in larger fish.

A final remark concerns the changing relation between distance on the retina and degrees in the visual field, illustrated in Fig. 7a. There are more μm/deg in the large eyes than in the small ones, which implies that the size of the receptive fields of retinal neurons must change as the eye grows. If the angular subtense of the receptive fields is kept constant, the diameter, in μm on the retina, must increase. If, on the other hand, the diameter in μm is fixed, then the angular subtense must decrease. There are no data available to suggest which stratagem, or combination of them, the animal follows. Since it is generally believed that receptive field size is correlated with dendritic spread (Brown, 1965), the first alternative (fixed angular subtense, increasing dendritic spread) implies neuronal growth and presumably an addition of synapses to individual neurons throught adult life. We intend to investigate this matter further.

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