Vision Research Vol. 21, pp. 1497 to 1504, 1981
Printed in Great Britain

0042-6989/81 101497-08$02.00/0
Pergamon Press Ltd

GROWTH-RELATED CHANGES IN THE SIZE OF RECEPTIVE FIELD CENTERS OF RETINAL GANGLION CELLS IN GOLDFISH

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(*Received* 4 *December* 1980)

Abstract—Intraocular recordings were made from the retinal ganglion cells of small (< 40 mm) and large (> 140 mm) intact paralyzed, submerged goldfish to determine how the size of their receptive field centers is influenced by the 2.5-fold increase in retinal magnification factor which accompanies growth. The angular subtense of the centers was only slightly smaller in large than in small fish, corresponding to a greater than 2-fold increase in the center diameter as measured in micrometers on the retinal surface. This statistically significant increase suggests that the number of centers which overlap a given point on the retina remains approximately constant during growth. Other implications of this result are also discussed.

INTRODUCTION

Throughout the life of a goldfish, new neurons are added to the periphery of a functional, active retina (Johns and Easter, 1977). Concurrently new synapses are added to the central retina, far from the site of neurogenesis (Fisher and Easter, 1979). Thus retinal anatomy changes continuously. In the preceding paper (Macy, 1980) and in this one, the possible changes in retinal function are investigated. In the first paper, the qualitative characteristics of the receptive fields of retinal ganglion cells were examined. Briefly, fields were quite similar in large and small animals, the one exceptional property being orientation selectivity, which was more frequently encountered when recording from larger animals. In this paper, we examine a more quantitative question; namely, how does retinal growth affect the sizes of the ganglion cells' receptive fields?

This line of inquiry arose naturally from a consideration of the goldfish's physiological optics. The shape of this animal's eye is independent of its size, and the distance from the center of the spherical lens to the retina is scaled proportionally to the diameter of the lens (Easter *et al.*, 1977). The lens, the only optically active element, has its secondary nodal point at its center (Charman and Tucker, 1973). It follows that the "retinal magnification factor", defined as the number of micrometers on the retinal surface per degree of visual angle, varies linearly with the diameter of the lens. In other words, the same visual solid angle projects to larger retinal areas as the eye grows. This increase can be substantial, since the lens diameter increases from about 1.5 to 4.0 mm from yr 1 to 5. During this time, the number of ganglion cells has increased and they have spread out on the retinal surface (Johns and Easter, 1977; Kock and Reuter, 1978). How has the retina managed to adapt to this continuous change? The general problem is as complex as visual functions are numerous, but one particular aspect—the size and overlap of receptive fields—is susceptible to experimental analysis. We have undertaken such an analysis by measuring the receptive fields of ganglion cells in large and small fish and then comparing them in the context of growth.

We suggest that three concrete hypotheses help to put the problem in perspective. Each of the three assumes that one aspect of the receptive fields is held constant during growth, and each predicts a different change of receptive field size. The three hypotheses are not the only ones possible, but they are probably the easiest to understand. They are described below.

(1) Constant micrometers hypothesis. The diameter of the center of a retinal ganglion cell's receptive field, as measured in μm on the retinal surface, remains constant. If this is true, it follows that the angular subtense of the field must decrease, reciprocally with the increase in retinal magnification factor.

(2) Constant degrees hypothesis. The diameter of the center of a retinal ganglion cell's receptive field, as measured in degrees of visual angle, remains constant. This predicts that the diameter of the field, measured in μm on the retinal surface, must increase linearly with the retinal magnification factor.

(3) Constant overlap hypothesis. The "overlap factor" (the number of receptive fields within which a given point on the retina is included: Fischer, 1973) remains constant. The prediction here is slightly more complicated than in the first two cases, as it depends upon knowing the planimetric densities of the ganglion cells (the number per mm^2) in small and large retinas. These figures are known, and lead to the prediction that the angular subtense of the centers of

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receptive fields should decrease with growth, but the decrease should be less than predicted by the constant micrometers hypothesis.

Depending on one's bias, each of the three has attractive features. For instance, if one accepts that the diameter of the receptive field's center is determined by the diameter of the ganglion cell's dendritic tree (e.g. Brown and Major, 1966), then the constant micrometers hypothesis suggests that the dendritic tree, once established early in life, would not have to change thereafter. This is an attractive simplifying feature to the anatomist, but it seems a complication to the visual physiologist, as a given optic fiber would then report on a steadily shrinking portion of the visual world. To the physiologist, the constant degrees hypothesis is probably more attractive, as it implies a constant relation between the outside world and an optic fiber. Similarly, the constant overlap hypothesis implies a constancy between an ensemble of fibers and the outside world. As it turns out, the data do not fit any of the three predictions perfectly, but one, the constant micrometers hypothesis, can be rejected. Retinal receptive fields, measured in micrometers on the retinal surface, enlarge as the animal grows.

METHODS

Measurement of retinal magnification factor

Retinal magnification factor was directly measured in five eyes from small goldfish (35–45 mm, standard length) and in two eyes from large goldfish (110 mm). Each eye was removed from an anesthetized fish and a small hole was cut in the fundus as close as possible to the intersection of the optic axis with the retina. The eye, supported by a metal ring, was submerged under water in a transparent, flat bottomed vessel on the stage of a dissecting microscope. The pupil faced downward to view two parallel bars drawn on a card. The angular subtense of the bars was calculated from their separation and their optical distance from the eye. The image of the bars formed by the optics of the eye came to clear focus at a plane close to that previously occupied by the retina. The separation of the bars in the image was measured at the plane of best focus with an ocular micrometer, and retinal magnification factor was calculated by dividing the distance between the images of the bars (in μm) by their angular subtense at the eye (in deg of visual angle). After each measurement the lens was removed and its diameter was measured.

Measurement of receptive field center diameter

Most of the methods used for this part of the study have been presented in the preceding paper (Macy, 1981). Briefly, paralyzed goldfish gazed through water and through a flat clear window at a rear-projection tangent screen. The activity of single retinal ganglion cells was recorded with metal-filled micropipettes inserted into the eye through a small hole in the dorsal-caudal sclera. Twenty-nine small goldfish (standard length, 39.7 mm $\pm$ 6.1 mm, mean $\pm$ SD) and 5 large goldfish (149.00 mm $\pm$ 10.9 mm) were used. Immediately following each recording session, the lens was removed and its diameter measured, for purposes of computation of the retinal magnification factor, according to the formula:

$$\text{retinal magnification factor} = 20.5 \times \text{lens diameter}$$

where retinal magnification factor is expressed as μm/deg, and lens diameter is measured in mm (Easter *et al.*, 1977).

Receptive fields were mapped initially with a flashing 5.6° dia red disk, on 60° dia green background (intensity 6.2×10^9 quanta/sec-mm^2), and the site of maximum sensitivity was located. The coordinates of this site, relative to the optic disk, were recorded. Subsequent stimuli (successively larger red disks) were centered there, and threshold was determined for each. Stimulus duration was 1 sec, interstimulus interval, 1 sec.

Stimulus intensity was set by calibrated neutral density filters. Log threshold was defined as the stimulus intensity which, for units with spontaneous activity, elicited a change in firing rate detectable in the output of an audio monitor, or, for non-spontaneous units, elicited a response of one or more spikes on 3 out of 6 stimulus presentations. All values of stimulus diameter and corresponding log threshold were entered into a digital computer, after the experiment, for further analysis.

The diameter of the center of each receptive field was determined from the relationship between the diameter of the stimulus and the sensitivity (1/threshold) of the cell to that stimulus. This was done in three ways, called the "peak-sensitivity," "equivalent" and "fitted gaussian" center methods.

The "peak-sensitivity" center diameter was defined as the stimulus diameter for which further increases in the size of the stimulus did not lead to an increase in log sensitivity of more than 0.15 log units. The factor of 0.15 log units was introduced to reduce the effects of random variations in sensitivity upon the measured center diameter.

Second, the "equivalent center" diameter was determined according to the procedure of Cleland and Enroth-Cugell (1968). A line with a slope of two was fit to the first two points (5.6° and 8.2°) of a log diameter–log sensitivity plot. The x-coordinate of the intersection of this line with a horizontal line drawn through the maximum log sensitivity was defined as the equivalent center diameter of the cell's receptive field.

Both the peak-sensitivity and equivalent center diameters were calculated for each cell by computer.

The "gaussian-fit" center diameter was estimated with the help of a set of computer-generated log diameter–log sensitivity plots modeled by assuming a receptive field sensitivity weighting function given by the sum of a positive and negative gaussian curve (Schade, 1956; Enroth-Cugell and Robson, 1966;

Rodieck and Stone, 1965). Several such theoretical area-sensitivity functions, corresponding to sensitivity profiles having different ratios of center/surround diameters and center/surround amplitudes were plotted on clear plastic, and fit by eye to the empirically derived log diameter–log sensitivity data of each cell.

RESULTS

Changes in retinal magnification factor during growth

In Figure 1 the retinal magnification factor is plotted as a function of lens diameter. The solid line shows the prediction by the empirical equation of Easter, Johns and Baumann (1977). The good fit supports the conclusion that retinal magnification factor changed in direct proportion to the diameter of the lens, and justifies use of the equation for later calculations of retinal magnification factor.

Changes in receptive field center diameter during growth

The center diameters of receptive fields were determined for 106 units: 55 from small fish, 51 from large fish.

Three typical log diameter–log sensitivity functions are shown in Fig. 2. Each point represents one measurement. Solid lines connect the mean log sensitivities of several replications. The measured peak-sensitivity center diameters are shown by the vertical lines, the x-coordinates of which are listed at the right. Note that the log sensitivity may level out or turn downward with large stimulus diameters. The downward slope results from an antagonistic surround region, and the value of the slope indicates the strength of the surround. The slopes obtained from large fish were significantly more negative than those of the small fish ($P < 0.001$, t-test, two tailed). Therefore, larger fish had stronger surrounds.

The relationship between the peak-sensitivity center diameter and lens diameter is shown in the scatterplots and histograms in Figs 3 and 4, respectively.

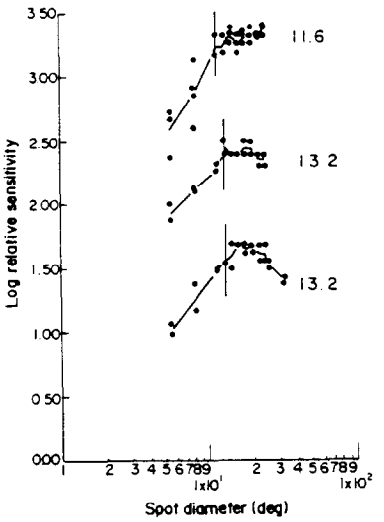

Fig. 2. This plot shows the log diameter–log sensitivity functions determined for three retinal ganglion cells. Log relative sensitivity (1/threshold) is plotted against log stimulus diameter. A sensitivity of 0.0 relative log units corresponds to a stimulus intensity of 6.8×10^{11} quanta/sec mm^2 at the surface of the retina, 1.3×10^7 636 nm-equivalent quanta/sec per red-sensitive cone, and 1.2×10^6 533 nm-equivalent quanta/sec per green-sensitive cone. The middle and bottom curves have been shifted downward by 0.5 and 2.0 log units, respectively. Each point is derived from one determination of sensitivity for a given stimulus diameter. The mean log sensitivities of several replications are connected by solid lines. The peak-sensitivity center diameters determined from these functions are listed at the right, and are indicated by the vertical bars which pass through the functions. The equivalent and gaussian fit center diameters determined from these area-sensitivity functions are: top function, 13.8 and 12.4 deg, middle function, 10.9 and 11.1 deg; and bottom function, 12.4 and 12.4 deg.

The analogous relationships for equivalent center diameters are shown in Figs 5 and 6, and for gaussian-fit center diameters in Figs 7 and 8. Note that the histograms are scaled in both degrees and micrometers.

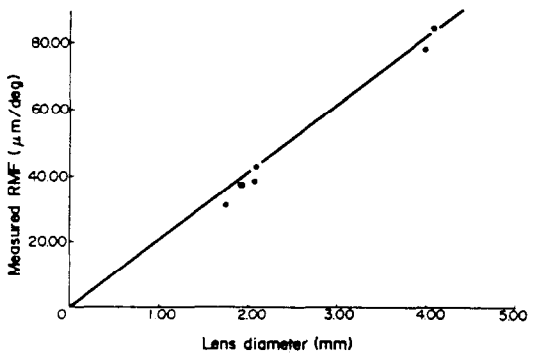

Fig. 1. Relationship between measured retinal magnification factor and lens diameter. Each point represents the retinal magnification factor as determined by direct examination of the image formed by the goldfish's eye. The solid line indicates the predicted change in retinal magnification factor according to the equation in Easter *et al.* (1977).

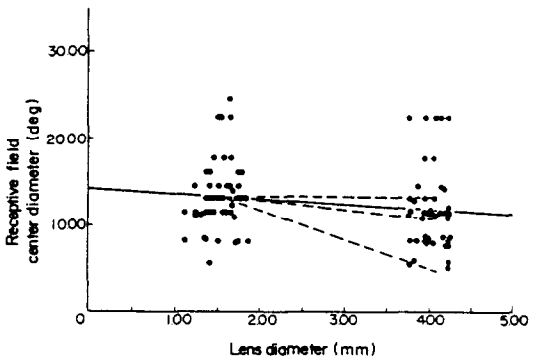

Fig. 3. Measured peak-sensitivity center diameters as a function of lens diameter. Each point represents a measurement of the peak-sensitivity center diameter for a single unit. The solid line is the best fitting least-squares linear regression. The three dashed lines represent, from lowest to highest, predictions of the constant micrometers, overlap, and degrees hypotheses, respectively.

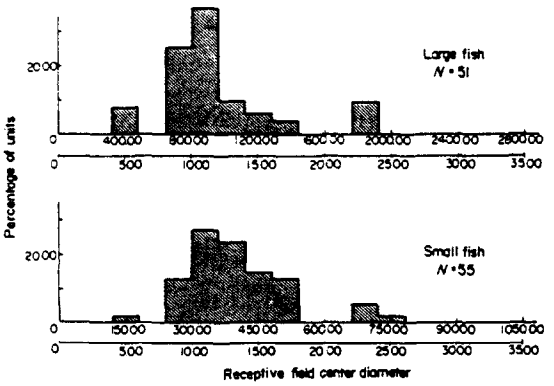

Fig. 4. The distribution of peak-sensitivity center diameters in small and large fish. Each of the two histograms is plotted vs center diameter in terms of deg of visual angle (lower axes) and μm on the retinal surface (upper axes). The mean retinal magnification factors for small and large fish were 32 and 83 μm/deg respectively. For clarity of presentation, values of 30 and 80 micrometers degree were used to calculate the values displayed on the μm axes. The bin width is 2 deg of visual angle.

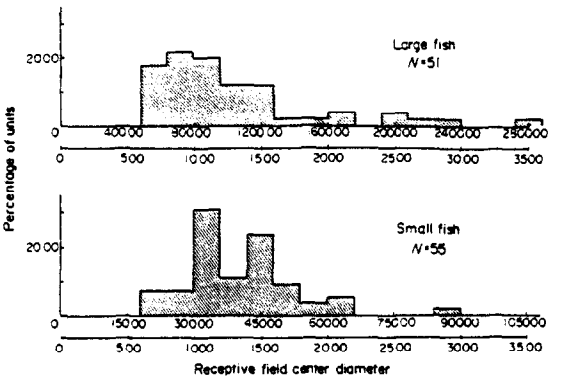

Fig. 6. The distribution of equivalent center diameters in small and large fish. Conventions are as in Fig. 4. The same unit that was omitted from Fig. 5 was also omitted here, although it was included in the calculations used to determine the percentage units in each bin.

In the scatterplots (Figs 3, 5 and 7) each point represents the measured center diameter of the receptive field of a single unit. The solid lines are the least-squares linear regressions to the data. The three dashed lines give the predictions of the three hypotheses: the lowest, middle, and highest show, respectively, the predictions of the constant micrometers, constant overlap, and constant degrees hypotheses. The basis for predicting the first and last of these is obvious, but the prediction of the constant overlap hypothesis requires knowledge of (1) the number of ganglion cells and (2) the area of the retina in small and large fish. The former is inferred from electron microscopic counts of optic nerve fibers in fish of comparable size (Easter *et al.*, 1979; Easter, in preparation), and the latter may be computed from the diameter of the lens (Johns and Easter, 1977). Since ganglion cells are distributed homogeneously across the retinal surface (Johns and Easter, 1977), these data allow calculation of the planimetric density of the ganglion cells, which may then be used, with average receptive field diameter, to compute overlap factor (Fischer, 1973).

Table 1 summarizes the results statistically and compares them with the predictions of the three hypotheses. The three columns display the results obtained with peak-sensitivity, equivalent, and gaussian-fit center diameters. The first two rows show the

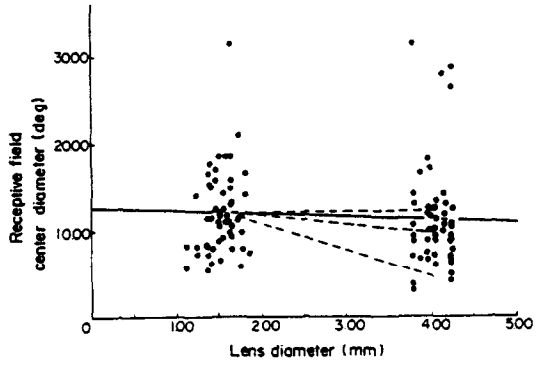

Fig. 7. Measured gaussian-fit center diameters as a function of lens diameter. Conventions are as in Fig. 3.

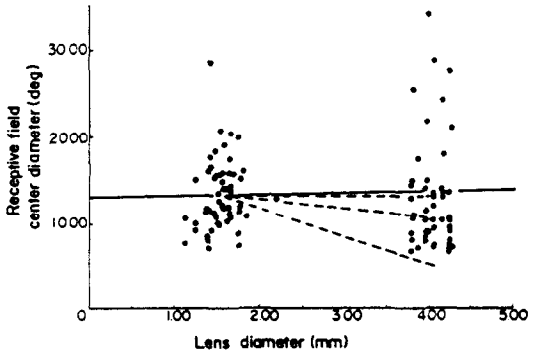

Fig. 5. Measured equivalent center diameters as a function of lens diameter. Conventions are as in Fig. 3. One unit with an equivalent center diameter of 64.3° recorded in a fish with a lens diameter of 3.9 mm is not represented.

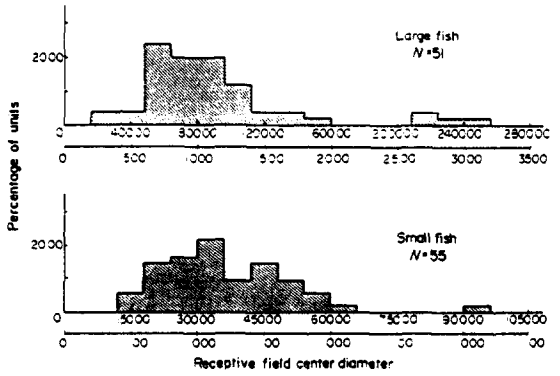

Fig. 8. The distribution of gaussian-fit center diameters in small and large fish. Conventions are as in Fig. 4.

Table 1. Center diameters in small and large fish: observations and predictions

	Peak-sensitivity center diameter	Equivalent center diameter	Gaussian-fit center diameter
Observations:			
Small fish	13.4	13.4	12.1
Large fish	11.9	14.0	11.1
Ratio:			
Large/small	0.89	1.04	0.92
Predicted ratios:			
Micrometers	0.38	0.38	0.38
Significance*	$P < 0.0005$	$P < 0.0005$	$P < 0.0005$
Overlap	0.80	0.80	0.80
Significance†	$P > 0.2$	$P < 0.001$	$P > 0.1$
Degrees	1.0	1.0	1.0
Significance*	$P < 0.05$	$P > 0.25$	$P > 0.1$

* One-tailed significance level.
† Two-tailed significance level.

mean diameters measured, by each procedure, in small and large fish. The observed ratio: (mean center diameter in large fish/mean center diameter in small fish) appears in the third row. The final six rows display, for all three procedures of measurement, the ratio of center diameters predicted by the three hypotheses, and the significance levels at which the observed ratios differ from the predicted ratios.

It is clear from the data in Figs 3–8 and Table 1 that the constant micrometers hypothesis is untenable. The receptive field center diameters, as measured in micrometers on the retinal surface, enlarged substantially as the animals grew. Although the three methods of estimating diameter gave slightly different values, they all showed large increases in the means: 429 to 988, 429 to 1162, and 387 to 921, by the peak-sensitivity, equivalent, and gaussian–fit methods, respectively. An increase is predicted by both of the other competing hypotheses and when both were tested statistically against the data, neither was ruled out consistently. The peak-sensitivity method favored the constant overlap hypotheses; the gaussian-fit method found both hypotheses acceptable; the equivalent center method favored the constant degrees hypothesis by virtue of the strong rejection ($P < 0.001$) of the constant overlap hypothesis. This latter conclusion must be slightly discounted, however, as it depended on inclusion of one receptive field which had a center diameter of 64 deg. This value is large compared with the peak-sensitivity and gaussian-fit center diameters of this unit (17.8 and 11.7 deg, respectively), because the initial slope of the log diameter–log sensitivity plot was much less than 2. When the equivalent diameter of this cell was replaced by that obtained by the peak-sensitivity or gaussian-fit analysis, the mean equivalent center diameter for large fish became 13.1 or 13.0 deg, respectively, lower than in small fish. With this change, the constant overlap hypothesis is still ruled out, but less strongly ($P < 0.01$).

In summary, the constant micrometers hypothesis is ruled out. Neither of the remaining hypotheses can be ruled out; whether one or the other fit the data better depended upon how the centers were estimated.

Several possible complications will now be evaluated.

When the data are pooled, as above, it is unclear if all types of units were affected by growth in the same ways. This was clarified by subdividing the data into three classes: on-, off, and on-off-center units. Table 2 gives the results. Although there were small differences in the mean receptive field diameters of the several types, all three changed similarly with growth.

The relation of center diameter to length of the recording session might be a problem, since recording sessions with large fish lasted longer than those with small fish. In particular, our results would be affected if units recorded late in a session had larger or smaller receptive fields. A regression analysis ruled out this concern; when receptive field diameters were

Table 2. Changes in the peak-sensitivity center diameters of on-center, off-center, and on-off-center cells

Field type	Small fish N	Small fish Peak-sensitivity center diameter	Large fish N	Large fish Peak-sensitivity center diameter
On-center	9	13.5	18	12.0
Off-center	29	14.5	19	12.6
On-off-center	17	11.4	14	10.8

regressed against (elapsed) times of recording, the two variables correlated very poorly ($r^2 < 0.06$ for small and large fish).

The relation of center diameter to retinal eccentricity might present a problem, particularly since the central 60° of the visual field contains more ganglion cells in a large retina than a small one. In the latter, the central 60° contains 15,640 ganglion cells, computed from the same information mentioned earlier for computation of overlap. Due to changes in retinal magnification factor and ganglion cell density, these occupy only the central 48° of the retina in large fish; 8500 new ganglion cells have been added to the sampled population. If the more eccentric cells had larger fields, as is the case in cats (Wiesel, 1961), then the difference in the populations sampled could affect the results. Once again, this can be dismissed. When center diameter and retinal eccentricity were regressed against one another, they correlated very weakly ($r^2 < 0.02$, for small and large fish).

Finally, differences in image quality between large and small fish might confound our results. Specifically, the scleras of the eyes of small fish were more pliable and delicate than those of large eyes. If the eye of the small fish were more susceptible to deformation during surgery than that of the large fish, this could degrade the small fish's image, which would lead to spuriously large estimates of center diameter. To assess the quality of the retinal image in small fish, drifting square-wave gratings of various spatial frequencies were used. Of 14 cells from small fish presented with grating stimuli, 11 gave clear responses to gratings with spatial frequencies as high as 0.36 c/deg (2.78 deg/c), even when the measured center diameter was as large as 14°. This suggested, as Schwassman (1975) concluded, that the paralyzed goldfish eye is roughly emmetropic, and that image quality is quite good. It is possible to be more precise, and to estimate the contribution of blur to the measured diameter of a receptive field. This will be taken up in the Discussion.

DISCUSSION

Relation to previous work on retinal ganglion cells

The receptive field center diameters measured in this study are within the ranges seen in other investigations of the goldfish visual system in which the eye was submerged during recording. Cronly-Dillon (1964) reported diameters ranging from 3 to 18 deg of visual angle and Schellart and Spekreijse (1976) found mean "on-" and "off-center" diameters of 7° and 13°, respectively. The agreement is especially good in light of the following two differences in procedure. First, these other studies involved tectal rather than retinal recordings. Therefore, the populations of units examined probably included intrinsic tectal cells as well as retinal ganglion cell terminals. These two types of units might display different distributions of receptive field center diameter, and neither study employed procedures to discriminate between the two. The second difference is that the others mapped receptive fields with small spots of light, which can give results very different from those of the diameter-sensitivity trade-off (Cleland and Enroth-Cugell, 1968).

In isolated retina and *in situ* eyecup studies, center diameters of receptive fields are reported in micrometers or millimeters on the retinal surface. In order to compare these diameters with measurements of the angular subtense of the centers, a knowledge of the retinal magnification factor is needed for each study. Since Wagner *et al.*, (1960) and Adams (1970) report only the tip-to-tip lengths of their fish, we have estimated the retinal magnification factors in these studies from the relationship between tip-to-tip length and lens diameter in the fish of the present investigation. Thus, Wagner *et al.* found field centers 8.4–33.6 deg in diameter, and Adams observed a mean center diameter of 15.0 degrees of visual angle. Adam's result is most pertinent to the present study, since it was obtained using diameter-sensitivity functions. The diameters reported by Daw (1968) are difficult to interpret in terms of angular subtense, since he gave an ambiguous measure of the size of the eye, and an unreasonably large retinal magnification factor.

The overlap factors calculated here (>700) are much larger than those seen in cats. Fischer (1973) found an overlap factor of approximately 35 for all positions in the cat retina. Peichl and Wässle (1979) calculated overlap factors of less than 20 for X and Y cells, and approx. 60 for sluggish cells and units with non-concentric receptive fields. They suggest that the latter number would be about 150 if the peak-sensitivity method of receptive field estimation were used, but this is still only about one fifth the overlap computed for fish. The species difference probably accounts for this large difference. Another possibility is that in the present study an electrode bias restricted sampling to only the largest ganglion cells of the retina, passing over small cells with small receptive fields. However, since the receptive field dimensions seen in this study are similar to those of units found in a variety of preparations (isolated retina, optic nerve, optic tectum and *in situ* eyecup), with a variety of microelectrodes, this requires that the same degree of sampling bias be present in all of these preparations, and is therefore an unlikely explanation.

Rusoff and Dubin (1977) found that the angular subtenses of the receptive field centers of the kitten's retinal ganglion cells were larger than those of the adult cat. Their results suggested that the center sizes, measured in μm on the retinal surface were approximately the same in the two populations. Again, the difference between their results and those of the present study can most likely be attributed to species differences, particularly as they relate to differences in retinal growth (Johns *et al.*, 1979).

Correlations with anatomy

If the diameter of a receptive field center and the size of the dendritic tree are positively correlated, as is strongly suggested by work of Brown and Major (1966), Boycott and Wassle (1974), and others (however, see Nelson *et al.*, 1978), the results imply that the diameters of the dendritic trees of retinal ganglion cells increase as the goldfish grows. This inference is supported by a methylene blue study of ganglion cells in the closely related Crucian carp (Kock and Reuter, 1978), in which the authors reported that, "In large eyes ganglion cells clearly have longer dendrites and wider dendritic trees than in small eyes...

The number of photoreceptors per ganglion cell receptive field can be calculated from the measurements in this report and the cone densities reported by Johns and Easter (1977). The average receptive field center (determined by the peak-sensitivity method) contains 2230 and 7600 cones in the small and large fish, respectively. One might expect this increased convergence to be accompanied by synaptogenesis in the retina, and an electron microscopic study of the central retina of young and old goldfish has shown a substantial increase during growth in the number of inner plexiform layer synapses per ganglion cell (Fisher and Easter, 1979).

Alternative models

Inasmuch as retinal ganglion cells enlarge as the animal grows, (Johns and Easter, 1977; Kock and Reuter, 1978) there could be a subpopulation of cells which are too small to be detected in small fish, but large enough to be detected in larger animals. This could account for all or part of the small decrease, during growth, in the measured angular subtense of the receptive field centers. If so, then the constant degrees hypothesis would be supported more strongly than the constant overlap.

A second explanation for the small decrease in the angular subtense of the centers could be the presence of stronger surround mechanisms in large fish. Depending upon the assumptions one makes about the shapes of the center and surround mechanisms, the mean angular subtense of the center mechanisms might have remained constant during growth, while the increasing strength of the surround components caused the measured subtense of the center to decline slightly. This should not be thought of as an artifact, but as one possible mechanism which causes the effective angular subtense of the center diameter to decrease slightly during growth.

As described in the methods of the companion paper (Macy, 1981), the angular subtense of a given distance on the tangent screen varied with position of the screen. Thus some scatter in the results could have been caused by differences in the positions of the receptive fields. However, any contribution of this sort must have been small, since no correlation was observed between the center diameters of receptive fields and their positions on the screen.

Quality of the optical image

Finally, the question of image quality must be addressed. Suppose that the small fish, for whatever reason, had a blurred retinal image. This would result in spuriously large receptive fields, and would weaken our conclusion that the angular subtense of fields was nearly constant with growth. It was pointed out earlier that units with receptive field diameters as big as 14° responded to drifting square wave gratings of 0.36 c/deg which suggested that blur was not important. Here we evaluate the issue more quantitatively. (We are indebted to Professor D. G. Green for introducing us to this analysis.)

If the optic point spread function is assumed to be a gaussian, and the harmonics of the square wave gratings are ignored, then the characteristic radius, r_c, of the point spread function may be computed from the equation:

$$S = e^{-(\pi r_c v)^2}$$

where S is the minimum contrast of the grating required to elicit a response from a cell, and v is the spatial frequency of the grating (Enroth-Cugell and Robson, 1966). For example, if the contrast required for detection of a 0.36 c/deg grating is assumed to be 10%, the characteristic radius of the point spread function must be less than 1.3 deg. Similarly, for a required contrast of 1.0%, r is at most 1.9 deg. If a gaussian shape is assumed to approximate the point weighting function of the receptive field (Schade, 1956; Enroth-Cugell and Robson, 1966; Rodieck and Stone, 1965), the effect of stimulus blur on the field width at half maximum sensitivity (FWHM, roughly the measured diameter) may be estimated by convolving the point spread function of the retinal image with the point weighting function of the receptive field. This is easily calculated, since the convolution of two gaussians is a new gaussian with a characteristic radius given by the square root of the sum of the squares of the individual characteristic radii. Thus, for optical point spread functions, calculated above, of 1.3 and 1.9 deg, a receptive field with a true FWHM of 12.0 deg would be measured as having a FWHM of 12.2 and 12.4 deg, respectively. Therefore, even if the units which responded to gratings with a spatial frequency of 0.36 c/deg required a contrast of only 1.0%, the blur would be estimated to increase the diameter of a 12 deg receptive field center by less than 0.4 deg. This supports the view that the receptive field center diameters in small fish are not significantly increased by blur.

If the small retinas did not have blurred images, perhaps the large ones did. It could be argued that the true mean receptive field diameter in the large fish was closer to 5°, the value predicted by the constant micrometers hypothesis, but a degraded image caused the measured value to be spuriously high. In order for

this to mask a true decrease in the mean angular subtense of the receptive field centers during growth, the scatter would have to cause receptive fields with a true diameter of about 5 deg to appear to have a diameter of over 11 deg. Assuming, as before, a receptive field center with a gaussian shape and a gaussian point spread function, it can be shown that such an increase would require image degradation having a point spread function with a FWHM of at least 9.8 deg. The image was much better than this; when it was observed during measurement of the retinal magnification factor, it had clear discrete bars separated by only 2 deg of visual angle. Therefore, the constant micrometers hypothesis cannot be resurrected by invocation of poor image quality in large fish.

Conclusion

There is a substantial increase, during growth, in the center diameters of the goldfish's retinal ganglion cells, as measured in micrometers on the retinal surface. The extent of this increase is consistent with both the constant degrees and the constant overlap hypotheses.

Acknowledgements—This work was supported by PHS Grant EY-00168 (to S.S.E.) and fellowships (to A.M.) from PHS (Training Grant EY-07022) and The Rackham School of Graduate Studies. We thank Drs D. G. Green, M. Alpern and A. Rusoff for useful discussions.

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