the hyperpolarization of cones. This proposal together with the suggestion that barium ions reduce the potassium efflux in cones predicts that the receptor potential amplitude of cones should decline in the presence of barium. Such a decrease is noted in this study and elsewhere.²

Also consistent with this interpretation is our present finding that barium ions delay the onset of rapid dark adaptation but that the rate of recovery, once begun, is unaffected. The onset of this adaptation process is highly temperature-sensitive and therefore may represent an enzymatic process which removes the blocking agent or the inhibitory substance from the sodium channels.³ It is not unreasonable that barium may act directly on this proposed enzymatic process so as to impede the removal of the sodium channel inactivator. Such a possibility is not remote since barium is known to affect enzyme systems.⁴, ⁵ Because the onset of the adaptation process in rods is also postulated to be governed by the enzymatic removal of an inactivator from the sodium channels,⁶ we anticipate that barium ions will increase the latency of the recovery process in rods as well. Research in our laboratory is currently under way to test this hypothesis.

We are indebted to Ms. Rita Dunford and Ms. Debbie Frechette for their expert technical assistance. We thank the IVAC Corporation of San Diego for their generous gift of the Model 200 gravity flow controller used in this study.

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Key words: barium, rapid dark adaptation, cones, bullfrog, retina, photoreceptor

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An estimate of image quality in the rat eye.

AUSTIN HUGHES AND HEINZ WASSLE.*

The point spread function on the optic axis of the rat eye is indirectly estimated to increase from a half-height width no greater than 12.5' to not less than 36' after dilation of a 0.33 mm pupil diameter to 3.0 mm.

A modulation transfer function (MTF) curve is not available for the rat. The following measurements provide an estimate of the minimum spatial frequency at which image contrast disappears close to the optic axis of the rat eye.

Methods. Observations were made on the eyes of five D.A. rats of between 115 and 130 days of age (215 to 230 gm weight). The animals were anesthetized by the intraperitoneal injection of 1 cc of 25% urethane solution and mounted in a head holder. Saline irrigation was employed instead of a contact lens. At first, the natural pupil was used, but later it was dilated by atropine. The apparatus of Fig. 1 is essentially that of Wässle.* A grating of transparent and opaque bands was
Fig. 1. Apparatus employed for the visual estimation of the double-pass spatial cut-off frequency of the rat optical system.

placed at the focus of a 110 mm camera lens (Super Takumar 55 mm; f2 plus APS Auto-Plus X 2), the ocular lens. The grating was illuminated by a collimating lens (Super Takumar 55 mm) with a pinhole source located at its focus. The necessary working distance and small pupil required the insertion of a 10 D lens at some distance in front of the observer’s eye in order to increase the field of view by the use of indirect ophthalmoscopy. The living eye was centered on the optical axis of the system with the source in Maxwellian view. For a given size of pupil, the grating was introduced into the collimated beam and moved until judged in optimal focus on the retina. The effective frequency of the grating was increased by rotating it up to 45° about its vertical axis (defocus at edge <0.5 D); if the grating was still visible to the observer, then the process was repeated with a grating of higher spatial frequency until the contrast of the retinal image appeared to be just zero to the observer; this was sharply defined and taken as the minimum cut-off frequency.

Results. The visual angle subtended at the rat retina by the gratings was determined from a count of the number of cycles of the image which fell within the borders of the optic disc or between two vascular landmarks. The disc, or separation of the landmarks, was subsequently measured in the eyecup by means of a traveling microscope. The optic discs were very similar in size in different rats; in the animal discussed below, it was 0.384 mm across. Thus, because 0.059 mm on the retina subtends an angle of 1°, the optic nerve head subtends 6.5° in the visual field. By inspection, four complete cycles of the image of a grating of 2.5 cycles/cm occupied the optic disc so that the spatial frequency of the retinal image of the grating was 0.615 cycles per degree (cpd). Frequencies expressed in grating cycles per centimeter may thus be converted to cpd in the retinal image by obtaining the product of the former with (0.615/2.5) = 0.246.

Over the period of an hour the natural pupil slowly changed size. The frequency at which grating contrast appeared to disappear in the retinal image was thus determined for three pupil diameters, 0.3, 1, and 2.5 mm, with the grating at the distance giving best focus on the retinal surface. This corresponded to about 8 or 9 D of extra power. The grating was also shifted to positions producing up to 8 D of defocus at each pupil diameter and the cut-off frequency for the defocused image again determined. The results of these observations are recorded in Table I.

Discussion. The results thus indicate a spatial frequency of 3.8 cpd (15.6° angular period) as the minimum frequency at which contrast disappears on axis in an emmetropic rat eye with a 0.33 mm pupil. Sampling theory leads to the expectation of local cone and ganglion cell densities at least matched to an optical image of this quality. Although the above result necessarily underestimates the true value of the cut-off frequency because the rays make a double passage through the optics of the rat eye and the contrast sensitivity function of the observer has not been taken into...
Fig. 2. Krueger and Moser have shown the form of the optical MTF to be very similar for different species of vertebrate eye. In the absence of a rat MTF we have positioned the double-and single-pass MTF profiles obtained for the cat by Wässle to approximately represent the situation for a rat eye with a 0.33 mm pupil. Assuming a 0.03 modulation threshold for the observer (not critical, see text), the double-pass profile has been arranged so that a 15.6' cut-off period just reaches the modulation threshold. The extrapolation of the single-pass MTF to the abscissa then indicates a single-pass cut-off period of 12.5'. The MTF obtained for the isolated rat retina by Ohzu et al. lies well above the estimated optical MTF and suggests that the overall MTF for optics and retina, as determined at the photoreceptor apertures, would be little different to that for a single passage to the retinal surface.

Table I

<table>
<thead>
<tr>
<th>Pupil diameter (mm)</th>
<th>Defocus relative to retinal surface (D)</th>
<th>Observed at cut-off</th>
<th>Nomographically computed single-pass angular period at cut-off (min arc)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rat 1:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1/3 mm</td>
<td>0.0</td>
<td>15.6</td>
<td>12.5</td>
</tr>
<tr>
<td>1.0 mm</td>
<td>6.0</td>
<td>13.0</td>
<td>14.9</td>
</tr>
<tr>
<td>2.5 mm</td>
<td>8.0</td>
<td>14.1</td>
<td>17.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.7</td>
<td>20.8</td>
</tr>
<tr>
<td>Rat 2:</td>
<td></td>
<td>10.0</td>
<td>24.3</td>
</tr>
<tr>
<td>1/3 mm</td>
<td>8.0</td>
<td>7.3</td>
<td>19.3</td>
</tr>
<tr>
<td>1 mm</td>
<td></td>
<td>7.3</td>
<td>26.4</td>
</tr>
<tr>
<td>Rat 3:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1/3 mm</td>
<td>0.0</td>
<td>14.9</td>
<td>13.0</td>
</tr>
<tr>
<td>1 mm</td>
<td>0.0</td>
<td>13.0</td>
<td>13.0</td>
</tr>
<tr>
<td>Rat 4:</td>
<td></td>
<td>14.3</td>
<td>13.9</td>
</tr>
<tr>
<td>3 mm</td>
<td>0.0</td>
<td>5.9</td>
<td>36.0</td>
</tr>
</tbody>
</table>

account, the cut-off value is already of interest because it is substantially better than the cut-off frequency calculated from either cone density, 1.86 cpd, or ganglion cell density, 2.3 cpd and exceeds the optimum behaviorally determined phototopic resolution of 1.5 cpd. The central region of the observer's pupil intersected the entire emergent beam at the smaller rat pupil diameters with the condensing lens and viewing distance employed. When the rat pupil was fully dilated, however, the performance of the rat optical system may be overestimated in Table I. The marginal rays of the rat pupil which pass through the marginal region of the observer's pupil have their efficacy reduced by the Stiles-Crawford effect, so that marginal aberrations which occur in the second pass through the rat optics will be underestimated by the observer. We thus consider only the small pupil data.

With assumptions we can assess the possible
underestimation of the true cut-off frequency resulting from the double pass when the rat pupil is small. The influence of equipment MTF would be negligible. For a rat eye of posterior nodal distance (PND) 3.4 mm, a 10 D condensing lens, and an observer viewing the real image of the emmetropic fundus from a distance of 33 cm, we calculate the grating image in the observer's eyes to be about 13 cpd at cut-off. The observer's modulation threshold in this region would lie between 0.1 and 0.01, and the properties of his visual system would not substantially influence the apparent cut-off frequency of the rat optical system. Krueger and Moser have shown the MTFs of a variety of species to be very similar in form, so we assume the shape of the cat single-passage MTF for the rat (Fig. 2) and compute the double-passage MTF as its square (Fig. 2). Assuming 0.03 for the observer's modulation threshold, the double-passage transform is set to intersect this modulation at the observed cut-off frequency, and the extrapolation of the single pass transform to the abscissa is read to obtain the minimum estimate of the single pass cut-off frequency. Estimates of this value have been included in Table I as well as data for other sizes of pupil and focus. Choice of between 0.1 to 0.01 for the modulation threshold varies the cut-off period from about 10' to 13', indicating the most probable range of the true cut-off period. In practice, this may be roughly equated with the half-height width of its inverse transform, the point spread function (PSF). It can be seen from Fig. 2 that the retinal MTF for the rat is substantially better than the single-pass optical MTF estimate, and a cut-off measured at the level of the photoreceptor apertures would differ little from that at the retinal surface.

Optical resolution close to the optic axis as estimated from the single-pass cut-off according to the Sparrow criterion is thus about 12', which is considerably better than Lashley's value of 30' obtained by transcleral imagery at an unknown pupil size. His value would be consistent with a fully dilated pupil according to Table I. The great depth of field of the rat eye established by single unit refraction results directly from the narrowness of the PSF relative to the ganglion cell receptive field sensitivity profiles when the pupil is small, and the above results are consistent with the literature. Pupil diameters from 0.33 to 1.0 mm are common in the rat under photopic conditions and small enough for diffraction effects to be significant. For yellow light Airy's disc is 7.5' diameter with a 0.33 mm entrance pupil, clearly outside the above range for minimum PSF width. It thus seems unlikely that more accurate measurements will show the image quality to be completely diffraction-limited; for a 1.0 mm pupil, Airy's disc is 2.5' diameter and not significant in relation to the estimated 15' single-pass PSF half-height width. The great obliquity of the fixation axis precludes assessment of the role of diffraction in limiting behavioral resolution.

From the Department of Physiology, John Curtin School for Medical Research, Australian National University, Canberra, Australia. Submitted for publication Jan. 24, 1979. Reprint requests: Dr. A. Hughes, Department of Physiology, J.C.S.M.R., A.N.U., P.O. Box 334, Canberra City, A.C.T. 2601, Australia. *Current address: Friedrich-Miescher-Laboratorium der Max Planck Gesellschaft, Spearmannstrasse 37-39, Postfach 2109, 74, Tübingen, West Germany.

Key words: rat eye, point spread function, modulation transfer function, optical quality

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