The Effect of Light History on the Aspartate-isolated Fast-PIII Responses of the Albino Rat Retina

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**Purpose.** To assess the effect of light-rearing history on the photon-capturing ability, amplitude, and kinetics of the fast-PIII response of the retina.

**Methods.** Albino rats were raised on 12-hour light-12-hour dark cycles, with illumination at 3 lux or 200 lux, and killed at approximately 12 weeks. Retinal rhodopsin content was measured spectrophotometrically. The morphology of the rod outer segments (ROS) and the thickness of the outer nuclear layer were determined histologically. Electoretinograms of isolated retinas to 3-µs flashes were recorded. The kinetics of fast PIII responses were assessed with a model of the phototransduction cascade.

**Results.** Total rhodopsin of 200 lux animals was reduced to 60% that of 3 lux animals: 2.3 ± 0.2 versus 1.4 ± 0.1 nmol/eye (mean ± SD). Length of ROS of 200 lux animals was reduced to 68% of the length of that of 3 lux animals: 20.1 ± 1.2 versus 13.7 ± 0.5 pm. The saturated amplitude of fast PIII of 200 lux animals was reduced to 56% that of the 3 lux group: 134 ± 27 versus 239 ± 37 µV (T = 22°C). Fast PIII responses of both groups are well described by the kinetic model before slow PIII intrusion (up to 100 ms). Estimated kinetic parameters of the transduction cascade did not differ reliably between the two groups.

**Conclusions.** Diminished saturated amplitude of fast PIII in 200 lux animals is accounted for by the hypothesis that fast PIII is directly proportional to the rod photocurrent and by the finding that the ROS of 200 lux animals are short compared to those of 3 lux animals. Similarity in estimated kinetic parameters of phototransduction suggests that the rods of the two groups differ little in the biochemistry underlying the activation phase of phototransduction. Invest Ophthalmol Vis Sci. 1996; 37:221-229.

Long-term structural and biochemical adaptation to environmental lighting is known to occur in the albino rat retina.1-4 Previous studies on the albino rat have shown that rhodopsin content and rod outer segment (ROS) lengths in the retina are inversely related to the intensity of the lighting they experience.3,4 Moreover, the rates of pigment regeneration also are altered by light experience, with the net consequence that albino rat retinas obey photostasis—the same number of photons is captured each day by the rods, even though the habitat intensity changes.3,5,6

In addition to affecting rhodopsin expression, light-rearing conditions affect the levels of expression of at least two other proteins of the phototransduction cascade, arrestin and transducin. Farber et al7 found that compared to animals raised in darkness, animals raised in cyclic light exhibit upregulation of the mRNA for arrestin and downregulation of those for opsin and transducin. Organisciak et al8 also reported that animals raised in cyclic light have higher levels of arrestin and lower levels of transducin than animals raised in the dark. Preliminary investigations in this laboratory on the relation of message levels to specific light-rearing intensities have revealed that animals raised in 200 lux environments exhibit no differences from animals raised in 3 lux lighting in the levels of mRNA for opsin and transducin; however, 200 lux animals do show an increased message level for arrestin over the level of arrestin message for 3 lux animals.

Recent work has established that the PIII (a-wave) component of the normal human electroretinogram
After 16 hours of dark adaptation, rats were killed at 12:00 PM by carbon dioxide asphyxiation. Each retina was extruded through a slit in the cornea, as described by Winkler.\textsuperscript{16} It was then placed in a centrifuge tube containing 10 ml physiological saline and disrupted with a spatula. After centrifugation at 12,000g for 15 minutes, the supernatant was poured off and 1 ml 1% Emulphogene (Sigma, St. Louis, MO) was added.\textsuperscript{17,18} The pellet was again broken up, and the extract was incubated for 1 hour at 4°C before being centrifuged again at 12,000g for 20 minutes. Absorbance spectra were recorded with an HP-8452A diode-array spectrophotometer before and after a complete bleach of the rhodopsin. Absorbance of rhodopsin at the $\lambda_{\text{max}}$ (500 nm) was determined from the difference spectrum. Rhodopsin concentration was then calculated, assuming $\varepsilon_{\text{max}} = 42,000 \text{ mol}^{-1} \text{ cm}^{-1}$.

**Histology**

The method of Penn et al.,\textsuperscript{19} which we now briefly describe, was used to determine the thickness of the outer nuclear layer (ONL) and the average lengths of ROS. Measurements were made on eight retinas of four different animals from each of the two different illumination-rearing conditions, for a total of 16 retinas. Rats were asphyxiated with CO$_2$ at 12:00 PM. Eyes were enucleated and fixed in a preparation of 1% paraformaldehyde and 2.5% glutaraldehyde fixative, buffered to pH 7.2 with 0.2 M Pipes. After 30 minutes in fixative, the corneas were removed and the eyes were placed in fresh fixative at room temperature for 2 hours and then refrigerated overnight. Lenses and nasal portions of the eyecups were removed the next day. After rinsing in 0.1M PIPES, the eyecups was dehydrated in an ethyl alcohol series, infiltrated with JB-4 embedding medium (Polysciences, Warrington, PA), and embedded in JB-4 catalyst medium. Four-micrometer thick sections were taken vertically through the optic disc with a Spencer 820 microtome. Sections were stained with either hematoxylin and eosin for ONL measurements or with sudan black for ROS measurements. The thickness of the ONL and the lengths of ROS were measured with an ocular micrometer on a Zeiss standard microscope (10X ocular, 40X objective; Zeiss, Oberkochen, Germany). Readings were taken every 250 microns along both the superior and inferior halves of the retina for ONL measurements and every 500 microns for ROS measurements. Because the albino rat eye has a standard diameter of 6.1 to 6.2 mm, with a hemicircumference of slightly less than 10 mm, an approximate total of 40 measurements of ONL thickness were made on each section, and approximately 20 measurements were taken of ROS length. Histologic data are reported without corrections for tissue shrinkage.

Although measurement of the thicknesses of the ONL provides a simple and secure method of assessing changes in the relative number of photoreceptors between groups of animals, the ONL measurements also can be used to obtain quantitative estimates of the spatial density of rods in each retina, as follows. The surface area of the retina is approximately 60 mm$^2$. An estimate of the volume of the ONL layer is thus obtained by multiplying its average thickness by 60 mm$^2$. In our fixed tissue, a photoreceptor nucleus in the ONL has a diameter of approximately 3 microns and, thus, a volume of approximately 113 microns$^3$. Dividing the total ONL volume by the volume of a photoreceptor nucleus yields an estimate of the total number of rods, on the assumptions that the packing fraction of photoreceptor nuclei in the ONL is near unity and that cone nuclei constitute a negligible fraction. These calculations neglect the variations in the regional thickness of the ONL (ref. 3, Fig. 1) and the volume occupied by the Müller cells; nonetheless, we expect them to be accurate in an average sense to approximately 20%.

**Stimulation of Retinas and Estimation of the Number of Photoisomerizations Per Flash**

A Type 1531-A Strobotac (General Radio) electronic stroboscope was used for light stimulation; its flash...
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Electrophysiology

Electrophysiological data were obtained from the retinas of four animals of each of the two illumination conditions. Animals were dark adapted overnight. All further experimental procedures began at 12 PM and were carried out under dim red light. After rats were anesthetized with intraperitoneal injections of 3 ml chloral hydrate—pentobarbital/kg body weight, eyes were removed and animals were killed by CO₂ asphyxiation. Retinas were removed in the same manner as for the measurements of rhodopsin. Each isolated retina was then placed in a petri dish that contained oxygenated (95% O₂, 5% CO₂) superfusion fluid and mounted in the recording chamber with the receptor side down. The recording chamber was constructed after the design of Sickel, as modified for by Winkler for recording from rat retinas. In the chamber, the retina was sandwiched between two fluid chambers with tight-sealing teflon rings at the edges.

Electrical recording was performed in a sheet-metal Faraday cage that shielded the retina electrically and excluded light. Two annular silver electrodes were situated on either side of the retina, at the rim of the chamber; these electrodes were polished and chlorided before each experiment. Electrodes were connected by shielded leads to a Grass P16 pre-amplifier whose output was digitized at 2 kHz by a Rapid Systems 4 x 4 digital oscilloscope for on-line signal processing, and storage for off-line analysis. Electrical signals were subjected to high- and low-pass filtering by the preamplifier. The high frequency cut-off of the filter was set for a rise time (10% to 90%) to 1 ms, corresponding to a bandwidth (at 3 dB attenuation) of 200 Hz. This filtering may have limited the rise time of the responses to the most intense flashes. The low frequency (AC) cutoff unfortunately was not recorded before the experimental apparatus had been disassembled, but it was probably set to 1 Hz.

The superfusion medium used to bathe the retina was modified from Reading and contained aspartate to isolate the PIII response. This solution contained (in mM): NaCl, 116.6; aspartate, 2.4; NaHCO₃, 25; MgSO₄, 1.2; K₂HPO₄, 1.2; KCl, 4.7; CaCl₂, 2.5; glucose, 7.0. After bubbling with 95% O₂—5% CO₂, the solutions were adjusted to pH 7.4 with small amounts of HCl. Bubbling with 95% O₂—5% CO₂ continued throughout the experiment. Each side of the retina was perfused at a rate of approximately 5 ml/minute. All recordings were performed at room temperature, 22°C to 23°C.

Rod Phototransduction Cascade Model and Curve Fitting

The model of the activation phase of the rod G-protein transduction cascade has been described elsewhere in detail and will be presented briefly here. Previous work has shown that the normalized circulating current $F(t)$ of amphibian and mammalian
we have made the substitution to the third line of equation 1, the product of the parameter \( \phi^{\text{eff}} \) is a brief “pure delay” that incorporates the effects of several “microsteps” in the constant of a single catalytic subunit of the activated PDE. The parameter \( \beta^{\text{sub}} \) is the Hill coefficient of the cGMP-activated channels.1315 In the transition from the second line of equation 2, with both A and varied \( t^{\text{eff}} \) to find the best fitting curve by the least-squares criterion. Analysis of the biochemical cascade leads to the expectation that A should be independent of \( \Phi \) at intensities that produce less than a few photoisomerizations per disc and that A and \( t^{\text{eff}} \) decline at higher intensities.13 Nonetheless, even at higher intensities, equation 2 has been shown to provide a useful parametric summary of the traces: In particular, the dependence of A on \( \Phi \) can be characterized empirically by a Weber-like saturation function:

\[
A(\Phi) = \frac{A_0}{1 + (\Phi/\Phi_{1/2})^n}
\]  

By virtue of the gaussian formula, equation 3 also yields a parametric characterization of the rate-saturation profile.11 The value \( A_0 \) is the maximum value that A achieves, whereas \( \Phi_{1/2} \) is the intensity at which A declines to half its maximum.

**RESULTS**

**Histologic and Rhodopsimetric Measurements**

Table 1 gives the average ONL thickness and ROS lengths obtained from the histologic measurements, and the estimates of total rhodopsin content, of the retinas of the two groups of animals. Retinas of the 200 lux animals exhibited a 6% decline in average ONL thickness relative to the 3 lux animals; this decline was not statistically significant. In contrast to the small difference in ONL thickness, the average length of the ROS of the 200 lux animals was much reduced, to 68% of the average length of the ROS of the 3 lux animals.

Outer nuclear layer thickness measurements were converted to estimates of the total number of rods by dividing the estimated total ONL volume of the retina by the volume of a rod nucleus (Methods). Estimates of the total number of rods are given in Table 1; estimates of the rod spatial density can be obtained by dividing the total number of rods by the assumed retinal surface area, 60 mm². These estimates of the total number of rods in the albino rat retina are close to those reported by Lashley22 and Hagins et al24: 1.5 × 10⁷ and 1.9 × 10⁷, respectively.

Retinas of animals raised in 200 lux lighting had on average 1.36 nmol of rhodopsin, which is only 60% of the 2.27 nmol rhodopsin of the 3 lux animals. Given that the number of rods in the retinas of the two
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200 lux

0
-200
-400

3 lux

0
-200
-400

0.0 0.1 0.2 0.3

FIGURE 1. Transretinal electroretinograms of isolated retinas of the two groups of animals. Responses are presented with the usual sign convention of ERGs, i.e., vitreal-positive is upward. Each trace is the average of four responses, one each from four retinas to a flash of the same intensity. The stimulation in each experiment used the same neutral density filter series: 3.0, 2.4, 1.8, 1.0, 0.5, 0.0 (the 0.5 filter was omitted for the series of 200 lux animals; see Methods). The number of photoisomerizations per rod produced by the unattenuated flash was estimated to be 1.1 × 10^6 for the retinas of the 3 lux animals and 6.6 × 10^5 for the retinas of the 200 lux animals (see Methods).

Fast PIII Kinetics

Figure 2 presents the normalized fast-PIII responses of the two groups (thicker, unbroken traces). Responses to the four most intense flashes of the two groups exhibit clearly the amplitude saturation mentioned in the description of Figure 1 and also show clearly the development of rate-saturation, another feature characteristic of the photocurrent. Also shown in Figure 2 are the best-fitting theoretical traces (dotted lines) produced by the kinetic model of the transduction cascade. It is noteworthy that the use of aspartate allows fast-PIII to be observed over a considerably greater time period than it can be observed in whole-eye ERGs, in which PII (the b-wave) intrudes. For example, the average response of the 3 lux group to the flash producing Φ = 1100 photoisomerizations per rod is seen to have the predicted kinetic form for at least 100 ms and over at least 90% of the fast-PIII amplitude range. In the ERGs of normal humans, comparable intensities produce a-wave responses that are truncated by the b-wave at less than 20 ms after the flash, at which time they have reached only approximately 30% of the saturated amplitude.

Figure 3 summarizes the quantitative properties of the fast-PIII responses obtained from the application of the theoretical analysis to the individual traces of all retinas. Panel A shows the maximum rate of rise at each intensity, and panel B plots the estimated values of the amplification constants. The most salient feature of these graphs is that the parameters of the two groups do not differ reliably—both sets of data can be described by the same first-order saturation function.

Maximal rates of rise of the responses of both groups are seen to saturate at approximately 200 s⁻¹. This value may be diminished by the rise-time of the analog filter, which was 1 ms. Estimates of A at the lowest intensity for both groups fall well below the

For each retina, we computed the average amplitude of the response plateau for the three (200 lux) or four (3 lux) individual records that exhibited the plateau; the group averages are reported in Table 1. The retinas of the 3 lux animals produced on average 239 μV, whereas those of the 200 lux animals produced only 134 μV; i.e., the saturated amplitude of fast-PIII of the 200 lux was reduced to 56% of its value in the 3 lux animals.

PIII: General Characterization

Figure 1 shows the average ERG responses of retinas of animals raised under the two lighting conditions to flashes producing between approximately 10⁷ and 10⁸ Φ per rod. Both sets of responses exhibit a clear-cut, though transient, amplitude saturation to the 1.8, 1.0, 0.5 (3 lux only), and 0 neutral density flashes. After this transient amplitude saturation, the responses relax into a slower negative-going phase. These features characterize the fast- and slow-PIII response components. At the lowest intensity (neutral density = 3.0), it is difficult to distinguish between the fast- and slow-PIII components of the ERG because there is no clear plateau separating them.

For each retina, we computed the average amplitude of the response plateau for the three (200 lux) or four (3 lux) individual records that exhibited the plateau; the group averages are reported in Table 1. The retinas of the 3 lux animals produced on average 239 μV, whereas those of the 200 lux animals produced only 134 μV; i.e., the saturated amplitude of fast-PIII of the 200 lux was reduced to 56% of its value in the 3 lux animals.
<table>
<thead>
<tr>
<th>ONL thickness (μm)</th>
<th>200 lux</th>
<th>3 lux</th>
<th>Ratio</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rods/retina (x 10^7)</td>
<td>(1.40 ± 0.08)</td>
<td>(1.49 ± 0.08)</td>
<td>0.94</td>
<td>NS</td>
</tr>
<tr>
<td>ROS length (μm)</td>
<td>13.7 ± 0.5</td>
<td>20.1 ± 1.2</td>
<td>0.68</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rhodopsin (nmol/eye)</td>
<td>1.36 ± 0.12</td>
<td>2.27 ± 0.17</td>
<td>0.60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>α_max: fast PIII amplitude (μV)</td>
<td>-134 ± 27</td>
<td>-239 ± 37</td>
<td>0.56</td>
<td>&lt;0.005</td>
</tr>
</tbody>
</table>

ONL = outer nuclear layer; ROS = rod outer segment; NS = not significant.

* Each data entry in the table is the mean ± SD of measurements made on four retinas from four different animals. The ONL thickness and ROS lengths were measured in histologic sections taken along the vertical meridian of the retinas, from both the superior and inferior quadrants; the standard deviations represent the square root of the variance between the mean values of the series of measurements made on each section. No corrections have been made for shrinkage in the ONL thickness or ROS lengths. The total number of rods was derived from the ONL thickness. For the a_max measurements, the mean values of all the saturated responses of an individual retina were taken as the estimate of the saturated amplitude for that retina; standard deviations in the table are those between the mean values for the individual retinas. Significance levels were computed with a t-statistic having 6 df because each number is the average of four independent observations; a one-tailed test was used because the expectation from previous studies was that each of the measured parameters would be lower for the 200 lux group than for the 3 lux group.

Theoretical curve, which predicts A to be constant at low Φ. A possible contributing factor to the decline in A at low Φ is the high-pass (AC) cutoff filter (see Methods).

Estimates of the delay parameter, t_eff, varied from a minimum of 6 ms for the most intense flashes (neutral density = 0), to 10 to 11 ms for the two least intense flashes (neutral density = 2.4, 3.0). There was a slight but systematic difference between the values of t_eff for the two groups; the responses of 200 lux animals had approximately 1 to 2 ms less delay. Shortening of t_eff at the intensities at which rate saturation...
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FIGURE 3. Summary descriptions of the kinetic features of the fast-PIII responses of Figure 2. (filled symbols) Results from the 3 lux group. (open symbols) Results from the 200 lux animals. Panel A presents the maximum rate of rise of each of the traces; panel B presents the estimated value of the parameter, $A$ (equation 1). Each plotted point is the mean ($\pm$ SD) of four observations from four different retinas, obtained by fitting equation 2 to the individual traces (as illustrated in Figure 2, where the model is applied to averaged traces.) The unbroken curve in panel B is the saturation function described by equation 3, with $A_0 = 2.0 \text{ s}^{-2}$, and $\Phi_{1/2} = 65,800$; the saturation function in panel A has the formula \( \frac{dR}{dt}\big|_{\text{max}} = \frac{dR}{dt\big|_{\text{sat}} \left[ \Phi / (\Phi + \Phi_{1/2}) \right]^{1/2}} \), with $dR/dt\big|_{\text{sat}} = 220 \text{ s}^{-1}$ and $\Phi_{1/2} = 65,800$.

sets in has been reported previously for amphibian rods.\(^{13}\) Approximately 1 ms of the overall delay is attributable to the filtering.

DISCUSSION

Fast PIII Saturated Amplitude Is Proportional to Rod Photocurrent

The simplest summary of the histologic and rhodopsinometric data reported in Table 1 is that the albino rat retina adjusts the length of its ROS to the illumination level over the illumination range 3 lux to 200 lux and that this adjustment results in little if any change in the amount of rhodopsin per disc. In other words, the lighting conditions give rise to adjustments in the rate of disc synthesis, phagocytosis, or both, but not to a significant change in the relative rates of synthesis of disc membranes and rhodopsin.

Histologic measurements of ROS lengths predict that $a_{\text{max}}$ of the 200 lux animals should have been reduced to 68% of $a_{\text{max}}$ for the retinas of 3 lux animals: $a_{\text{max}}$ for the 200 lux animals was found to be 56% that of the 3 lux animals (Figure 1, Table 1). The prediction of the magnitude of the reduction rests on two premises: first, that the circulating current of the rods in each group is proportional (with the same proportionality constant) to the length of the ROS; second, that all relevant factors other than ROS length are nearly equal for the two groups. A partial basis for the first premise can be found in previous investigations of the circulating current of rat retinas\(^{34}\) and investigations of individual toad rods.\(^{35}\) Both investigations found evidence that the current density of the light-regulated cation channels is uniform along the length of the ROS. Given the weak dependence of the cyclic guanosine monophosphate (cGMP)-activated current on voltage in the normal operating range of the rod,\(^{32}\) if animals in each light-rearing condition express the same number of ion channels per unit membrane, it is plausible that the same uniform current density would be present in the different length rods of the two groups.

Longitudinal uniformity of outer segment cGMP-channel current density in the two groups of animals alone, however, will not lead to proportional changes in transretinal ERG a-wave amplitude. The second, \"all other relevant factors nearly equal,\" premise must also be invoked: Among the factors included in this premise is the transretinal resistance profile, which is a distributed factor involved in the scaling between the photocurrent and the transretinal photovoltage. For example, if the thickness of retinal layers other than the ROS layer were altered seriously (particularly the ONL), or if the retina were otherwise pathologic, the transretinal resistance profile would not likely be the same for the two groups, and a single scaling factor between photocurrent and photovoltage would not be expected to apply to the retinas of both illumination groups. Based on the essentially identical histology of the two groups of retinas, however, we think it unlikely that the transretinal resistance profile has been altered. Nonetheless, experiments designed to test this are needed.

Fast-PIII Kinetics Are Similar in the Groups

As reported in Figure 3, we found no material differences in the saturated rate of rise, in the maximal amplification constant ($A_0$), or in the dependence of $A_0$ on $\Phi$ between the two illumination groups. Interestingly, the theory underlying equation 2 predicts that, other things being equal in the rods, shorter length rods should exhibit a higher value of $A_0$ than longer rods.\(^{14}\) This prediction follows because if everything but the ROS length is the same, at any instant each photoisomerization should cause the closure of the same number, but a proportionately larger fraction, of the total cGMP-activated channels. Thus, it might be expected that the retinas of the 200 lux group would
be approximately 1.4-fold more sensitive than those of the 3 lux group. The lack of any apparent difference between the groups in $A_0$ is consistent with the hypothesis that one or more of the activation steps has actually been downregulated in the 200 lux group, as predicted by the results of Farber et al.\textsuperscript{7} and Organisciak et al.\textsuperscript{5} Unfortunately, the current experiments were not designed, nor are the relevant data of the current experiments adequate, for reliably detecting a 1.4-fold shift in $A_0$ or, conversely, for convincingly demonstrating that such a shift does not occur.

The saturated rate of rise we measured, approximately 220 s\textsuperscript{-1}, is only 38% of the value (576 s\textsuperscript{-1}) reported for human a-waves.\textsuperscript{11} The saturated rate of rise of the extracellular voltages measured by Penn and Hagins,\textsuperscript{29} in their investigations of the albino rat retina, were approximately 20% higher than the values for human a-waves. Although the saturated rate of rise in our experiments may have been diminished somewhat by the amplifier rise time (see Methods), we think that the most likely explanation of the lowered value obtained in the current experiments is that it is an effect of the recording temperature, which was 22\textdegree C to 23\textdegree C. Saturated rates quoted for the albino rat experiments of Penn and Hagins\textsuperscript{30}—and of course, those for the human data—were obtained at or near 37\textdegree C.

The maximum value of the amplification constant found in the present experiments was $A_0 = 2.0$ s\textsuperscript{-2}. This value depends on estimates of $\Phi$; however, we emphasize that our estimates of $\Phi$ are based on measurements of the amount of rhodopsin bleached in situ. Previous population average estimates of the value of $A_0$ from human a-wave data range from 4 to 7 s\textsuperscript{-2} (refs. 11, 12, 33); these estimates depend on assumptions about the transfer of light from the human cornea to the rod outer segments, as well as assumptions about the size and rhodopsin content of the rods. Estimates of $A_0$ based on the responses of isolated primate rods\textsuperscript{34} yielded values of 4 to 7.7 s\textsuperscript{-2} (ref. 14) whereas estimates based on isolated human rods produced values of 1.2 to 2 s\textsuperscript{-2} (ref 35). The estimates of $A_0$ we found were likely diminished by the lowered temperature of our experiments relative to rat body temperature. An analysis of the temperature dependence of $A_0$ of toad rods showed it to have a $Q_{10}$ of 3.5\textsuperscript{16}. If the temperature dependence of $A$ in rat rods is similar to that in toads, as might be anticipated from the work of Penn and Hagins,\textsuperscript{29} the value of $A_0$ predicted for rat body temperature would be near 10 s\textsuperscript{-2}. A recent analysis of the corneally recorded a-waves of living mice reports the average value $A_0 = 7.2$ s\textsuperscript{-2} (ref. 36), reasonably consistent with this expectation.

In summary, the regulation of the rod that occurs in response to illumination rearing conditions over the nearly 100-fold intensity range of 3 lux to 200 lux results in rod outer segments with greatly altered lengths, proportionately diminished circulating currents, and no reliable differences in the activation phases of phototransduction.

**Key Words**

electroretinography, photoreceptors, photoreceptor–transduction, rhodopsin, rods

**References**


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