The Distribution and Kinetics of Visual Pigments in the Cat Retina

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An imaging fundus reflectometer has been used to study the distribution and regeneration of visual pigments in the retina of the adult living cat. Measurements were made over an area of tapetal retina extending 25° nasal and 40° temporal to the area centralis on the horizontal meridian and 5° inferior to 40° superior on the vertical meridian. The measured density differences show large variations with retinal location, with values in the central retina up to 60% higher than those in the superior region. The area of high density differences forms a horizontal streak. There are two peaks of density difference values, one centered on the area centralis and the second in the nasal section of the streak. Spectral measurements indicate that the contribution of cone pigments is negligible everywhere except at the area centralis, where it is about 5%. The distribution of density differences is shown to correlate well with anatomical data if the effects of fundal stray light are taken into account and if it is assumed that the cross section of light capture by the rods is determined by the dimensions of the inner segments. The time required for essentially complete regeneration of rhodopsin depends on retinal location, varying from about 80 min in the superior retina to more than 90 min in the regions of peak densities. Invest Ophthalmol Vis Sci 29:1056-1065, 1988

Previous studies have shown that the cat retina contains predominantly rod photoreceptors, and that even at the area centralis, the rods outnumber the cones by a factor of at least ten. The anatomical data suggest that the rod population reaches its greatest density a few degrees away from the area centralis and diminishes again towards the more peripheral retina. They also indicate that the dimensions of the photoreceptors vary with retinal location.

The noninvasive technique of fundus reflectometry can be used to obtain estimates of the relative levels of visual pigment at different retinal positions, and thus provide an indication of the distribution of the photoreceptors. However, the use of fundus reflectometry for such studies has been limited by the prohibitively long time needed for determinations to be made at a sufficient number of retinal positions to provide an adequate map of any such variations.

The development of an imaging fundus reflectometer (IFR) based on a high-sensitivity television camera allows circular areas of retina 25° in diameter to be “mapped” for visual pigment in a single experiment, and we have used this apparatus to investigate the distribution of rhodopsin in the living cat eye, across an area of tapetal retina extending from 25° nasal to 40° temporal on the horizontal axis and from 5° inferior to 40° superior on the vertical meridian, relative to the area centralis. This portion of retina includes the few locations which have previously been used for nonimaging fundus reflectometric studies on the cat. The data obtained at these locations in the present study are similar to those of the most recent of these investigations. However, the distribution of rhodopsin, as measured by the double densities, is found to vary substantially with retinal position.

Previous studies have yielded conflicting estimates of the duration over which rhodopsin regeneration continues in the cat following extensive bleaching. Bonds and McCleod reported that regeneration was essentially complete in about 30 min, while Ripps et al found that in their experimental conditions it continued for more than 60 min. Regeneration rates have therefore been reexamined. The present results indicate that the time during which rhodopsin regenerates varies with retinal location, but is never less than 70 min.

The contribution of cone pigment(s) to the double density values was found to be near the limits of detectability of the instrument at the area centralis and negligible elsewhere.
Materials and Methods

Animals

Only adult cats (greater than 150 days old) were included in the study. Animals were maintained under anesthesia with intravenous infusion of 14.5 mg/kg/hr of alphaxolone alphadalone acetate (Glaxo, Greenford, UK). The pupil was dilated with cyclopentolate (1%) and phenylephrine (10%) and the cornea was protected by a contact lens. The animal’s head was supported in a metal framework and the eye was immobilized by conjunctival sutures attached to an eye ring. All procedures were carried out in accordance with the ARVO Resolution on the Use of Animals in Research.

Fundus Reflectometry

One version of the IFR used for this study has been described in detail elsewhere. In outline, the instrument is based on a clinical fundus camera, modified to provide monochromatic illumination of the retina, and attached to an ISIT (Intensified Silicon Intensified Target) television camera equipped with an electronic zooming facility. For a given state of visual adaptation a series of televised images of an area of retina covering approximately 25° was obtained with monochrome illumination using narrow-band interference filters centred on 470, 500, 560, 598 and 670 nm. The images were recorded on an analogue videorecorder, digitized using a transient recorder and averaged by a microcomputer both temporally, over 32 successive TV fields, and spatially, to produce picture elements each of which corresponded to a rectangular area of retina of approximately 1.2° square. Each measurement series thus produced five two-dimensional arrays, one for each interference filter used. When the retina underwent adaptational changes in the intervals between measurements the density changes were as expected for changes in visual pigment levels: this was the case in experiments where no eye movements had occurred. At times was focused on the changes at 500 nm. The calculated bleaching effect of the measuring beam at 500 nm was less than 1%, which is at the limits of detectability of the apparatus. The luminances used for measurements at all other wavelengths were calculated to produce substantially smaller degrees of rhodopsin photolysis.

Treatment of Data

The large numbers of data generated by each experiment necessitated some further abstraction for purposes of display. Mean values obtained from the 196 central picture elements at all wavelengths were inspected to ensure that the spectral variations of their density changes were as expected for changes in visual pigment levels; this was the case in experiments where no eye movements had occurred. Attention was then focused on the changes at 500 nm, which yielded the best signal to noise ratio. Except in experiments where the area centralis was being examined at high spatial resolution, these data were further smoothed by applying centrally weighted nine-point averaging to each element. For greater clarity, the data were also displayed as contour maps.

Procedure

Either the view through the eyepiece of the fundus camera, or that obtained from a TV monitor of the camera output, was used to inspect the position of the animal’s eye, and enabled the test location to be set accurately. When the animal had been aligned with the reflectometer, the position of one or more retinal features (e.g., the area centralis, or the retinal vasculature) on the TV monitor was used throughout the
During the setting-up procedure, the animal's eye was deliberately light-adapted, to ensure that the retina contained relatively little visual pigment. The experiment was initiated with a 9.5 min "clearing" exposure to a bright white light, estimated to produce a retinal irradiance of 5.2 log scotopic trolands when appropriate corrections for the parameters of the feline eye had been made.\textsuperscript{12,13} The intensity of the light was then increased by a factor of 20 and the eye was further exposed for 30 seconds. Immediately after this bleaching sequence the reflectances of the bleached retina at each of the wavelengths were recorded, the series of measurements being completed within 12 seconds. The animal was then allowed to dark-adapt for at least 90 min, during which intermittent recordings of fundal reflectance were made. A second exposure to the 30 second white light (equivalent to 8.0 log scotopic troland seconds) was then used to bleach more than 95% of the pigment which had been regenerated.\textsuperscript{12} In order to avoid complications from bleaching products which absorb in the visible wavelength range, such as metarhodopsin 3,\textsuperscript{11-15} the animal was again allowed to dark-adapt for 15 min, by which time these products have largely disappeared, and then subjected to a third bleaching exposure lasting 15 seconds and equivalent to 7.5 log scotopic troland seconds. (This last bleaching light was of diminished duration to avoid possible side effects of repeated high exposures.\textsuperscript{4,16} Photoproduct interference during the measurement period immediately following the third conditioning exposure would be expected to be less than 3% of the total pigment bleached,\textsuperscript{12} a level which is near the limits of detectability of the apparatus. Thus, measurements made after the final bleach, like those obtained immediately after the first one, provided reflectance data for the retina essentially devoid of visual pigments or of photoproducts which absorb appreciably at the wavelengths examined. In contrast, the data obtained after the intermediate bleach allowed the formation and decay of metarhodopsin 3 to be monitored.

In Vitro Spectrophotometry

In vitro spectral measurements were made on the retinas of one dark-adapted animal which died under anesthesia. All experimental procedures were carried out in dim red light (Philips PF712B safelights). Following enucleation, the eyes were hemisected and the eyecups bathed in a mammalian Ringer's solution.\textsuperscript{17} The tapetal region of the eye cup was cut into sections, from each of which the retina was detached from the pigment epithelium. Spectra were obtained from the fragments of retina with a Shimadzu MPS 50L spectrophotometer.\textsuperscript{15}

Results

Figure 1A shows representative measured double density difference spectra obtained from a single cat. Two sets of data are shown, one (squares) from the area centralis\textsuperscript{*} and the other (circles) from a location 10° superior to it, which is in the region where measurements have been made in previous studies.\textsuperscript{11,12}

\textsuperscript{*} Although the term "area centralis" is commonly used to describe a region of retina extending over about 10°, it is used throughout this report to denote the location within that region where the measured density differences were greatest.
Although similar in their spectral characteristics, the values obtained from the two locations are very different in overall size. This pattern of variation was seen in all six animals examined; values obtained from the peripheral position ranged from 0.249 to 0.416 (mean 0.324) at 500 nm, while those from the area centralis lay between 0.470 and 0.580, with a mean of 0.507.

In Figure 1B, the IFR data are shown normalized, together with the normalized difference spectrum obtained postmortem from a small patch of isolated retina examined by transmission spectrophotometry (solid curve). There is good agreement between the spectrophotometric data and those obtained by IFR from the peripheral location (circles) and in each case the spectral characteristics conform well to a rhodopsin nomogram, centered at about 505 nm. However, the two sets of IFR data do not superpose, those obtained at the area centralis (squares) showing relatively larger density differences occurring at both 560 and 598 nm than is the case in the periphery. This is not likely to be simply spectral broadening caused by stray light, since there is no discrepancy at 470 nm. The divergence is consistent with a spectral contribution from cone visual pigments amounting to about 0.025 density units, i.e., about 5% of the total measured density changes. There are problems with obtaining data from the area centralis with this experimental protocol, however, since the region with a relatively large concentration of cone photoreceptors corresponds to an angular subtense of little more than 1°, a size slightly smaller than that of a single IFR datum. Identifying the precise location of the area centralis is therefore critical for comparisons to be valid. Further, since no secondary spatial averaging such as nine-point smoothing (see Materials and Methods) can be applied, the data are noisier than normal and less certainty can be attached to them. In order to confirm that the spectral differences at the area centralis are due to cone pigments, this location was examined at greater magnification, using the electronic zoom facility on the TV camera. Experimental design was based on the assumption that the regeneration of cone pigment(s) would be faster than that of rhodopsin. Figure 2A shows the spectral variations observed in the double density differences at the area centralis 4 min (diamonds) and 8 min (triangles) after the retina had been exhaustively bleached. At 4 min the changes are almost as large at 560 nm and 600 nm as those at shorter wavelengths, but at 8 min the 500 nm value is substantially the largest. The wavelength-dependence of the changes during the first 8 min is shown in Figure 2B. The 600 nm values (circles) increase over the first 4 min and then cease to change. In contrast, those obtained at 500 nm (squares) continue to rise. Both the spectral characteristics of the density differences observed initially and the wavelength dependency of regeneration indicate contributions from more than one pigment, with the rapidly regenerating component arising from cone pigment(s). Results similar to those illustrated in Figure 2 were obtained from three other experiments. Thus, it is apparent that the contribution of the cone pigment(s) is relatively small at the area centralis and insignificant elsewhere in the cat retina, both on the basis of the present data, and from the published anatomical data which show that the rod-to-cone ratio is very high. Therefore, the density differences measured when the IFR was used at normal
Fig. 3. Contour maps of the double density changes observed at 500 nm after 90 min of dark adaptation following an extended light exposure which bleached essentially all visual pigment from the measurement area. The contours were derived from data which had been smoothed by weighted nine-point averaging. The data cover the central 25° of tapetal retina and are from two cats. The cross on each map marks the area centralis, the point of highest double density, which was 0.580 in A and 0.560 in B.

magnification were treated as though they arose entirely from changes in the levels of rhodopsin.

The distribution of pigment densities in the central retina is illustrated in Figure 3, where data obtained from the left eyes of two cats are shown as contour maps. The choice of contours has been made on the basis of the inherent signal/noise ratio of the measurements, and some smoothing of the data has been made by eye. In each case there is a localized region of highest measured density differences. The range of pigment densities is not radially symmetrical; rather there is a stripe of retina where values are all relatively high.

Figure 4 gives examples of the double density differences obtained from the 25° region of retina nasal to the disc and along the horizontal meridian, from the same animals as those of Figure 3. The nasal retina also contains a horizontally elongated region of higher density differences which appears to form an extension of the horizontal streak seen in the central retina. Within it there is a peak where the density values are similar to those found in the area centralis.
This pattern was found in all four animals in which this nasal portion of retina was examined, with peak values at 500 nm ranging from 0.462 to 0.584 and a mean of 0.521.

Spectral analysis of the double density changes in the nasal region of the retina did not indicate the presence of a significant contribution from cone pigments, though the precision of the experiments does not exclude the possibility that there is an increased population of cones there relative to other peripheral locations.

In Figure 5, the double density distributions obtained from four experiments centered on different areas of the retina of a single animal have been combined in a single contour map. Also shown are the optic nerve and the major blood vessels. The regions of the retina examined were chosen to provide overlapping areas between some of the images, so that the reproducibility of the data could be verified. The map obtained covers an area of retina extending 25° nasally and 40° temporally from the area centralis along the horizontal axis, and 5° inferiorly to 40° superiority in the vertical axis. From the large retinal area covered by the data of Figure 5, it is clear that apart from the region of relatively high pigment densities centered on the area centralis and its counterpart in the nasal retina, the measured double density differences are fairly constant, with only slight decreases occurring towards the periphery. The “saddle” of slightly reduced values between the high density region of the nasal retina and that around the area centralis which can be seen in Figure 5 was found consistently (cf Figs. 3, 4).

Figure 6A shows two sets of regeneration measurements derived from the density differences monitored at 500 nm, following a full bleach lasting 10 min. The data were obtained from a single experiment and illustrate the changes which occurred at the area centralis (triangles) and at a point 10° superior to it (circles). At all times following the bleach the measured density differences are greater at the area centralis than in the peripheral location. In Figure 6B the data have each been normalized to the value reached at 120 min of dark adaptation. It is evident that although all measurable changes ceased by 80 min at the peripheral location, they continued for about 100 min at the area centralis. In most experiments measurements were continued for only 90 min of dark adaptation. At the end of this period the data displayed a similar pattern of changes in density, with these having reached completion in the periphery, but not at the area centralis. A similar pattern was found at the region of high density differences in the nasal retina, with a faster recovery of the measured double density differences than in the periphery, but a more extensive period required for their completion.

The formation and decay of the bleaching intermediate metarhodopsin 3, measured following the 30 second bleach at the end of the initial extended dark adaptation period (see Methods), were found to adhere closely to the pattern previously reported. At the area centralis, the absolute levels of the intermediate were higher than in the periphery, in the same proportion as the measured rhodopsin density levels for the two locations. There was no detectable differ-
ence in the relative rates at which the intermediate appeared or decayed between different retinal positions.

Discussion

Contributions of Rod and Cone Pigments

The spectral characteristics of the double density changes observed in the present study confirm the anatomical observation that the rod population greatly exceeds that of the cones throughout the area of retina examined.\textsuperscript{1,2} Thus, at all locations, the spectrum approximates to that expected for rhodopsin. Even at the area centralis the deviation from this pattern is small (Fig. 1B), and would be difficult to measure with the rather lower spatial resolution that has usually been adopted for fundus reflectometric studies (ie, data averaged over an area of retina 2° in diameter.\textsuperscript{11,12}

This result is not surprising, in view of the anatomical observation\textsuperscript{3} that in most areas of the cat retina there are about 65 rods for every cone. Although it was found anatomically that the cone population density rose sharply in a localized region of the central retina, their numbers still only reached about 10% of the total population over an area of about 1° angular subtense.\textsuperscript{2}

Even though the present fundus reflectometric measurements are able to detect the presence of the cones, interpretation of the data is hampered not only by the sparsity of these receptors, but also by the probability that they contain more than one class of pigment. Psychophysical and electrophysiological studies\textsuperscript{19-22} indicate that the cat's photopic visual system is trichromatic, and that the three classes of cones have maximal sensitivities at about 450, 500 and 560 nm.

The double density differences measured at 560 nm for the cone pigments are only of the order of 5% of those of the rods in the same central retinal region (Figs. 1B, 2), while anatomically they are estimated\textsuperscript{2} to reach about 10% of the photoreceptor population at the area centralis. However, anatomical data (Table 1) suggest that the cone outer segment is only about half the length of that of the rod, so that even allowing for the funneling of incident light by the inner segment, which almost certainly occurs,\textsuperscript{23} relatively reduced double densities are to be expected. Further, if there is more than one class of cone pigment, it is the sum of their density changes which should correlate with the anatomical cell count.

Distribution of Measured Rhodopsin Density Changes in Relation to Anatomical Studies

Although the present data appear to be reasonably consistent with anatomical data on the relative population densities of rods and cones in the cat retina, the topographical variations in the measured rhodopsin density differences initially appears surprising. Cell

### Table 1. List of rod and cone dimensions at the area centralis and a retinal location 10° superior to it (O.S., outer segment; I.S., inner segment)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Area centralis value</th>
<th>Periphery value</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rod density</td>
<td>$2.7 \times 10^3/mm^2$</td>
<td>$4.7 \times 10^7/mm^2$</td>
<td>2</td>
</tr>
<tr>
<td>Cone density</td>
<td>$2.7 \times 10^3/mm^2$</td>
<td>$9.1 \times 10^7/mm^2$</td>
<td>2, 33, 34</td>
</tr>
<tr>
<td>Rod O.S. length</td>
<td>25 (\mu)m</td>
<td>16 (\mu)m</td>
<td>35-38</td>
</tr>
<tr>
<td>Rod O.S. diam</td>
<td>1.5 (\mu)m</td>
<td>1.0 (\mu)m</td>
<td>2</td>
</tr>
<tr>
<td>Rod I.S. diam</td>
<td>2.0 (\mu)m</td>
<td>1.35 (\mu)m</td>
<td>38, 39</td>
</tr>
<tr>
<td>Cone O.S. length</td>
<td>10 (\mu)m</td>
<td>6 (\mu)m</td>
<td>36, 40</td>
</tr>
<tr>
<td>Cone O.S. diam</td>
<td>(av) 1 (\mu)m</td>
<td>1.5 (\mu)m</td>
<td>35</td>
</tr>
<tr>
<td>Cone I.S. diam</td>
<td>4 (\mu)m</td>
<td>5 (\mu)m</td>
<td>34, 35, 39</td>
</tr>
</tbody>
</table>
counts indicated that there was a reduction in the number of rods per unit area at the area centralis compared with more peripheral locations (see Table 1). However, an increase in the diameter of both the inner and outer segments in the central retina was observed, and a lengthening of the outer segment has also been noted.

The absolute size of the measured density changes in the central retina is also noteworthy: it is well known that fundus reflectometric measurements generally underestimate true pigment levels because of the "diluting" effects of stray light. There are two chief sources of this light: the preretinal scattering (S) of the measuring light by the ocular media and their interfaces, and the passage of light between, rather than through, photoreceptor outer segments as it traverses the retina. Although the former source can be shown to have a profound effect on measured density changes if it becomes a sizeable fraction of the light reaching the photodetector, it can be treated as a constant for a given eye and instrument to a first approximation. In the cat, where the presence of the tapetum leads to a relatively high reflectance from the fundus, S is likely to play a significantly smaller part than it would in animals with nontapetal retinas. Stray light reflected from behind the photoreceptors, on the other hand, depends on the fraction, f, of the area which is covered by the photoreceptors, and this will vary from one retinal location to another if the receptor numbers and dimensions change. If the stray light component S is relatively very small, it has been shown that the measured density change, $D_m$, is given by

$$\log \left[ 1 \left/ (1 - f) + f \times 10 (\exp^{-2D_r}) \right. \right]$$

(1)

where $D_r$ is the true axial density of the receptor outer segment. The values found in the present study in the superior retina are similar to, though rather larger than, those reported previously for the same region, suggesting that the IFR suffers from a value of S no greater than or even slightly larger than S. The elliptical pattern from them could bring about a reduction in measured density values close to them. However, inspection of the data strongly suggests that this is not the case, since the diminution of the measured density levels begins to occur nearly $10^6$ away from the vessels. Moreover, there is evidence that the nasal region does contain a separate peak, since cats fed on a diet deficient in taurine can develop focal lesions first at the area centralis and later in a position corresponding to the peak in the nasal retina.

It is known from microspectrophotometric studies that the axial density of rhodopsin in rod photoreceptors is about 0.018 $\mu$m$^{-1}$. Substituting this value in equation (1) together with the receptor dimensions given in Table 1 for the central retina, yields a value of 0.34 when f is derived from measurements of receptor packing density and outer segment diameter. However, if it is assumed that f is determined by the diameter of the inner segment, which is substantially larger, the measured density change at the area centralis predicted by substitution of the parameters in Table 1 is 0.58, in good agreement with the measured values. Similarly, substitution of the parameters applicable to a location $10^6$ superior to the area centralis (Table 1) into equation (1) leads to a predicted value of only 0.14 if f is derived from the outer segment diameter, but 0.30, close to that found experimentally, when the inner segment diameter is used. The fundus reflectometric data strongly suggest, therefore, that light funnelling plays an important role in the cat's rod system.

Although the increased density changes measured at the area centralis are due in part to funnelling and to the larger value of f that applies in this region, it is noteworthy that the amount of rhodopsin per unit area, as given by the product of the outer segment coverage factor, the axial density of rhodopsin and the outer segment length at the area centralis is 0.215, whereas that found at the peripheral location is only 0.106. The area centralis therefore contains approximately twice as much rhodopsin per unit area as the periphery.

The region of high density in the central retina is not radially symmetrical, and the elliptical pattern followed by the contour maps (Figs. 3, 5) closely resembles the population distribution of ganglion cells and, with the exception considered above, of photoreceptors. An unexpected finding was that there was a second region of maximal density changes in the nasal retina (Figs. 4, 5). It is possible that this region is in fact only an elongate extension of the streak-like distribution in the central retina and that its apparent separation results from an artefact of the method. The two peaks are separated by several major blood vessels (see Fig. 5), and light scattering from them could bring about a reduction in measured density values close to them. However, inspection of the data strongly suggests that this is not the case, since the diminution of the measured density levels begins to occur nearly $10^6$ away from the vessels. Moreover, there is evidence that the nasal region does contain a separate peak, since cats fed on a diet deficient in taurine can develop focal lesions first at the area centralis and later in a position corresponding to the peak in the nasal retina.

**Rhodopsin Recovery**

The time course over which changes in the density differences occurred in the superior periphery during dark adaptation (Fig. 6) was very like that reported in a previous study carried out at a similar retinal location, with a half-return time of about 30 min. The changes, which cannot be described by a single exponential, correlate well with the recovery of scotopic sensitivity in the cat measured electrophysiologically. The pattern of recovery is appreciably...
different from that observed in a second fundus reflectometric study. The reasons for the discrepancy are not clear.

The differences between the time course of rhodopsin recovery peripherally and at the area centralis (Fig. 6), which were consistently observed, were unexpected. The dependency on location is not likely to be due either to contamination of the data by the presence of bleaching intermediates or variations of fundal stray light. The former, which is in any case unlikely in view of the extended bleach durations used, would be expected to lead to different apparent time courses of recovery when monitored at 560 nm, and analysis demonstrated that this was not the case; although noisier, because of their smaller amplitudes, the normalized data were essentially superposable on their counterparts measured at 500 nm. Similarly, use of equation (1) to estimate the apparent recovery, assuming that fundal stray light varies in a manner dependent on the dimensional data of Table 1, and assuming identical real rates of rhodopsin regeneration, shows that the opposite of what is found experimentally would be predicted. Since the area centralis contains a higher density per unit area of rhodopsin, the clear implication is that the absolute rate of regeneration of rhodopsin is higher at the area centralis.

The difference in the time course of recovery of measured density was not specific to the area centralis, since it was also observed in the region of high density in the nasal retina. As at the area centralis, the absolute rate at which rhodopsin regenerated was greater than in the periphery, though at any given time the fraction of the full recovery which had occurred was lower.

Inspection of the normalized curve obtained at the area centralis suggests that it not only continues for longer, but that its form is also different from that for the superior periphery. At the former location, the measured density changes appear to follow an essentially linear pattern for about the first 60 min, while any tendency to linearity in recovery in the superior periphery was limited to the first 20 min. A similarly extended linear period was also observed at the nasal periphery was limited to the first 20 min. A similarly extended linear period was also observed at the nasal region of high density changes. Such a time course suggests that the rate-limiting process in these regions is saturated during this period. It is unlikely that this process involves the photolytic sequence, since the kinetics of formation and decay of metarhodopsin 3 did not vary with location, and the regeneration data were obtained after extended bleaching periods. However, one of several protein-dependent steps in the visual cycle such as chromophore isomerization or transport could readily account for this behaviour. While our present data do not allow us to distinguish between them, it is possible that experiments in which the bleaching regimens are varied will make this feasible.

Key words: cat, imaging fundus reflectometry, regeneration, rod, visual pigment

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References