Am J Physiol Heart Circ Physiol 286: H419–H423, 2004.
First published August 28, 2003; 10.1152/ajpheart.00643.2003.

Low oxygen consumption in the inner retina of the visual streak of the rabbit

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Submitted 7 July 2003; accepted in final form 25 August 2003

Yu, Dao-Yi, and Stephen J. Cringle. Low oxygen consumption in the inner retina of the visual streak of the rabbit. *Am J Physiol Heart Circ Physiol* 286: H419–H423, 2004. First published August 28, 2003; 10.1152/ajpheart.00643.2003.—The oxygen requirements of different retinal layers are of interest in understanding the vulnerability of the retina to hypoxic damage in retinal diseases with an ischemic component. Here, we report the first measurements of retinal oxygen consumption in the visual streak of the rabbit retina, the region with the highest density of retinal neurons, and compare it with that in the less-specialized region of the retina underlying the vascularized portion of the rabbit retina. Oxygen-sensitive microelectrodes were used to measure oxygen tension as a function of retinal depth in anesthetized animals. Measurements were performed in the region of the retina containing overlying retinal vessels and in the center of the visual streak. Established mathematical analyses of the intraretinal oxygen distribution were used to quantify the rate of oxygen consumption in the inner and outer retina and the relative oxygen contributions from the choroidal and vitreal sides. Outer retinal oxygen consumption was higher in the visual streak than in the vascularized area (means ± SE, 284 ± 20 vs. 210 ± 23 nl $O_2 \cdot min^{-1} \cdot cm^{-2}$, $P = 0.026$, $n = 10$). However, inner retinal oxygen consumption in the visual streak was significantly lower than in the vascular area (57 ± 4.3 vs. 146 ± 12 nl $O_2 \cdot min^{-1} \cdot cm^{-2}$, $P < 0.001$). We conclude that despite the higher processing requirements of the inner retina in the visual streak, it has a significantly lower oxygen consumption rate than the inner retina underlying the retinal vasculature. This suggests that the oxygen uptake of the inner retina is regulated to a large degree by the available oxygen supply rather than the processing requirements of the inner retina alone.

retinal metabolism; oxygen supply; avascular retina

THE RETINA IN MOST MAMMALS, including humans, is nourished from a dual blood supply. The choroid, lying immediately behind the retina, supports the outer retina, whereas the retinal circulation primarily supports the inner half of the retina. One of the major roles of the vasculature is the provision of sufficient oxygen to maintain retinal function. Lack of oxygen is known to be the initiating cause of the loss of vision in humans when ocular blood flow is halted (4), so oxygen can be said to be the most critical metabolite required for retinal function. Oxygen supply to the retina is delicately balanced. Even in healthy retinas, the oxygen supply from the highly vascular choroid is only just sufficient to support the outer retina, particularly in the dark (15), when the oxygen requirements of the photoreceptors are increased (20). It has been shown that under light-adapted conditions, the oxygen requirements of the inner retina in the rat (9) and the cat (6) are higher than those of the outer retina. This helps explain why the retina is particularly vulnerable to disruption of the retinal vascular supply and why retinal hypoxia is thought to play a role in many retinal diseases with a vascular component. However, in humans, not all regions of the inner retina are vascularized. The foveal avascular zone is completely devoid of retinal capillaries. This is intriguing because part of the foveal avascular zone also has a high density of inner retinal neurons (12, 16). How the energy demands and nutritional requirements of the high-acuity region of the avascular zone are met from the surrounding annular capillaries and/or the choroidal circulation is not presently known.

The rabbit offers a useful animal model to investigate the relationship between the level of neural processing and the oxygen demands of the retina in both vascularized and avascular regions of retina. The rabbit possesses a relatively high-acuity region of avascular retina, forming a horizontal band correlating with the visual horizon (18). The rabbit also has a narrow band of vascularized retina (Fig. 1*A*) (10), so microelectrode-based techniques can be used to make a direct comparison between oxygen distribution in vascular and avascular areas of the retina in the same eye (Fig. 1*B*). In the vascularized area of the retina in the rabbit, the deepest retinal capillaries are confined to the nerve fiber layer. In the remaining avascular layers, the oxygen distribution can be analyzed to extract quantitative information about the local oxygen consumption. Thus, in the vascularized area, the oxygen uptake from the inner retina deeper than the nerve fiber layer, and all of the outer retina, can be quantified. In the avascular visual streak, all of the inner retina and the entire outer retina can be included in the analysis.

Previous measurements of preretinal oxygen tension in the rabbit (21) have suggested that lateral diffusion of oxygen across the vitreous from the vascular area may play a role in supporting the inner retina of the avascular area. However, only measurements of oxygen gradients across the retinal-vitreal boundary can precisely determine the significance of such an effect in terms of oxygen supply to the inner retina. The present study describes the first measurements of oxygen supply and consumption in the inner and outer layers of the rabbit retina in the vicinity of the vascular streak and in the avascular area of the retina in the high-acuity visual streak.

MATERIALS AND METHODS

Intraretinal oxygen profiles. The experimental techniques were similar to those reported by our previously studies in other species (23, 24). All procedures conformed to the "Guiding Principles in the Care and Use of Animals" and were approved by Animal Ethics Committee of the University of Western Australia. A total of 14 adult rabbits was used. Oxygen-sensitive microelectrodes were used to

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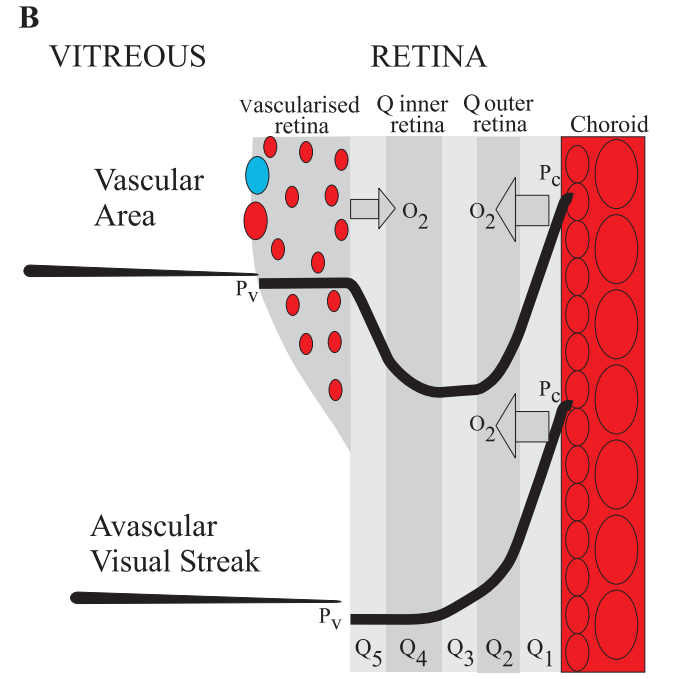

Fig. 1. *A*: fundus photograph of the posterior pole of the rabbit retina. The band of retinal vasculature and the whitish background of the myelinated region of the nerve fibers are clearly visible. Intraretinal oxygen measurements were made in the vascularized area inferior to the major retinal vessels and in the avascular retina in the region of the visual streak. *B*: schematic illustration of the intraretinal oxygen measurements in the vascularized area and in the avascular visual streak. The five layers constituting the avascular portion of the retina (Q_1–Q_5, where Q is oxygen consumption) are shown along with a representation of typical oxygen distributions in the two regions. The arrows indicate the delivery of oxygen from the choroidal and retinal sides in each location. P_c, oxygen tension in the choriocapillaris; P_v, oxygen tension in the vitreous.

measure the oxygen tension across the retina of anesthetized, mechanically ventilated rabbits under light-adapted conditions. Anesthesia was induced by an intramuscular injection of ketamine (50 mg/kg) and xylazine (3 mg/kg) and followed by an intravenous infusion of ketamine (10 mg/kg) and xylazine (3 mg/kg) infused at a rate sufficient to maintain anesthesia throughout the experiment. The animals were ventilated with air at 30 breaths/min using a tidal volume sufficient to produce blood gas levels within the normal range. Arterial blood pressure was monitored continuously throughout the experiment. We manufactured our own oxygen-sensing microelectrodes using techniques developed by Whalen et al. (22). The electrodes were calibrated in air-equilibrated saline before and after the experiment. The electrode entered the eye through a small hole just behind the limbus. The small size of the electrode tip (1 μm) coupled with high-acceleration piezoelectric translation of the electrode through the retina produces highly reproducible measurements of intraretinal oxygen distribution. Intraretinal oxygen profiles were measured in 10-μm steps ~2 disk diameters nasal to the optic disk in either the vascularized area just inferior to the major vessels or close to the center of the visual streak. Under microscopic observation, the electrode tip was placed just anterior to the chosen area of retina. The electrode was then stepped through the retina, under computer control, until a peak oxygen level within the choroid was reached. The measurement was then repeated during step-wise withdrawal of the electrode. Although very close agreement between the insertion and withdrawal profiles was routinely achieved, the withdrawal profiles were used for data analysis because they tended to be less influenced by artifacts associated with mechanical stress on the electrode tip during penetration (23). When more than one artifact-free data set was available from a particular location, all data were analyzed and the mean values for the fit parameters were calculated. Only one set of parameters from either the vascular or avascular areas in each animal was used in calculating the mean across animals. Artifact-free data suitable for analysis were obtained from a total of 10 eyes in either the visual streak or vascularized area of the retina.

Mathematical models. For the analysis of the oxygen profiles from avascular regions of the retina, a modified form of the model of Haugh et al. (11) was employed. The model was expanded to include five layers, which allowed us to separate out the oxygen consumption rates of the outer and inner retina along with the oxygen gradients in diffusion zones at the boundaries with the choroid and vitreous and between the dominant oxygen-consuming zones in the inner and outer retina (Fig. 1*B*). For the analysis of the oxygen profiles from vascularized areas of the retina, a further layer was added to allow for the oxygen input from the retinal circulation. This allowed us to determine oxygen consumption in the avascular layers of the inner and outer retina in an identical manner to that employed in the five-layer model. The retinal capillaries in the rabbit extend only to the deepest margin of the nerve fiber-ganglion cell layer (13), so the inner plexiform layer and all deeper retinal layers can be included in the consumption analysis. The oxygen consumption analysis is based on multilayer solutions to Fick's law of diffusion, but the essence of the analysis is that the oxygen consumption is greatest where the oxygen gradient changes most rapidly. A full description of the principles for the derivation of similar models of retinal oxygen consumption are presented elsewhere (8, 9). Briefly, oxygen consumption (Q) is proportional to the rate of change of oxygen flux with distance

$$Q = Dk \frac{d^2P}{dx^2} \quad (1)$$

where P is P_{O_2}, x is distance, and Dk is the product of oxygen diffusion (D) and solubility (k) coefficients. Integrating twice gives an equation for the oxygen tension P in each *layer j* as a function of x

$$P_j(x) = \frac{Q_j}{2Dk} x^2 + \alpha_j x + \beta_j \quad (2)$$

where α and β are constants. At $x = 0$, the oxygen tension is equal to that in the choriocapillaris P_c, so from *Eq. 2* we get $\beta_1 = P_c$. Similarly, at the boundary with the vitreous, the oxygen tension is equal to P_v. We can determine the other constants, α and β, in each layer by applying boundary conditions, which reflect the fact that both oxygen tension and oxygen flux are continuous across boundaries. This approach applied at each boundary allows all the required constants to be determined. The oxygen distribution can then be expressed in terms of the oxygen tension on the choroidal and vitreal sides and the position and oxygen consumption rate of each of the five retinal layers. The model assumes that the product of oxygen solubility and diffusion coefficients (Dk) remains constant across the retina, an

assumption that has been confirmed experimentally (19). We used a value of *Dk* of 2.84×10^{-6} (ml O_2·cm^2)/(100 g·min·mmHg), a value based on a previous study (1) in cats and monkeys. The model was simplified by assuming that all of the oxygen consumption was concentrated into *layers* Q_2 and Q_4, with Q_2 being located in the outer retina and Q_4 located in the inner retina. The total oxygen consumption of the outer retina was calculated from the product of Q_2 and the thickness of *layer 2* and that of the inner retina from the product of Q_4 and the thickness of *layer 4*. A least-means squared fit between the mathematical models and the intraretinal oxygen distribution was performed to extract the oxygen consumption and oxygen gradient parameters. No constraints were imposed on the thickness or position of the different retinal layers. These parameters were determined by the best fit between the model and the data. In common with earlier modeling studies (6, 9), the most reliable parameters determined from the model were the total oxygen consumption of the outer and inner retina, which is determined by the product of the consumption rate and the thickness of the consuming layer.

RESULTS

Typical intraretinal oxygen profiles are shown in Fig. 2 for a vascularized area and in the avascular visual streak. A correction factor assuming a penetration angle of 30° from the perpendicular has been applied throughout. The best fit of the mathematical models to the data is shown superimposed in Fig. 2 ($r^2 = 0.996$ and 0.997, respectively). Oxygen gradients from the choroid to the outer retina are high in both regions. In the vascular region, there is also a significant oxygen gradient from the retinal vascular bed to the avascular layers of the inner retina. In contrast, in the avascular visual streak, there is no significant oxygen delivery from the vitreal side. The fit between the mathematical models and the experimental data was good in all the profiles accepted for analysis ($r^2 = 0.98 \pm 0.02$, $n = 20$). The averaged data (±SE) for these oxygen gradients are summarized in Table 1 along with the calculated oxygen consumption rates for the inner and outer retina. Outer retinal oxygen consumption was significantly higher in the visual streak than in the vascularized area (284 ± 20 vs. 210 ± 23 nl O_2·min^{-1}·cm^{-2}, $P = 0.026$, $n = 10$). However, inner retinal oxygen consumption in the visual streak was significantly lower than in the inner retina underlying the vascular area (57 ± 4.3 vs. 146 ± 12 nl O_2·min^{-1}·cm^{-2}, $P < 0.001$). In the visual streak, the average oxygen gradient between the vitreous and retina was not significantly different from zero ($P = 0.97$), indicating that there was no significant flux of oxygen from the vitreous into the retina or from the retina into the vitreous. In the vascularized area, the average oxygen contribution from the overlying retinal vasculature to the underlying avascular portion of the retina was 33 ± 2% of the total oxygen uptake of the avascular portion of the retina. Choroidal oxygen levels (P_c) were high in both locations (59.2 ± 4.6 and 72.2 ± 4.1 mmHg), with that in the avascular area being slightly higher ($P = 0.042$). Oxygen levels at the vitreal boundary (P_v) were significantly higher ($P < 0.001$) in the vascularized region (39.3 ± 5.5 mmHg) compared with the avascular visual streak (9.5 ± 2.3 mmHg).

DISCUSSION

The most novel finding of the present study is that, although the functional requirement of the inner retina in the visual streak in the rabbit is presumably maximal, the total oxygen consumption of the inner retina in this region is significantly lower than that in the included portion of the inner retina underlying the vascular streak. In the vascular region, the innermost retinal layers, containing the nerve fibers and ganglion cells, are not included in the analysis due to the unknown input from the retinal capillaries within these layers. The total oxygen consumption of the full thickness of the inner retina in the vascularized region is therefore very likely to be higher than that calculated in the present study, further increasing the contrast with the oxygen requirements of the inner retina of the visual streak. Our calculations determined the total oxygen consumption per unit area of the retina (in nl O_2·min^{-1}·cm^{-2}) for the inner and outer retina. This has the advantage of allowing a direct comparison between the total retinal oxygen consumption of the outer retina and the included portion of the inner retina without taking into account differences in the thickness of these two regions in the vascularized and avascular regions of retina. Ahmed et al. (1) used a similar approach in analyzing foveal and parafoveal measurements in the primate retina and reported light-adapted outer retinal oxygen

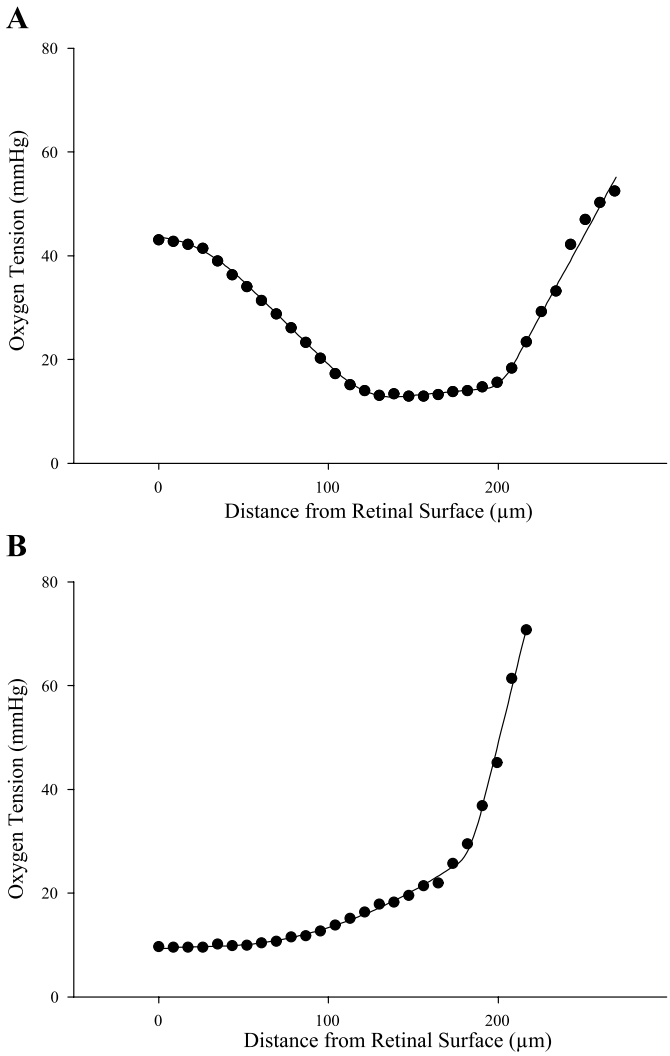

Fig. 2. Typical oxygen distribution data from a vascularized area (*A*) and in the avascular visual streak (*B*). Data are expressed as oxygen tension as a function of electrode penetration depth from the retinal surface. Data points (●) are shown along with the best fit (solid lines) of the data to the mathematical model from which the oxygen consumption was calculated.

Table 1. *Retinal oxygen consumption and oxygen gradients in the vascular area and visual streak*

	Vascular Area (n = 10)	Visual Streak (n = 10)
Q_{or}, nl O_2·min^{-1}·cm^{-2}	210±23	284±20
Q_{ir}, nl O_2·min^{-1}·cm^{-2}	146±12	57±4.3
Oxygen flux from the choroidal side, nl O_2·min^{-1}·cm^{-2}	239±20	341±18
Oxygen flux from the vitreal side, nl O_2·min^{-1}·cm^{-2}	117±12	0±1.0
Total of measured Q supplied from the choroid, %	67±2.0%	100±0.3%
P_c, mmHg	59.2±4.6	72.7±4.1
P_v, mmHg	39.3±5.5	9.5±2.3

Values are means ± SE. Q_{or} and Q_{ir}, total oxygen consumption (Q) in the outer and inner retina, respectively; P_c, oxygen level at the choroidal boundary with the retina; P_v, oxygen level at the vitreal boundary.

consumption rates of ~280 and ~320 nl O_2·min^{-1}·cm^{-2}, respectively. Our measurement of total outer retinal oxygen consumption in the visual streak in the rabbit (284 ± 20 nl O_2·min^{-1}·cm^{-2}) is therefore very similar to that seen in the vicinity of the primate fovea and about twice that recently reported for the outer retina in the rat (148 ± 11 nl O_2·min^{-1}·cm^{-2}) (8). In the primate study of Ahmed et al. (1), the inner retinal oxygen consumption was not quantified, but it was noted that proximal to the region of high oxygen consumption in the outer retina of the foveal area the profiles were linear most of the way toward the vitreous, indicating a low oxygen consumption in the proximal retina. Judging by the considerable track lengths to the retinal surface in their study, it seems unlikely that the profiles were measured in the very center of the foveola, where there are very few inner retinal neurons. If that is the case, then their evidence suggests that the oxygen consumption of the inner retina in the avascular region of the primate fovea is low, an interpretation consistent with our present findings in the rabbit visual streak. In contrast, in vivo studies (6, 9) have shown the inner retinal oxygen consumption in species with vascularized retinas to be similar to or greater than that of the light-adapted outer retina. The low oxygen requirements of the inner retina in the visual streak in the rabbit therefore appears to be a specific adaptation to the limited oxygen availability in this avascular region, a property that may well be true of the avascular region of the human retina.

To compare our results with other studies that express the oxygen consumption in terms of oxygen consumption per unit volume, an estimate of the thickness of the outer and inner retina is required. This is relatively simple for the visual streak, where the thickness of individual cell layers is relatively uniform. Defining the boundary between the inner and outer retina to be the deepest margin of the outer plexiform layer, conventional retinal histology gives an outer retinal thickness of ~80 μm and a value of ~93 μm for the inner retina in the rabbit. It was assumed that fixation of the tissue resulted in uniform shrinkage to 70% of the original thickness. This gives an oxygen consumption estimate of 3.5 ml O_2·min^{-1}·100 g tissue^{-1} for the outer retina and 0.6 ml O_2·min^{-1}·100 g tissue^{-1} for the inner retina. In the vascular area, the corresponding estimate of outer retinal thickness is ~94 μm, which gives an oxygen consumption rate of 2.2 ml O_2·min^{-1}·100 g tissue^{-1} for the outer retina. No attempt was made to estimate the inner retinal thickness in the vascular area because it is very dependent on location, and the vascularized portion of the inner retina was not included in the oxygen consumption analysis.

Braun et al. (6) reported a light-adapted oxygen consumption rate of 1.4 ± 0.9 ml O_2·min^{-1}·100 g tissue^{-1} for the outer retina of the cat and an inner retinal oxygen consumption rate of 3.7 ± 1.5 ml O_2·min^{-1}·100 g tissue^{-1}. Thus, in the cat, the inner retina is the major oxygen consumer under light-adapted conditions. In the avascular retina of the guinea pig, the opposite is true, with outer retinal oxygen consumption (2.07 ml O_2·min^{-1}·100 g tissue^{-1}) constituting 95% of the total retinal oxygen consumption (7). Taken together with the present findings in the rabbit, it would seem that a relatively low oxygen consumption rate of the inner retina may be a feature of avascular retinas and of the avascular region of partially vascularized retinas.

Examining the oxygen gradients at the inner and outer boundaries of the retina indicates that the choroid is the only significant source of retinal oxygenation in the visual streak. The lack of any significant oxygen gradient from the vitreous to the retina in the visual streak indicates that oxygen diffusion from the retinal vasculature via the vitreal route plays no significant role in supplying oxygen to the avascular inner retina. This finding is similar to that reported in the primate fovea, where it was noted that oxygen diffusion from the vitreous contributed very little to foveal oxygen use (1). While we did not measure oxygen tension in the vitreous far away from the retina, it is reasonable to expect that some oxygen enters the vitreous via diffusion from the major retinal arteries, in a similar manner to that reported for the cat (2). However, the relatively large diffusion distances required for this oxygen to reach the avascular retina result in a negligible contribution to inner retinal oxygenation in the avascular area. For example, an oxygen level of 20 mmHg in the central vitreous, 10 mm away from the retina, could produce a maximum oxygen gradient of ~1 mmHg/mm toward the avascular retina of the visual streak, which is less than one-thousandth of the oxygen gradient from the choroid. It would appear that delivering oxygen to the avascular retina via the vitreal route may require more dynamic processes, such as that proposed for the avian pecten, where mechanically induced convection within the vitreous may effectively reduce diffusion distances (17).

The average values for the oxygen tension at the retinal boundary with the vitreous are in close agreement to previously published measurements of preretinal oxygen tension in vascularized and avascular areas of the rabbit retina (21) and span the value for the vitreous as a whole (22 mmHg) in the vitrectomized rabbit eye (5). The measured values for oxygen consumption rates in the outer retina in the rabbit are higher than those recently reported for the light-adapted rat retina in vivo (148 ± 11 nl O_2·min^{-1}·cm^{-2}) (9). Inner retinal oxygen consumption in the rabbit in the vascularized area is slightly lower than that in the rat (184 ± 17 nl O_2·min^{-1}·cm^{-2}) (8). Although the oxygen consumption of the inner retina in the visual streak is lower still, it remains higher (in percentage terms) than that seen in the avascular guinea pig retina, which consumed only 5% of the total retinal oxygen uptake (7). This presumably reflects the relatively poor visual acuity in the guinea pig and the presence of intraretinal hypoxia under normal physiological conditions (24).

How the inner retina in the visual streak of the rabbit is able to function with such a low oxygen requirement is not known.

One possibility is that a high rate of glycolytic metabolism provides the required energy, which is supported by evidence of both high concentrations of glycogen in the inner retina (14) and a metabolic study (3) in in vitro rabbit retinas. If the human retina behaves in a similar way, then understanding the ability for the inner retina to modulate its oxygen requirements to match the limited oxygen supply may open up new avenues for ameliorating the hypoxic component of ischemic diseases of the retina and brain.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the technical assistance of Dean Darcey, Paula Yu, Judi Granger, Megan Dallas, and Chris Barry.

GRANTS

This study was supported by National Health and Medical Research Council of Australia Grant 211901.

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