Control of Choroidal Blood Flow by the Nucleus of Edinger-Westphal in Pigeons: A Laser Doppler Study

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Anatomical studies in birds have suggested that choroidal blood flow may be regulated by a circuit involving the following serially-connected components: the retina—the suprachiasmatic nucleus (SCN)—the medial subdivision of the nucleus of Edinger-Westphal (mEW)—the ciliary ganglion—the choroidal blood vessels. In order to better clarify the role of this circuit, we examined the effects of electrical stimulation of EW on choroidal blood flow in the ipsilateral eye, using laser Doppler velocimetry to monitor choroidal blood flow in the superior pole of the eye. Baseline choroidal blood flow values (144-311.3 mg/min per eye) were found to be comparable to those previously reported in rabbits, cats and primates. Stimulation of EW dramatically increased choroidal blood flow. The increases were current-related and the average maximal increases ranged between 300–700% above baseline values. In contrast, EW stimulation had little or no effect on overall bodily blood flow. All EW stimulation sites were later verified histologically. These results indicate that the SCN-mEW circuit in birds may be involved in mediating increases in choroidal blood flow, possibly in response to the levels of retinal illumination. Such adaptive neural regulation of choroidal blood flow may play an important role in mitigating the potentially deleterious effects of light on the retina. Invest Ophthalmol Vis Sci 31:2483–2492, 1990

The major source of blood supply to the outer retina is the choroid in all vertebrates. In species with an avascular retina, such as rabbits and pigeons, the choroid serves as the major, if not sole vascular supply to the entire retina. The choroid functions to provide oxygen and nutrients to the retina as well as to remove waste products. Photoreceptors are particularly dependent on the choroid since disruptions of choroidal blood flow lead to pathological changes in photoreceptors as well as in other retinal cell types. The choroid with its high blood volume and low oxygen extraction may also be involved in the dissipation of heat, which is produced by light absorption by the retina and pigment epithelium. Increases in retinal illumination in both monkeys and humans have been shown to cause an increase in blood flow in the choroid. This increase in blood flow could presumably cool the retina, thus protecting the photoreceptors from thermal damage.

Control of vascular tone in these choroidal vessels is under external neural influence, unlike the retinal vessels which are reported to autoregulate. These neural projections originate from several peripheral ganglia (the superior cervical ganglion, the sphenopalatine ganglion, the trigeminal ganglion and the ciliary ganglion) and have diverse influences on blood flow. For example, the innervation of the choroid by the superior cervical ganglion provides a vasoconstrictory sympathetic influence on the choroid, while the ciliary ganglion appears to exert a vasodilatory parasympathetic influence on choroidal blood flow. However, little information is available on the central brain regions or peripheral stimuli that activate these fibers.

Anatomical studies in birds have demonstrated a neural circuit by which ambient light may be able to reflexively regulate choroidal blood flow. The serially connected components of this circuit consist of: the retina—the suprachiasmatic nucleus (SCN)—medial Edinger-Westphal (mEW)—the ciliary ganglion—the choroid. The precise role of this circuit in controlling blood flow, however, has not been determined. Since oculomotor nerve stimulation in cats...
and rabbits has been found to have a vasodilatory effect on the choroid and since retinal illumination has been shown to increase choroidal blood flow in monkeys and humans, it is possible that the SCN-EW circuit in birds mediates increases in choroidal blood flow in response to increases in retinal illumination. Such putative increases in blood flow may either dissipate an increased heat load on the retina or provide additional nutrients required by the retina due to increased metabolic demands. In order to begin to determine the role of the SCN-EW circuit, we investigated the influence of mEW on choroidal blood flow. This study was conducted using direct electrical stimulation of EW while recording changes in blood flow in the choroidal vessels using laser Doppler techniques. A brief report of these findings was previously presented at the 1989 ARVO meeting.

**Materials and Methods**

White Carneaux pigeons (6-9 mo, Bowman Gray) (n = 22) were deeply anesthetized with ketamine (0.66 ml/kg) and xylazine (0.33 ml/kg) and positioned in a stereotaxic device. Body temperature was maintained at 38°C with a Harvard heating blanket and rectal thermoprobe. A subcutaneous injection of lidocaine was made into the scalp, and skin, fascia and bone were removed to expose the brain. An insulated stainless steel stimulating electrode was then stereotaxically placed in or near EW, with confirmation of electrode placement determined by miosis in the ipsilateral eye with low current levels (less than 50 /xA anodal current pulses of 0.5 msec duration, 100 Hz). Bone, fascia and muscle overlying the superior pole of the eye were removed, the superior rectus and superior oblique muscles were retracted, and the remaining extracocular muscles topically curarized. The laser probe (arrow) was positioned against the sclera and records were systematically obtained from the region normally underlying the superior rectus or superior oblique muscles via a TSI Laserflo® Blood Flow Monitor (arrow, TSI). An insulated stainless steel stimulating electrode (curved arrow, SE) was stereotaxically placed in or near the ipsilateral mEW.

Fig. 1. A schematized depiction of the experimental preparation is shown. Pigeons were deeply anesthetized and positioned in a stereotaxic device. Bone, fascia, and muscle overlying the superior pole of the eye were removed, the superior rectus and superior oblique muscles were retracted, and the remaining extracocular muscles topically curarized. The laser probe (arrow) was positioned against the sclera and records were systematically obtained from the region normally underlying the superior rectus or superior oblique muscles via a TSI Laserflo® Blood Flow Monitor (arrow, TSI). An insulated stainless steel stimulating electrode (curved arrow, SE) was stereotaxically placed in or near the ipsilateral mEW.

though the ultrasound gel was not necessary to obtain good blood flow measurements, it did prevent tissue drying during the experiment and it was used in all experiments. Microstimulation of EW was in trains of 100 Hz, 0.5 msec anodal current pulses delivered by a Grass stimulator (S48) and stimulus isolation unit. The amplitude of the current pulses was varied between 100–400 μA. The stimulation protocol involved delivering 15–30 sec trains of pulses with intervening 2–5 min rest periods. At least three trials were conducted per current level at each blood flow recording site. The duration of the experiments was from 5–9 hours, with supplemental doses of anesthetic administered to maintain deep anesthesia. During the blood flow recording session, the room and surgery lights were off. Control blood flow measurements while stimulating EW were also made from the skin of the shoulder region of the wing of three pigeons. Relative arterial blood pressure was also monitored in two animals via a cannula placed in either the brachial or ischiadic artery, with the cannula connected to a pressure transducer interfaced with the D.C. Differential Channel of a Stoelting Physiograph II.

Although a variety of techniques have been used to measure choroidal blood flow, the use of laser
Doppler velocimetry (LDV) has allowed us to continuously monitor choroidal blood flow while periodically stimulating EW. The principals of LDV have been described in detail by others. The LDV probe had no obvious unwanted effects on the tissue from which blood flow was being measured, as reflected in the stability of the baseline records at each recording site. The TSI LASERFLO® blood perfusion monitor is specifically designed to measure blood flow in a microvascular bed. The LASERFLO® probe directs the laser beam into tissue up to a depth of 1 mm at the probe tip. The photons scattered and Doppler shifted by the moving red blood cells are collected by a photodetector in the probe which converts the light into electronic signals. The blood perfusion monitor uses an algorithm to convert this signal into either blood flow rate, velocity or volume information. The flow rate is the product of the average number of Doppler shifts per photon (m) (which is proportional to the blood volume) and the frequency shift (f) (which is proportional to the average velocity of the moving red blood cells), (Blood flow = m X f). The LASERFLO® blood perfusion monitor gives blood flow measurements in ml/min/100 g tissue, which are displayed both digitally and on a chart recorder. As will be detailed further in the discussion, the precise accuracy of the LASERFLO® blood flow values for the pigeon choroid has not been validated by other types of measurements. Nonetheless, the blood flow values obtained for the choroid in pigeons are consonant with those obtained by other means for other animals. Further, we are primarily using this methodology to assess the relative changes in choroidal blood flow obtained in response to EW stimulation, thereby allowing us to unambiguously use this instrument to provide clarification of the influence of EW on choroidal blood flow.

At the end of each experiment an electrolytic lesion (100 \( \mu A \), 30 sec, constant current) was made, and the animal was transcardially perfused with 0.75% saline followed by a fixative of 4% paraformaldehyde in a 0.1 M lysine-0.01 M sodium periodate in 0.1 M phosphate buffer (pH 7.4). The brain was removed, cryoprotected with 20% sucrose-10% glycerol in 0.1 M phosphate buffer with 0.02% sodium azide, frozen and these data were used to convert the blood flow measurements obtained at the superior rectus were significantly different throughout the experimental session by both ANOVA and Dunn's multiple comparison procedure (\( P < 0.05 \)). One hundred microampere data were not used in the statistical tests because these data could not be obtained in all animals.

### Results

#### Baseline Choroidal Blood Flow

Stable baseline choroidal blood flow measurements from recording sites beneath the superior rectus (SR) and superior oblique (SO) muscles were first obtained prior to any stimulation (Table 1). Although baselines varied to some degree between animals, they were consistently between 20–30 ml/min/100 g beneath the SO and 35–60 ml/min/100 g beneath the SR. The baseline measurements obtained at the superior rectus were consistently and significantly higher than those obtained at the superior oblique site. This was statistically confirmed by a two-way ANOVA for the same group of nine pigeons as above (Table 1, Two-way ANOVA, \( P > 0.05 \)). During the five to nine hour course of an experimental session, the baselines were stable and no significant changes in baseline levels were observed. This was statistically confirmed by a two-way ANOVA for the same group of nine pigeons as above (Table 1, Two-way ANOVA, \( P > 0.05 \)).

In order to compare our baseline blood flow values to those previously obtained in other vertebrates (in whom the measurements have been reported in mg/min), the pigeon pigment epithelium, choroid, retina, and surrounding sclera were weighed from 4 animals and these data were used to convert the blood flow values obtained from the LASERFLO® monitor into mg/min for the choroid. The mean value of the weight for the posterior pole of the pigeon eye was 0.55 g. Correcting for the specific gravity of blood (approximately 1.06), the baseline blood flow values for the pigeon choroid were calculated to be 144 mg/min at the superior oblique site and 311.3 mg/min at the superior rectus site, which compares favorably with data obtained for various mammalian species.

#### Effects of EW Stimulation

Microstimulation of EW yielded dramatic increases in choroidal blood flow at both recording sites (Fig 2A-C). These EW-elicted increases in blood flow were rapid (<200 msec) and their magnitudes were directly related to the current amplitude (Fig. 2A-C). The choroidal

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### Table 1. Average baseline blood flow values (in ml/min/100 g) prior to onset of each current level

<table>
<thead>
<tr>
<th>Current Level</th>
<th>Superior oblique site—prestimulus baseline</th>
<th>Superior rectus site—prestimulus baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>100 ( \mu A )</td>
<td>22.5 ± 8</td>
<td>49.5 ± 13</td>
</tr>
<tr>
<td>200 ( \mu A )</td>
<td>24.3 ± 5</td>
<td>53.2 ± 7</td>
</tr>
<tr>
<td>400 ( \mu A )</td>
<td>27.3 ± 4</td>
<td>57.4 ± 7</td>
</tr>
</tbody>
</table>

Changes in baseline during the course of an experimental session were not significant by a two-way ANOVA (\( P > 0.05 \)), but the differences between the SR and SO sites were significantly different throughout the experimental session by both ANOVA and Dunn's multiple comparison procedure (\( P < 0.05 \)).

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Fig. 2. Chart recorder data from the TSI Blood Flow Monitor showing the effects of microstimulation of mEW (using trains of 100, 0.5 msec pulses/sec) on choroidal blood flow. Stimulating current onset and offset is indicated by arrows. Chart records of blood flow responses (with a 30 sec stimulus duration and a 2–3 min interstimulus interval) obtained from a single site beneath the superior oblique muscle with 200 μA (A) or a 400 μA (B) current pulses are shown. An example of responses from a single site beneath the superior rectus muscle (C) with 400 μA pulses is also shown. As can be seen, microstimulation of mEW yielded dramatic increases in choroidal blood flow. These increases were rapid and the magnitude of the increase was directly related to the current amplitude. X-axis, one large square = 50 ml/min/100 g, and Y-axis, one large square = 15 sec.

blood flow response would occasionally peak and begin to return to baseline prior to stimulus offset (Fig. 2C). All blood flow responses returned to baseline at stimulus offset with a latency of 2–5 seconds. The blood flow increases from each recording site for each current level were obtained and the average percentage increases in blood flow were calculated for each current level (Table 2). Additionally, mean peak choroidal blood flow was calculated for each current level for each recording site and these values were then plotted in comparison to the mean prestimulus baseline value prior to each current level (Fig. 3). Both Table 2 and Figure 3 clearly show that the increase in choroidal blood flow was directly related to current level, with choroidal blood flow (with 400 μA stimulus current) beneath the SO maximally increased by 700% above baseline (on the average) and beneath SR by 300% (on the average). Two-way ANOVA on a sample of nine pigeons indicated that the percentage increase in choroidal blood flow with 400 μA was significantly greater at the SO site than at the SR site (p < .01).

In contrast, blood flow in the microvasculature of the skin on the shoulder showed little, if any, increase while stimulating EW, thus arguing that the increases in choroidal blood flow observed with EW stimulation were not being mediated by systemic increases in blood flow. For example, 200 μA anodal current pulses (0.5 msec duration, 100 Hz) were never observed to have an effect on blood flow in the skin. Similarly, 400 μA anodal pulses had no consistent effect on shoulder blood flow, although slight increases were occasionally observed. In contrast, stimulation of midbrain sites known to increase systemic blood flow yielded large stimulus-related increases in cutaneous blood flow. Similarly, stimulation of EW had little or no effect on arterial blood pressure.

| Table 2. Mean percent increases in choroidal blood flow obtained for each animal at each current level |
|---------------------------------|---------------------------------|---------------------------------|
|                                 | 100 μA                          | 200 μA                          | 400 μA                          |
| Superior oblique site           |                                 |                                 |                                 |
| CG19                            | 294%                            | 638%                            | 679%                            |
| CG20                            | —                               | 276%                            | 683%                            |
| CG21                            | 42%                             | 223%                            | 698%                            |
| Superior rectus site            |                                 |                                 |                                 |
| CG22                            | 435%                            | 225%                            | 320%                            |
| CG24                            | 173%                            | 383%                            | 600%                            |
| CG25                            | —                               | 361%                            | 349%                            |
| CG30                            | 336%                            | 212%                            | 181%                            |
| CG33                            | —                               | 133%                            | 148%                            |
| CG34                            | —                               | 106%                            | 175%                            |

Blood flow data could not be obtained with 100 μA current pulses in all animals due to variability in response threshold. Two-way ANOVA showed that the percentage increase in choroidal blood flow with 400 μA was significantly greater at the SO site than at the SR site (p < 0.01) but not at 200 μA (100 μA current responses were not included in statistical analysis due to incomplete sample).
Superior Oblique Site

Superior Rectus Site

Fig. 3. Graphs illustrating the choroidal blood flow increases recorded at the SO (A) and SR (B) sites with 100 μA, 200 μA and 400 μA current pulses. For each animal and each site, three measurements were taken of the peak blood flow at each current level. Mean peak blood flow (stim) was then calculated for each current level and each site and graphed in comparison to mean base line blood flow (pre-stim) prior to current onset.

Discussion

These results demonstrate that EW microstimulation increases choroidal blood flow in the superior portions of the eye, thereby suggesting that normal activation of EW by its inputs promotes upregulation of choroidal blood flow via the projection of mEW to the choroidal neurons of the ciliary ganglion, which themselves innervate the choroidal vessels. Our findings are consistent, in principal, with previous studies in cats and rabbits on the control of choroidal blood flow by the oculomotor complex and they may help explain the deleterious consequences of EW lesions on the health of the retina. Our findings, unlike those in previous studies of this type, are based on the use of laser Doppler velocimetry (LDV) and showed much greater changes in choroidal blood flow than previously observed. LDV offers some advantages in comparison to the techniques used in other previous studies on the neural regulation of choroidal blood flow.

Technical Considerations

While a number of different techniques have been used to measure choroidal blood flow, most methods allow only a limited number of measurements in the same animal. These methods include the radiolabelled microsphere method and techniques involving monitoring the clearance of a substance from the blood, either a gas or dye. While each method has its own advantages and disadvantages, the laser Doppler instrument we have used is ideally suited to continuously and quantitatively monitor blood flow in a shallow vascular network such as the choroid. The LDV probe has no obvious unwanted effects on the tissue from which blood flow is being measured (personal communication Dr. R. F. Bonner, NIH; John Borgos, TSI). The use of LDV has made it possible for us to monitor the effects of stimulating EW with different current levels (with repeated measures) in individual animals. In contrast, the microsphere technique requires considerably larger numbers of animals to obtain comparable data, since only 2–3 data points can be obtained from each animal. Further, the use of microspheres may not provide information on the dynamic properties of the choroidal response to neural stimulation (e.g., the latency of the onset and offset of the response and the stability of the response during the stimulus).

While the absolute blood flow values yielded by the TSI LASERFLO® monitor for the pigeon choroid have not been corroborated by other techniques, the values yielded by this monitor have been validated in other tissues. For example, Lindberg et al. compared the results obtained in rat CNS with radiolabelled microspheres to those obtained with LDV (using the TSI LASERFLO® monitor). Using two laser Doppler probes to monitor the microcirculation in the spinal cord, they observed decreases in blood flow in the spinal cord after systemic administration.
of phenylephrine. They reported that the magnitude of the changes observed with LDV were extremely similar to those observed with radiolabelled microspheres and provided highly reliable results. Other investigators have also tested the accuracy of LDV (some using different models of the TSI LASER-FLO® monitor than the one we used and others using similar monitors by other manufacturers) on other tissues (cochlea, intestinal mucosa, nasal mucosa, kidney, skin, and retina) and similarly found that values obtained with LDV were highly similar to those obtained with microspheres. Similarly, we believe that the values for baseline choroidal blood flow in the pigeon eye (24.7–53.4 ml/min/100 g; 144–311.3 mg/min) are likely to be largely accurate since our values (when converted to choroidal blood flow in the eye in mg/min) compare favorably to the values for choroidal blood flow obtained in monkeys (677 mg/min), cats (734 mg/min), and rabbits (809 mg/min) using radiolabelled microspheres and those obtained in baboons (463 ml/min/100 g) using krypton gas clearance. The larger volume of choroidal blood flow in these mammalian species than in pigeons can be accounted for by the relatively greater size (and hence the greater volume of the choroidal vascular bed) of the eyes of the mammalian species.

While LDV proved to be very useful in our experiments, there are some limitations that must be overcome. For example, LDV is extremely sensitive to movement. To overcome this limitation we immobilized the extraocular muscles by topical application of curare. This prevented any eye movement, either naturally-occurring or occurring due to current spread from our EW stimulation site to the nearby somatic parts of the oculomotor nuclear complex (which occurred with some of our electrode placements in EW). We found that curare also dilated and fixed the pupil (and presumably immobilized the lens, although we did not experimentally verify this), as would be expected since transmission between the ciliary ganglion and the constrictor muscles of the iris and the muscles of the ciliary body is nicotinic. Other than making the recording of choroidal blood flow more stable and reliable, curare had no effect on baseline choroidal blood flow or on the responses to EW stimulation. It should be noted further that the observation that pupil and lens immobilization by curare had no effect on the EW-elicited increases in
choroidal blood flow argues against the notion that the EW-elicited effects are mediated by traction on the choroidal bed produced by the lens and pupil movements attending EW stimulation. A second limitation of LDV, is that it is only possible to sample a small region of tissue at any one time with a single probe. In order to overcome this limitation we sampled from two general sites at the superior pole of the eye, one beneath the superior rectus muscle and the other beneath the superior oblique muscle. The baseline blood flow values for each site were consistent from animal to animal, as were the magnitudes of the current-elicited increases in choroidal blood flow. There were statistically significant differences, however, between the two sites in the baseline blood flow values and in the maximum increases in choroidal blood flow that could be elicited. The bases of the differences in choroidal blood flow at these two sites are unclear, but they may stem from differences in the geometry of the choroidal vascular bed at these two sites (e.g. differences in vessel abundance or diameter). We chose to sample only from the superior portion of the retina for two reasons. First, access to this part of the eye can readily be achieved without bleeding. Secondly, this region in pigeons contains the red field, which is an area of increased cone density that is specialized for high acuity vision. The choroidal blood flow in this region may therefore possess some of the characteristics found in the choroid of the macular part of the primate eye. The macular region in mammalian retina is known to have a higher basal choroidal blood flow when compared with other areas of the retina. Consistent with this finding in mammals, histological observations indicate that the vessel abundance and size in the choroidal vascular bed appears greater in the superior part of the pigeon eye (Reiner and Fitzgerald, unpub. obs.).

Comparisons to Previous Studies: Consistent with our findings, oculomotor stimulation has been shown to cause vasodilation of choroidal vessels in cats and rabbits. Vasodilation was observed after electrical stimulation of either the oculomotor nerve or the oculomotor nuclear complex. The increases observed in choroidal blood flow in mammals have seemingly not been as dramatic as those that we observed in pigeons. For example, choroidal blood flow in cats was observed to maximally increase only by 30%. This difference may be a reflection of the differences in methodology (most prior studies have used microspheres to measure choroidal blood flow) or of the differences in species. Nonetheless, based on our results in pigeons, the findings in cats and rabbits suggest that EW in mammals may also be involved in producing choroidal vasodilation via activation of ciliary ganglion neurons projecting to the choroidal vessels. Although this conclusion is consistent with the physiological studies, innervation of choroidal blood vessels by ciliary ganglion neurons has not yet been demonstrated anatomically in mammals.

In birds, control of choroidal blood flow by the choroidal neurons of the ciliary ganglion is mediated by muscarinic cholinergic mechanisms (16, Reiner, Vana and Fitzgerald, unpub. obs.), suggesting that the effects of oculomotor stimulation on choroidal blood flow in mammals may also be mediated by muscarinic cholinergic transmission between ciliary ganglion neurons and choroidal blood vessels. Studies of the effects of systemic administration of muscarinic antagonists or of ganglionic blockade on the vasodilation in response to oculomotor stimulation have yielded results largely consistent with this conclusion. In cats, significant blockade of stimulation induced increases in choroidal blood flow were observed with systemically administered atropine (to block muscarinic transmission) or hexamethonium (to block transganglionic transmission). Similarly, systemic administration of biperiden (to block muscarinic receptors) or hexamethonium in rabbits also greatly attenuated the oculomotor stimulation-induced increases in choroidal blood flow. The interpretation, however, of the results of experiments involving systemic administration of pharmacological agents such as these, is not unequivocal. For example, in studies examining pharmacological effects directly exerted on blood vessels, systemic administration of drugs may lead to equivocal results because the drugs, due to a local blood-tissue barrier, may have only restricted access to the abluminal side of the vasculature where the relevant postsynaptic receptors are located. Further, systemic administration could lead to cardiovascular changes in the tissue of interest indirectly, either by influencing other neural cardiovascular centers or by affecting blood pressure. Nonetheless, the results of our own preliminary studies in pigeons (Reiner, Vana and Fitzgerald, unpub. obs.), in which we infused atropine directly into the choroid, are in agreement with the findings in cats and rabbits. We found that such intrachoroidal infusion of atropine (10^-3 M to 10^-2 M) significantly attenuated the EW-microstimulation elicited increase in choroidal blood flow. Thus, the role of EW in regulating choroidal blood flow may be very similar in birds and mammals.

Functional Implications

In birds and mammals, the choroid is innervated by several types of autonomic fibers. Adrenergic sympathetic fibers arising from the superior cervical ganglion are known to exert a vasoconstrictory influence
on the choroid.8,47 Parasympathetic VIP-containing fibers, which arise from the sphenopalatine ganglion, are known to cause choroidal vasodilation,5,9,15,48,49 as are parasympathetic cholinergic ciliary ganglion fibers, as discussed in this paper and reported by others.12,17,18 Finally, substance P/calcitonin gene-related peptide (CGRP)-containing sensory fibers in the choroid, which arise from the trigeminal ganglion,9,15,50-52 have been shown to exert a vasodilatory action on the choroidal vessels.9,10,53 Little is known, however, about which types of stimuli or which central circuits control these different populations of peripheral fibers.

In our studies on pigeons, we have determined the components of one of the circuits controlling the ciliary ganglion fibers innervating the choroid. As noted, the components of this circuit are the retina-SCN-EW-ciliary ganglion-choroid.14-16,54 Various stimuli that may act through neural circuitry are known to influence choroidal blood flow. These stimuli include intraocular pressure, hypoxia, systemic blood pressure, and light.8,9 It seems likely that the circuit we have described reflexively mediates choroidal blood flow changes in response to light. Our finding that large vasodilatory responses can be elicited by EW stimulation supports the notion that the SCN-EW circuit may mediate increases in choroidal blood flow in response to increased levels of light. Further consistent with this possibility, we have found that discrete microstimulation of SCN in pigeons also results in increases in choroidal blood flow and that retinal illumination in pigeons leads to increases in choroidal blood flow.56 It is possible that increases in choroidal blood flow are necessary to provide the retina with necessary nutrients for photoreceptor renewal and it thus play an important role in maintaining a constant physiological environment for retinal photoreceptors. 3,4 The present results suggest that these adverse effects on the retina following EW lesions may have occurred due to an inability to adaptively increase choroidal blood flow in response to some parameters of the normal illumination states to which the animals were exposed. The effective neural control of choroidal blood flow may thus play an important role in maintaining a constant physiological environment for retinal photoreceptors and disruption of neural regulation of choroidal blood flow may underlie or contribute to retinal pathologies.

Key words: choroid, Edinger-Westphal, blood flow, birds, Laser-Doppler

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