Pressure in the canal of Schlemm and its relation to the site of resistance to outflow of aqueous humor in the eyes of Ethiopian green monkeys

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A simultaneous recording of pressures in the anterior chamber and in the canal of Schlemm in living and dead monkey eyes was used to analyze the site of resistance to outflow of aqueous humor. The results were interpreted to indicate that under the experimental conditions the greatest part of resistance to outflow lay distal to the inner wall of the canal of Schlemm. A value for episcleral venous pressure was obtained by direct measurement. It was also determined that a significant back pressure builds up rapidly with increasing intraocular pressure. Possible sources of error were discussed. Species differences as well as the experimental design and technique may account for the contrasting observations made in human eyes.

The purpose of this investigation was to define the site of resistance to the outflow of aqueous humor in the eyes of normal monkeys. Earlier studies of this question included measurements of the pressure in aqueous veins, the effect of goniotomy on outflow resistance, or direct manometry of both the anterior chamber and canal of Schlemm. Goldmann and Linner determined the pressure in the canal of Schlemm of human eyes indirectly by measuring the pressure required to collapse an aqueous vein connecting with the canal. In normal eyes at an intraocular pressure of 15 mm. Hg they estimated the pressure in the canal to be lower by 3 or 4 mm. Hg. Since the pressure in nearby recipient vessels had an essentially similar or slightly lower value, it was concluded that the principal resistance to outflow was located in the inner wall of Schlemm's canal. Bárány found that goniotomy caused a marked fall in the outflow resistance of the enucleated chicken eye, and concluded that structures close to the inner wall of the canal provided the main resistance to outflow of aqueous humor. Grant, using an improved technique for goniotomy and perfusion in enucleated human eyes, drew similar conclusions, and estimated that 75 per cent of the resistance to aqueous outflow in the dead human eye was located in the inner wall of Schlemm's canal. Perkins, on the other hand, employing direct manometry, measured simultane-
viously the pressures in the anterior chamber and in the canal of Schlemm of three rhesus monkeys. He found that the pressure in the canal was only 10 per cent less than that in the anterior chamber, and concluded that the site of resistance to outflow of aqueous must lie distal to the inner wall of the canal.

Lack of information concerning the site of outflow resistance in living normal primate eyes and need for a system to study the mechanism and locus of action of facility increasing agents prompted the present work. It was felt that further information might be obtained with improved cannulation and manometric technique.

Methods

A. Experimental animals. Freshly killed rhesus monkeys were made available following nephrectomy through the courtesy of Dr. Frank Black, Department of Epidemiology, Yale University School of Medicine. Several live rhesus monkeys were also obtained. *Cercopithecus aethiops* (Ethiopian green or green vervet monkeys) were mostly used for in vivo study. The animals weighed between 2 and 3 kilograms and were maintained on a diet of Mother Hubbard crackers and water ad libitum supplemented by fresh fruit and vegetables. Phencyclidine,* 1.0 to 2.0 mg. per kilogram, was first administered intramuscularly so that the animals could be more easily handled. The effect of phencyclidine lasted for approximately one hour during which time a femoral artery and vein were cannulated with suitably sized polyethylene tubing. The former was led to an electric strain gauge transducer via polyethylene tubing filled with heparin sodium* in saline. The cannulated vein was connected to a constant drive infusion apparatus. Tracheotomy was performed next and followed by a stabilization period of approximately 15 minutes during which the animal's respiratory movements were observed. A Phipps-Bird respirator was then adjusted so that the monkey's respiratory efforts were just eliminated without change in pulse rate or femoral artery blood pressure. For anesthesia at a level where corneal reflexes were preserved, thiopental sodium† was administered intravenously at a rate of 10 to 15 mg. per kilogram per hour. Gallamine‡ was given at a rate of 5 mg. per kilogram per hour to eliminate undesirable body and eye movements. Finally, 6 mg. per kilogram of heparin sodium was added to the intravenous infusion.

B. The eye.

Dissection. A canthotomy was performed and the lateral margins of the upper and lower lids gently retracted with No. 4-0 silk sutures so as not to exert pressure upon the globe. Lidocaine,§ 2 per cent, anesthesia was used topically. The temporal limbus was dissected free of conjunctiva, associated pigment, and underlying connective tissue until a fine gray line, and in some instances, a red line became apparent through the thinned corneoscleral tissue. This line corresponded to the canal of Schlemm. The anterior chamber was then cannulated mechanically. When the intraocular pressure had stabilized, outflow facility measurements were made.‡ The external wall of the canal was then incised parallel to its long axis for a distance of approximately 1 to 2 mm. The opening was slit shaped. Examination of the opening under the dissecting microscope showed

\*Liquemin, Organon, Inc., West Orange, N. J.
†Abbott Laboratories, North Chicago, Ill.
‡Flaxedil, Lederle Laboratories, Pearl River, N. Y.

![Manometric System](image-url)
that above pressures of about 10 mm. Hg aqueous humor exited discretely from the opening. At pressures below 10 mm. Hg blood usually oozed from the slit. The next step was to repeat the facility determinations after which the canal was cannulated directly.

Cannulation system. The anterior chamber was cannulated mechanically with stainless steel cannulas. Special attention was given to the cannula tubing leading to the canal of Schlemm. A large bore polyethylene tubing was pulled out over a hot plate so that the tapered end of the cannula tip did not exceed 0.10 mm. in outer diameter. Cannulas larger than this perforated the inner wall of the canal. The internal diameter of the cannulas ranged from 40 and 50. The cannulas were tested prior to use by inserting them into the previously cannulated anterior chamber of an eye of an anesthetized rabbit through a shelved self-sealing corneal incision. The pressure in the anterior chamber was then varied by its connection to a reservoir through the preplaced stainless steel cannula (O.D. 0.5 mm.). Intraocular pressure was measured through both cannulas and recorded. If the response of the polyethylene cannula was comparably brisk and accurate as that of the larger steel cannulas, it was considered satisfactory for use. It was then marked with ink at 5 and 10 mm. from its tapered end. It was filled with cooled boiled saline by means of a needle and syringe. Once filled and bubble free it was joined to a short piece of metal tubing which in turn inserted into polyethylene tubing connected to a transducer which would measure the pressure of the canal (see Fig. 1). During this maneuver saline exited from the metal joint (a) at a reservoir pressure of 40 mm. Hg to eliminate the chance of trapping air bubbles within the cannula. The reservoir and intraocular pressure levels were then equalized. The cannula tip was manipulated with sponge-padded forceps under the dissecting microscope and inserted into the canal usually for a distance of 5 mm.

The cannula appeared to fill and seal the opening. Two methods were used to ensure a seal. One consisted simply of drying the sclera surrounding the cannula with a fine stream of air. This usually proved satisfactory. On several occasions tetramethyl thuram disulfide was used. This methacrylate resin formed a seal.

Cannulation system. The anterior chamber was cannulated directly.

Examination of the chamber angle. The animals were killed and the anterior chamber cannula was removed. The anterior segment of the eyes was then excised by means of a circumferential equatorial incision so it could be delivered with the canal of Schlemm still cannulated. Gross examination of the chamber angle was done under the dissecting microscope and photographs were taken. For gonioscopy and photography it was sometimes necessary to excise portions of the pupillary margin of the iris since it had a tendency to flap over the chamber angle. The base of the iris was never disturbed. The anterior segment was then fixed in 4 per cent neutral formaldehyde. For purposes of histologic examination, meridional sections were cut at 8 μ, both in the region of the cannulated area of the canal and opposite this area in the unmanipulated portion of the chamber angle.

Results

1. Intraocular pressure and outflow facility are recorded in Table I. The values for intraocular pressure are higher than those obtained for monkeys studied under deep barbiturate anesthesia when no secretion of aqueous humor was apparent and lower than those observed for monkeys under phencyclidine anesthesia. They are comparable to the levels reported for animals under intravenous pentobarbital sodium.

The mean determined for outflow facility, 0.41 ± 0.08 (12) μL per minute per millimeter Hg, is close to previously reported values. In those eyes studied by both constant rate and constant pressure perfusion, very small differences were noted. These differences are not reported. The latter method had the obvious advantage of speed.

A comparison of outflow facilities measured before and after the external wall...
of the canal was slit open, and again after the canal was cannulated, did not show important differences (Table I). Neither was a difference in intraocular pressure apparent before and after cannulation. After the external wall was slit open there was an immediate and transient drop in intraocular pressure in those eyes which had a pressure greater than episcleral venous pressure (Fig. 2, top and bottom tracings). This decrease was restored to original levels (±1.0 mm. Hg) within 10 to 15 minutes. A fall in intraocular pressure did not occur in those eyes which had a pressure nearer to episcleral venous pressure (Fig. 2, middle tracing).

During experiments performed to determine the relationship between pressures in the anterior chamber and in the canal of Schlemm, the pressure in the former was purposefully made to approach zero. At this time red blood cells could be seen bobbing around the tip of the cannula which had been placed within the canal of Schlemm. The pressure in the canal remained above the pressure in the anterior chamber and settled at what must have been episcleral venous pressure, directly determined. The value found by this method was about 6 mm. Hg (Table I) and corresponds to indirect estimates of episcleral venous pressure made by Goldmann.11

2. The relationship between pressure in the anterior chamber and in the canal of Schlemm over a wide range of pressures was successfully studied in 6 live and 3 in situ dead eyes (Table I and Figs. 3 and 4). Above 10 to 15 mm. Hg a linear relationship was regularly found between the two pressure compartments. In large measure the pressure in the canal of Schlemm reflects the pressure in the anterior chamber. The relationship between the two may be expressed in the following way and the resistances across the internal wall of the canal and across the external wall and collector channels derived accordingly:

\[ P_\text{c} = \text{the pressure in the anterior chamber; } P_s = \text{the pressure in the canal of Schlemm; } R_i = \text{the resistance across the inner wall of the canal of Schlemm; } R_v = \text{the resistance across the collector channels and outer wall of the canal in the dead eye and in the living eye at normal pressures of } P_\text{a} = 15 \text{ mm. Hg; } R' = \text{the virtual resistance along the collector channels, in addition to } R_v, \text{ which would account for flow at pressures greater than normal; } \]

### Table 1: Intraocular pressure, outflow facility, episcleral venous pressure in 12 living monkeys

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<td>11.4</td>
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Facility values are reported as microliters per minute per millimeter of mercury. C1 is facility determined in the eye after cannulation of the anterior chamber; C2 after slitting of the external wall of the canal of Schlemm; C3 after cannulation of the canal of Schlemm.

Epv is episcleral venous pressure in millimeters of mercury measured when pressure in the anterior chamber was zero.

Slope values are determined from the plots recorded in Fig. 3; one additional experiment (No. 32) not shown in Fig. 3 is also included in this table.

Iop and C are recorded as mean ± s.e.m. (n).
F is flow;
d is the drop in pressure along the collector channels in excess of the amount accounted for by Rv.

Then the independent equations are:

\[ F = \frac{P_s - d}{R_s} \quad (1) = \frac{P_s}{R_s + R_v} \quad (2) = \frac{P_s - P_v}{R_s} \quad (3) = \frac{P_s - d}{R_s + R_v} \quad (1 + 3) \]

From experiment No. 29, for example, the equation of \( P_s \) vs. \( P_v \) for \( P_v > 15 \) is

\[ (4) \quad P_s = 11 = \frac{9}{10} (P_v - 15), \text{ and} \]

\[ (5) \quad d = 0 \text{ when } P_v = 11 \text{ since, at normal pressure, } R_v \text{ accounts for all the pressure drop along the collector channels.} \]

From equations (1) and (3) we find that

\[ \frac{R_s}{4} = \frac{11}{9} \text{ at normal pressure } P_v = 15, \text{ and, from (4)} \]

\[ P_s - 15 = \frac{10}{9} P_v - \frac{110}{9} \]

\[ \therefore \quad P_s - P_v = \frac{1}{9} (P_v - 110) + 15 = \frac{1}{9} (P_v + 25) \]

and from (1) and (3)

\[ \frac{P_s - d}{R_s} = \frac{P_v - P_s}{R_v} \]

or \[ d = \frac{R_v}{R_s} \cdot \left( \frac{P_v - P_s}{P_s} \right) \]

\[ dR_v = P_v R_v - R_v (P_v - P_s) \]

\[ d = \frac{P_v - P_s}{R_s} \cdot \left( \frac{P_v}{P_s} - 1 \right) \]

\[ = P_v \cdot \frac{11}{4} \cdot \frac{1}{9} (P_v + 25) \]

\[ = \frac{25}{36} P_v - \frac{25}{36} \cdot 11 = \frac{25}{36} (P_v - 11) \]

\[ = .7 (P_v - 11) \]

This formula shows that \( d \) varies linearly with \( P_v - 11 \).

From (2) and (3):

\[ R_v' = R_v \cdot \frac{P_v}{P_s - P_v} - R_v \]

\[ = R_v \left( \frac{9P_v}{P_v + 25} - \frac{R_v}{R_s} \right) \]

\[ = \frac{9P_v}{P_v + 25} - \frac{11}{4} \]

\[ = \frac{R_v}{4} \cdot \frac{25}{P_v + 25} (P_v - 11) \]

and \[ \frac{R_v}{R_s} = \frac{25}{4} (P_v - 11) \]

This formula shows that \( R_v' \) varies with \( P_v - 11 \), the excess pressure, although not linearly.

The slope of \( \frac{R_v'}{R_s} \) against \( P_v - 11 \) is \[ \frac{1}{4} \cdot \frac{25}{(P_v + 25)} \]

which varies from \( .17 \) to \( .10 \) as \( P_v \) goes from 11 to 41. \( \frac{R_v'}{R_s} \) varies from 0 at normal pressures to 3 at 41 \[ .10 (41 - 11) \].

Thus \[ \frac{R_v + R_v'}{R_s} \] varies from \[ \frac{11}{4} \text{ to } \frac{11}{4} + 3 \cdot \frac{R_v}{R_s} \]

\( R_v' \) is the total resistance to flow in the collector channels and it essentially doubles as \( P_v \) increases to 40.

It seems that \( d \) is better accounted for physically by a back pressure rather than by an increased resistance, and, for this reason, \( R_v' \) has been called a "virtual" resistance. The critical mathematical facts underlying the assumption that \( d \) is due to back pressure rather than to an increased resistance are that \( P_s \) vs. \( P_v \) is linear for \( P_v \geq 15 \) (normal intraocular pressure) and \( R_v \) remains constant.

3. Gonioscopy was done at the end of each experiment (Figs. 5 and 6). In experimental failures usually the cause was immediately apparent. The cannula could be seen poking through the trabecular meshwork, or resting on, and, in one instance, behind the iris. On one occasion the canal was perfectly cannulated but satisfactory measurements were not obtained. Later a fine clot was found within the tip of the cannula. In another experiment the cannula seemed to have been perfectly placed, but identical pressures
Fig. 2. Record of intraocular pressure during dissection of outer wall of Schlemm's canal. In each case arrow indicates moment at which the outer wall of the canal was actually entered. Vertical lines in anterior chamber pressure record reflect knife strokes upon the outer wall. Top and bottom tracings show examples of a sudden transient fall in intraocular pressure with recovery. The middle tracing shows no fall in intraocular pressure after the exterior wall of the canal was opened. Deflections after the arrow resulted from attempts to ensure that the outer wall had been opened.
Fig. 3. The relationship between anterior chamber and canal of Schlemm pressures in 3 dead and 5 living monkey eyes. The slopes of the former average 0.74. The latter average 0.85. Each point (except No. 23) represents two measurements, one derived from progressive stepwise increments in pressure, the other taken during descending stepwise measurements (see text).
were recorded from anterior chamber and canal. Gonioscopic examination of the chamber angle revealed that the cannula had perforated the inner wall of the canal of Schlemm exactly at the site of interesting and unusual anterior synechiae.

4. Histologic examination of the canal by light microscopy of serial sections did not reveal damage to the inner wall (Figs. 7 and 8). No evidence of damage could be detected by these methods, but it was not felt that the possibility of minute trauma to the trabecular meshwork and the inner wall was completely excluded.

Discussion

These manometric studies indicate that in the living monkey eye the significant part of resistance to aqueous outflow lies in the outer wall and its collector channels. The ratio, $R_w/R_{in}$ was generally found to be about 3. The increase in pressure in the canal of Schlemm with increasing intraocular pressure is quite marked. The linear relationship between the two above normal pressures has a slope value of 0.85. In this respect, therefore, the monkey eye behaves qualitatively at least like four human eyes which were studied by Goldmann. Goldmann found that the plot of $P_t$ vs. $P_c$ was linear. The slope differed from those of the present experiments. Nevertheless, a sizable increase in the pressure of the aqueous veins at their point of emergence occurred when the intraocular pressure was increased by the application of an ophthalmodynamometer. Whether the increased pressure in the aqueous veins reflected an increase in intraorbital pressure or whether the pressure recorded reflected directly (through direct connec-
Fig. 5. An excised quadrant of a monkey eye with cannula in place. The iris has been flapped posteriorly to allow photographing. Note ink mark on cannula. Inset, enlargement showing from the inside cannula within Schlemm's canal, scleral spur immediately posterior, and finally ciliary body. Clear area overlying length of cannula is the place where limbal pigment has been removed during dissection.

Fig. 6. Polyethylene cannula, O.D. 0.09 mm., I.D. 0.05 mm., in place. The iris has been partly excised to facilitate previous gonioscopic photography.
tions with the canal of Schlemm) the pressure in the canal of Schlemm is not definitely decided. If partly the latter, however, Goldmann's results indicate that a part of the resistance to aqueous outflow lies in the distal part of the aqueous veins and their episcleral and conjunctival connections. The difference between the monkey and the human eye as regards the sites of outflow resistance, then, would be best explained by a difference in a quantitative rather than a qualitative distribution of these sites.

Another finding of great importance for the monkey eye is the high rate at which back pressure builds up. For example, as \( P_e \) increases to 30, \( R_e \), additional "resistance," becomes 2.3 \( R_e \). As \( P_e \) increases to 50, \( R_e \) equals 12.5 \( R_e \). It is clear that for both the monkey eye and the human eye direct experimental investigation of this back pressure is necessary. Our analysis depends on the assumption that \( R_e \) is constant throughout, that the relationship between \( P_e \) and \( P_a \) above normal intraocular pressures is linear, and that episcleral venous pressure varies within very narrow

Fig. 7. Enlargement of Fig. 6 showing inner wall and trabecular meshwork at arrow.

Fig. 8. The excised anterior segment has been cut meridionally and the cannula pushed around within the lumen of the canal so that it now appears through the open cut end.
limits above normal intraocular pressures. Direct measurements of episcleral venous pressure and facility determinations made via the canal cannula are needed to obtain data for or against these assumptions.

Some interesting anatomic features of the canal of Schlemm were revealed during preparatory dissections. Jocson and Grant have found that liquid silicone injected into the canal of Schlemm of dead human eyes flowed around easily within the canal. In the present experiments this observation was confirmed for the monkey eye. There was no impediment to circumferential flow of an injected solution of fluorescein. Also, a human hair could be passed circumferentially within the lumen of the canal without obstruction (Fig. 9). Of course physiologic considerations may normally operate against this type of flow in favor of an outwardly directed radial flow.*

When the external wall of the canal was slit open, the inner wall did not protrude through the small slitlike opening. The inner wall was extremely fragile and it is perhaps just because porosity contributed to its fragility that no bulge in the inner wall occurred. Often a small drop of aqueous would exit through the slit. A steady ooze of aqueous was observed if the lips of the opening were held apart. Since it was difficult to hold the lips steadily open, the finding of an unchanged outflow facility after slitting of the external wall is not surprising. On the other hand, the initial opening through the external wall into the lumen of the canal certainly bears on the abrupt transient drop in intraocular pressure. If the total outflow resistance is distributed over an area which includes the external wall, and if a large part of the resistance resides in the external wall and collector channels, then a significant drop in intraocular pressure might be expected. Intraocular pressure would be restored as the slit closed over. In about half the experiments which showed a decrease in intraocular pressure, a return to original pressure levels occurred. In the other experiments new steady state values for intraocular pressure returned to a slightly

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*In equation (2), an expression for episcleral venous pressure, $P_e$, can be included as $F = \frac{P_e - P_r}{R_e + R_r}$. 

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Fig. 9. A human hair has been threaded around within the lumen of the canal with the help of several separate openings in the exterior wall.
higher or slightly lower (±1.0 mm. Hg) level. In some of these latter a very small increase in outflow facility was evident but not striking. Other possible sources for the transient intraocular pressure decrease would include a very small volume loss from exit of intracanalicular fluid, and, of course, the occurrence of actual injury to the inner wall.

Trauma to a tiny area of the inner wall cannot absolutely be excluded and certainly it is important to consider what possible physiologic distortions are induced by dissection of the external wall of the canal of Schlemm.

The recorded pressures in the canal might be falsely low or falsely high. If the former, a leak around the cannula might account for this record. Even at pressures greater than normal, however, $R_{c}$ increased. One might anticipate a larger leak at higher pressures and consequently little or no change in $R_{c}$. Then, too, the hypothetical leak around the cannula would need to be rather constant from eye to eye to account for the similar values obtained in successful experiments. This "fixed" leak is unlikely. Finally, in those cases where there was a known leak around the cannula, considerably lower pressures were anticipated and indeed recorded in the canal.

Now, could the recorded pressures in the canal be falsely high? A leak within but around a stopcock could transmit pressures from the reservoir. But, again, the leak would need to be constant in amount and this hypothesis is destroyed by comparing successful with unsuccessful experiments as well as by observing the uniform nature of successful experiments. A second more likely cause of false high pressures in the canal would be penetration of the inner wall during dissection. This possibility cannot be absolutely excluded, but it is felt that histologic examination of the specimens, the regularity of successful experiments, and the contrast with the results in unsuccessful experiments when the inner wall was clearly penetrated indicate that injury of consequence probably did not ordinarily occur. Finally, when pressure in the anterior chamber was reduced to zero, no blood was found to enter into the anterior chamber through the trabecular meshwork from the canal of Schlemm. (This phenomenon as well as the observation that the pressure in the canal of Schlemm remains higher than the pressure in the an-

Fig. 10. A human hair within one of the bifurcations of the canal of Schlemm of a rhesus monkey.
terior chamber at low chamber pressures suggests that a certain type of inward unidirectional resistance may be present within the lamellae of the trabecular meshwork and inner wall.) The mechanics of the mesh may also explain the (extrapolated) above atmospheric pressure levels noted in two dead eyes when the pressure in the canal of Schlemm was zero (Fig. 3).

Another factor could have contributed to our results, namely, an undetected artifact of the system. Where this artifact might reside and how it would exert its effect is open to speculation.

Can these findings be reconciled with those of Grant for dead human enucleated eyes and with Goldmann's measurements in living human eyes? First, there is probably an overlooked important species difference between the human and monkey eye. The tenuity of the inner wall of the monkey canal compared with that of the human being becomes evident during dissections. Electron-microscopic studies confirm this difference. Second, just as it is difficult to exclude trauma to the inner wall during dissection of the outer wall, it is similarly difficult to exclude damage to the outer wall during the performance of goniotomy. Maumenee has observed that the thickness of the human trabecular meshwork from Schlemm's canal to the anterior chamber is about 0.1 to 0.2 mm. He observed that it was very difficult to understand how a surgeon controls an incision of this depth particularly if the incision were made at an oblique angle to the surface of the meshwork with less than ideal optics. The earlier findings of Perkins are not pertinent to this "dissection" discussion since the cannula used by Perkins was three times the diameter of the cannula used in the present work. Furthermore, Perkins did not include histologic proof of the success or failure of his cannulation experiments. Third, our cannulation experiments may present an extreme condition. In reality, the canal of Schlemm may be only a potential cleft, ordinarily collapsed, so that apposition of the inner wall with the outer wall in the human eye gives the impression of a considerable resistance to the inner wall as well as making it difficult to open the outer wall without injury to the inner wall. The present experiments may tell only about a "dilated" canal. These speculative considerations should probably yield to the idea that the differences described are related to a difference between the inner wall of the monkey and the human eye. Therefore, these experiments need not be interpreted as necessarily bearing upon the physiology of the human eye or upon the human condition of glaucoma.

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REFERENCES