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ON THE EYE OF THE OX AND ITS INTERNAL BLOODVESSELS*

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A FEW words in the first place on the original purpose of this investigation.

We know that the blood-streams that pass through the eye fall in pressure as they do so: their exit pressure is considerably lower than their entrance pressure. We do *not* know how the fall is distributed: how much of it occurs in the arteries, how much in the capillaries, how much in the veins. If we did, we could better understand certain processes whose nature is still questioned, e.g., the secretion of the intraocular fluid by certain vessels, and its absorption by others. Now, if it were possible to measure and count the channels through which the blood has to pass at different parts of its course, one could, with the help of physical principles, learn in some degree how the fall is distributed—one could construct a pressure line for the intraocular circulation. That is what I desired to do.

The initial steps of the enquiry were published in this Journal several years ago (BRITISH JOURNAL OF OPHTHALMOLOGY, 1917, pp. 48 and 657; 1918, p. 257). The present paper exhibits some of the anatomical material collected since that time. It leaves the

*Many of the preparations reproduced at the end of this article were shown under the microscope and on the screen to the Section of Ophthalmology of the Royal Society of Medicine on Nov. 12, 1920, and to the Midland Ophthalmological Society at an earlier date.

question of blood-pressure aside for the moment. Many counts and measurements have been made, but these, and the inferences they suggest, must be dealt with in a separate article.

Leber's unrivalled description of the bloodvessels of the eye¹ was consulted on every point, but it does not afford sufficient data for the purpose. One could not work out the subject on human eyes; such material fresh and healthy is not to be had. I turned, therefore, to the albino rabbit, the absence of uveal pigment offering evident advantage. The results have, I think, some interest.

Rabbit No. 1 was killed by chloroform. It was then suspended by the hind feet; pressure was made on the abdomen; the ears and conjunctiva became visibly congested. The neck was then tightly ligatured, and severed between ligature and body, and the head was placed in normal saline with formalin 5 per cent. These steps were designed to fill the intraocular vessels with blood and to fix them in that state. They failed. Excised and opened a week later the eyes were internally almost bloodless. Only the larger veins of the choroid and ciliary processes contained broken blood-columns; the other vessels were nearly empty. Had they failed to fill during the external congestion, or had they emptied themselves later? A second observation answered that question.

Rabbit No. 2, without disturbance of any kind, was viewed ophthalmoscopically with regard to the natural tint of the fundus-reflex. It was then killed by coal gas instead of chloroform, to relax the arteries, and suspended as in the first case. A long elastic cord was wound round the body from thighs to shoulders, with a pad on the abdomen. Intense congestion of ears and conjunctiva, with protrusion of the eyes, immediately ensued. *The fundus tint, viewed ophthalmoscopically, was no deeper than in the normal living eye, perhaps even a little paler.* The left cornea was now punctured with a cataract needle. The aqueous escaped with abnormal force and the iris instantly assumed a deeper colour. The fundus-tint was now found to be much deeper than in the unpunctured eye. The animal was suspended in a jar with head and shoulders immersed in saline-formalin solution, the compressive cord being left in place. Examined ten days later the *unpunctured eye* was found to be nearly as bloodless as those of rabbit No. 1, whereas the *punctured eye* showed intense injection of the uveal tract and retina.

In this latter experiment blood was driven with great force into the orbital vessels, as proved by the protrusion of the eyeballs, yet it failed to fill the intraocular vessels until the cornea was punctured. Why so? Evidently its entrance was prevented by high pressure in the chambers, caused no doubt by pressure on the sclera from without. The forcible afflux of blood to the head, chiefly venous blood moving in the wrong direction, would distend the large orbital veins and drive the eyes outwards, raising thereby their internal pressure, before it could fill the internal vessels. When further displacement of the eyeballs became impossible the whole contents of the orbit, both within and without the eye, would stand at a uniform high pressure and the blood would cease to move, until the puncture of the cornea suddenly lowered the chamber pressure and allowed it to rush in.

This method of injecting the intraocular bloodvessels for the microscope, viz., killing by an anaesthetic, compression of the trunk, puncture of the cornea, and immersion in a fixing fluid, gave some interesting preparations. Further trial, using less compression, would probably have given better ones; hence this description of it. I do not know whether others have used it. I did not employ it further because more valuable material came into my possession.

For all my best material I am indebted to Mr. Frederick C. Lowe of Wednesbury. Mr. Lowe is an expert with the microscope and camera, not professionally, but for love of the work. He has exceptional skill in injecting minute blood-vessels, especially the intraocular vessels of animals of several kinds. Happening to hear of my efforts he kindly offered me his help, and he has given it most

amply and generously. As regards injection and photography, the preparations here reproduced are his work. The section cutting was done by myself, with assistance. Some statement of the methods used is probably desirable.

Injecting. The following details are given by Mr. Lowe. The eye is excised, together with muscles, nerve and fat, without dragging, immediately after the animal is killed, and injected as soon as possible. The canula is inserted into the larger of the two arteries found by the side of the nerve; the other is tied. The vessels are washed out with warm normal saline under a pressure of 40 mm. Hg, the eye being under warm water. The reservoir holding the injection mass and the water containing the eye are then gradually heated to about 100° F. The reservoir is connected on the one hand with the canula, air being excluded from the tube, and on the other with a pump, air-chamber, and U-shaped mercurial manometer, and the injection is begun under a pressure of 40 or 50 mm. Hg. The cornea is usually punctured. When the mass flows freely from the cut veins these are closed with clips. The pressure is then raised gradually to 100 mm. Hg. (of late to 80 by preference) and kept at that height for 10 or 15 minutes. When successfully injected the eye feels elastic, not hard, between the thumb and finger (the pressure in the vessels is largely borne by their own walls, not fully transmitted to the fluid in the chambers); if the eye feels hard a vessel has ruptured; the aqueous is clear not clouded, the external vessels are visibly injected. The injection being completed, the eye is cooled with cold water, time being allowed for the injected mass to solidify. Canula and clips are then removed and the eye is placed in 3 per cent. formalin solution.

The injection-fluid, until lately, was usually a suspension of precipitated lead chromate in a gelatin solution; of late, finely ground vermilion similarly suspended and cleared of coarse granules by filtration has given excellent results.

Removal of pigment epithelium. After the eye is opened the ciliary processes are denuded of epithelium by letting a fine jet of water play forcibly upon them. The outer surface of the choroid is treated in like manner and by supplementary brushing with a camel-hair pencil.

Embedding, section-cutting and mounting. I used a non-alcoholic method for three reasons. First, because I was familiar with no other. Second, because I feared the effect of dehydration on the gelatinous casts of the vessels. And third—perhaps the only good one of the three—because alcohol, at the time when I began, was not obtainable, whereas I possessed a little glycerin.

The tissue to be cut is laid in a small china saucer and covered with melted "water jelly"—(gelatin, 1 part by weight; water containing 1 per cent. of carbolic acid, 7 parts). When firmly set, the slab so formed is removed from the saucer and placed in 1 per cent. formalin solution to render it incapable of subsequent melting. Suitable slices are cut from it with scissors or razor and these are sectioned in the usual way on the freezing microtome, in gum. Each section is floated on to a slide under water, drained, and mounted in glycerin jelly—(glycerin, 1 part; water-jelly as described above, 2 parts.) The "water jelly" before being used must contain no formalin, or it will not melt, and no glycerin or it will not freeze.

The illustrations on special paper are reproductions, by the Arthur Cox Illustrating Co., of micro-photographs by Mr. Lowe. Those in the text are from hand drawings made with the Leitz drawing-prism.

The Eye of the Ox

FIG. A shows certain differences between the ox's eye and the human eye:—(a) The axis of the eyeball diverges widely from the median line of the head. With the help of a folding two-foot rule I judged the angle to be about 45°; using a goniometer designed for the purpose Lindsay Johnson² estimated it, probably more correctly, to be 52°. The two eyes, therefore, diverge at an angle of more than 90°. The optic nerve joins the eye in its temporal hemisphere, not in the nasal as in man. The difference evidently lies in the position of the eyeballs rather than in that of the nerves.

In spite of the divergence the ox has a certain power of binocular vision and uses it when he wishes to see his best. Walk quietly across a field where cattle are grazing, and many of them will be content to regard you with a single eye; make an unusual noise or take a lively dog with you, and they will turn so as to watch the intruder with both. This implies that the ox sees well with a peripheral part of the retina and by means of a visual axis differing widely from the geometric axis of the lens. Other evidence to the same effect will appear later.

Because of the divergence the ox sees further round than we do. With his two eyes he commands, I think, at least three quarters of a circle in the horizontal plane. Some animals certainly command

FIG. A.

a still wider field. I tested a sheep on this point. While she lay resting on the grass I approached slowly from behind, trying to remain unseen. But whatever line I took I could always see one or other of her eyes: when I stepped a little to one side to get this eye out of sight, she moved her head a little and I saw the other; when one of her ears hid the effective eye, she lowered that ear, but not the other. She kept an eye on me with very little trouble. Different animals differ much in this respect. Safety seems to explain the difference. Animals that live by hunting others, e.g. lions, wolves, eagles, owls, have little need for backward vision and their eyes are directed chiefly forwards; while those in danger from

beasts or birds of prey can keep a look-out further round (see Lindsay Johnson's table of divergence in mammals). Oxen and sheep in their wild state are among the hunted.

(b) Viewing the eye in the line of its axis one sees that the cornea is oval, the broader end being towards the nose, the narrower towards the temple; also that the pupil is oblong, its long diameter corresponding with that of the cornea. The long diameter of the pupil is about parallel with the lower border of the jaw, and about horizontal when the neck is in line with the back; when the animal is grazing it is directed towards the ground a little in advance of the nose. These adaptations help to extend the field of vision laterally. The ox, unlike the rabbit for example, whose cornea and pupil are round, has no need to keep a look-out upwards.

(c) Viewing the posterior hemisphere from within, we see that the centre of the papilla lies about 10 mm. below the horizontal meridian and about 7 mm. to the outer side of the vertical.

The most conspicuous feature, however, is the tapetum lucidum, a shining area of resplendent peacock blue occupying a large part of the choroidal surface in the upper hemisphere, and extending in the lower down to the level of the papilla and almost to the ora serrata on each side. Its colour is due to "interference" (Hess³), this part of the choroid being lined with a fibrous tissue which throws back certain rays of the spectrum but not the others. Under the microscope thin sections of the tapetal tissue appear highly coloured when lighted in certain directions from above, but colourless and transparent when lighted from below. In its normal condition it strongly reflects certain coloured rays and hides the underlying pigment cells, but it is not opaque in the ordinary sense.

The tapetal area corresponds with the most valuable part of the ox's visual field: the part that pictures the ground and the objects near it, not the sky. The broader temporal portion looks chiefly forwards and downwards, the narrower nasal portion chiefly backwards. It certainly affords aid to vision. How does it act? Helmholtz suggested that by reflecting incident rays back along their paths through the retina it gives additional stimulus to the retinal elements. This accords with the fact that animals active in the dusk have commonly a tapetum lucidum. But the explanation is incomplete, for some other animals have it also. And what of the special colour, which differs much in different species? Does the tapetum so stimulate certain colour-sensations rather than others as to aid the animal in distinguishing objects of those colours from their surroundings, e.g., one kind of herbage from another in the case of the ox, an animal from ground or grass in the case of the carnivora? Or is the colour a by-product without physiological significance?

(d) Looking at the eyeball from behind, one sees the nerve attached to the lower outer quadrant, and near to it the main

trunks of the posterior ciliary arteries passing from the inner side of the nerve to become attached to the outer surface of the sclera, on both sides of the nerve.

FIG. B, drawn from measurements of several eyes, represents the anterior part of the eye incised radially and laid out flat, viewed from behind. It is given to show the eccentricity of the ciliary body. The tips of the processes lie in a circle concentric with the lens, whereas the ora serrata, the posterior boundary of the ciliary body, comes further forward at the nasal side than elsewhere. Its distance from the tips of the processes here is about 5.5 mm., on the temporal side 10 mm., above about 11 mm., and below 8 mm. Between the ora serrata and the corneal margin as seen externally, the want of concentricity is greater still. A needle passed through

FIG. B. Natural size.

the ora serrata from within emerges on the nasal side at about 2 mm. from the limbus, on the temporal at 5 or 6, above at 12, and below at 11 mm. The angle of the anterior chamber does not follow the contour of the cornea; it is nearly circular, for the opaque sclera overhangs it widely above and below, and hardly at all at the sides.

The advance of the retina on the nasal side, aided by the shape of the cornea and pupil, extends the field of vision in the backward-outward direction. A similar advance on the temporal side would be useless, for in the ox, as in man, the field is limited in the inward-forward direction by the nose. At both sides, be it noted, the tapetum reaches forward on the horizontal meridian almost to the limit of the retina, so that the animal may not only see, but see well, as far round as possible.

Orientation of an excised ox eye is easy. Turn the cornea towards yourself with the long diameter horizontal, and with the optic nerve below the horizontal meridian. Now, if the broad end of the cornea is to your right, you have the ox's right eye, if to

your left, his left. After the eye is bisected, the tapetum and the nerve will distinguish the upper hemisphere from the lower, or the temporal from the nasal. In an anterior segment, the lie of the pupil will show the horizontal meridian, and the breadth of the ciliary body will distinguish the temporal side from the nasal.

THE BLOODVESSELS.

The posterior ciliary arteries.—FIG. 1 is from a section about 10 mm. behind the eyeball. It shows the two main arteries that supply the interior of the eye lying to the inner side of the optic nerve. One of these comes from the internal carotid, the other indirectly from the external (Leber). Near to the eye they communicate freely with each other, sometimes uniting for a few millimetres to form a single trunk. Fluid injected into either escapes immediately and copiously through the other unless this latter be tied; if it be tied, there is little or no escape from any vessel until, after about fifteen seconds, a flow from the cut vortex veins begins (Lowe). This proves two things: first, that if there be a difference of pressure in the two trunks, it is neutralized before the blood reaches the eye; and, second, that these two trunks convey little, if any, blood to parts outside the eye.

Near to the eyeball the two arteries separate, one of them passing round below the nerve to the temporal side. They give off many branches here. On reaching the sclera, they traverse its outer surface tortuously for some distance before they disappear; they groove it, are bound firmly to it, and send many branches into it. But what look like single trunks here prove, when cut across, to be groups of vessels contained in wide fibrous tunnels. The largest lie on a level with the nerve on its nasal and temporal sides.

FIG. 2. A thin layer has been sliced away from the back of the sclera in the region of the nerve. Many small vessels are divided just above and below the nerve, a group of larger ones a little higher up; the largest enter the sclera outside the limits of the picture; none pass deeply into it here. The fissure for the retinal vessels begins to appear; these vessels enter the nerve through the sclera, not behind the eyeball as in man.

FIG. 3 is from the same eye. The section is parallel with the last, and deeper in the wall of the eye. At this depth the sclera, which is more than 2 mm. thick here, shows hardly any vessels. The retinal vessels are seen entering the nerve.

FIG. 4, again from the same eye, shows a section almost on a level with the papilla. Above, it passes obliquely out of the sclera into the outer layer of the choroid, and exposes some of the small choroidal arteries.

FIG. 4 A shows the retinal vessels emerging from the papilla—somewhat displaced by the removal of the retina. The papilla is

partly hidden by the overhanging choroid. Above it the tapetal area is seen, below it the non-tapetal.

To see the multitudinous vessels that enter the sclera near to the optic nerve, one must cut perpendicularly to the surface, not tangentially. In a rectangular piece measuring 20 mm. horizontally by 15 mm. vertically and having the optic nerve at its centre, I found nine vessels in the upper cut edge, nine in the temporal, nine in the nasal, and three in the lower, nearly all arteries, and all near to the outer surface.

FIG. 5 shows a group of arteries in the sclera 10 to 15 mm. behind the equator and below the horizontal meridian. They are still near to the outer surface. The sections are parallel with the equator. The narrower strip is the anterior of the two. Small branches pass steeply through the sclera to the choroid.

FIG. 6. These sections are anterior to the foregoing; the broader lies just in front of the equator, the narrower a few millimetres further forward. They show the long posterior ciliary arteries. In the human eye a single such artery on each side runs forward between sclera and choroid on the horizontal meridian, and bifurcates on reaching the ciliary body. In the ox, the chief artery on each side, after sending many branches to the choroid, bifurcates behind the equator while still near to the outer surface of the sclera, and so forms the twin vessels here seen. These, running forward close together, one above the other, and still giving off branches to the choroid, reach the inner surface of the sclera a few millimetres from the ciliary body. They lie not in the horizontal meridian but below it, corresponding in position with the lower edge of the tapetum. They will be seen again in the picture of the ciliary body.

These successive sections show how greatly the thickness of the sclera diminishes towards the front of the eye.

FIG. 7 shows one of the upper *vortex veins* on its passage through the sclera. Care was taken to cut it at right angles with its course and with the surface of the sclera so as to avoid modification of its shape by oblique sectioning. The yellow cores that filled the lumen have dropped out. The upper section shows the vein entering the inner surface of the sclera near to the ora serrata; the lower shows it about to reach the outer surface near to the equator.

The anterior ciliary vessels are very much smaller than those which enter the posterior hemisphere. The two main arteries seen in Fig. 1 have, as a rule (under an injection-pressure of 100 mm. Hg.), an aggregate cross-section of approximately 2 sq. mm. The anterior ciliary arteries and veins together, so far as I could discover them in a circum-corneal zone of sclera 15 mm. wide

(there were about 32 in all) gave an aggregate of less than 0.05 sq. mm. Evidently a very large proportion of the blood that reaches the interior of the eye enters by the posterior vessels.

The larger vessels of the choroid are brought to view by separating the membrane from the sclera and brushing away its outer loose pigmented coat. As in the human eye, the arrangement of the arteries differs widely from that of the veins. The area drained by the upper pair of vortex veins is marked off from that drained by the lower by a horizontal seam or raphé extending right across the membrane about 5 mm. above the centre of the nerve. Innumerable veins arise here and, joined by others as they go, pass upwards and downwards in long sweeping curves to unite ultimately in the vortex veins. The arteries are less conspicuous. On reaching the choroid through the sclera they are already much smaller and much more numerous than are the veins that leave it to pass out through the sclera. They enter chiefly in the neighbourhood of the nerve and horizontal raphé. Their branches lie at first outside the veins, often crossing them at large angles and showing remarkable tortuosity; later they take the same direction as the veins and run between them towards the periphery. In doing so they decrease in diameter while the veins increase. The arrangement has an exceptional result: arterial and venous streams running side by side move in the same direction.

FIGS. 8 to 12 show these vessels in various parts of the choroid under the same enlargement as used for the previous series.

FIG. 8. The nerve-aperture and the horizontal raphé.

FIG. 8a. The plexus surrounding the aperture for the optic nerve. Many arterial twigs are seen overlying the veins and directed towards the nerve.

FIG. 9. An artery cut through where it leaves the sclera, with branches passing in various directions. In two entire choroids with well injected vessels I found no larger artery than this; nearly all were smaller.

FIG. 10. A vortex vein together with most of its choroidal tributaries. The latter, anastomosing freely as they pass forward, coalesce near to the anterior limit of the choroid to form great transverse veins which, with slight interruptions, make a circle round the eye (the circle of Hovius) at the posterior edge of the ciliary muscle and beneath the ora serrata. These transverse veins receive also numerous tributaries from the ciliary body and iris, hidden here by the ciliary muscle. They unite to form the great vortex trunks, giving pictures that remind one of a "weeping" ash tree. The trunks, usually 4 in number but occasionally 5 or even 6, lie obliquely between the vertical and horizontal meridians of the eye, and rather nearer to the former than to the latter, an upper and a lower pair, as in the human eye.

FIG. 11 shows the meeting place, on the vertical meridian, of the areas served by the upper (or lower) pair.

FIG. 12 shows the meeting place, on the horizontal meridian, of an upper with a lower area. Here the twin long posterior ciliary arteries are visible between their emergence from the inner surface of the sclera (see Fig. 6) and their entrance into the ciliary muscle.

The capillaries of the choroid and their stems.—The capillary network lining the choroid differs in character in different places. All the figures in this group have an enlargement of 50 diameters, and each of the squares represents 1 sq. mm. of surface.

FIG. 13 is from the tapetal area at a point near to the posterior pole of the eye. Here the network shows numerous roundish figures, the "stars of Winslow," in which the freely anastomosing tubes tend on the whole towards a central stem, as the spokes of a wheel to the axis. Around the axis the meshes are at their smallest, many of them being minute rounded apertures covering less space than the surrounding tubes; nearer to and at the circumference of the wheel they are elongated, but much less so than in the non-tapetal area.

The wheels join each other without clear lines of demarcation. They have an average diameter of about 0.2 mm., but they vary in size and in some places are hardly definable. Each wheel is joined below not only by a stem at its centre but by others at or near to its periphery. The axial stems are the larger, the peripheral the more numerous. It will be shown immediately that the former are probably venous, the latter arterial.

FIGS. 14, 15 and 16 are from the non-tapetal region below the horizontal dividing line. Here the meshes elongate more and more as the periphery is approached. The wheels are gradually replaced by larger tree-like or feather-like forms with larger and fewer stems. The membrane becomes thinner. Near to the periphery the large veins lie close beneath the capillary layer and are seen through it almost as clearly as from the outer side. FIG. 14 was taken from a spot a few millimetres below the edge of the tapetum and near to the vertical meridian. FIG. 15 from the same preparation, but nearer to the equator. FIG. 16 from the same eye as FIG. 13, but near to the periphery. In the first and last the injection was fuller than in the others.

The difference between the tapetal and non-tapetal areas as regards the capillary network is significant: one can hardly doubt that the smaller meshes correspond with greater retinal activity. Is there any difference of this kind between one part of the tapetal area and another?

FIG. C represents an attempt to answer the question. An exceptionally well injected choroid was skilfully removed in one

piece by Mr. Lowe. It was flattened out by radial incisions and mounted as here shown. The capillary surface, under enlargement of 65 diameters, was examined in many places. At the sites figured 0, 1, 2, etc., the axes of the wheels, so far as distinguishable, were plotted on paper by means of the Leitz prism. A piece of glass, 65 mm. square, laid on each drawing in turn, showed the number of wheels in 1 sq. mm. at each site. Here are the numbers:

Site ...	0	1	2	3	4	5	6	7	8	9	10	12
Wheels	21	23	22	24	23	21	21	17	23	18	11	14

The counts could not be made with great precision for reasons already given, but I think they are accurate enough to show that the distribution of the wheels is fairly uniform over a large part of the tapetal area. Near to its upper curved margin (7, 9, 10, 12)

FIG. C. Natural size.

they certainly lie less closely. Near to the lower straight margin (1, 2, 3, 4, 5) they seem nearly uniform throughout; at the two ends of this strip (4, 5) the capillaries are less well filled than in the middle (1, 2, 3), but the network does not appear to be less close.

So far as this observation goes it shows that the nourishment of the retina by the choroidal capillaries is fairly uniform over a large part of the tapetal area, and supports the supposition (of Lindsay Johnson and others) that animals devoid of a macula lutea have an area of relatively good vision much larger than that afforded by the macula in man. But it does not preclude the idea that certain parts of the tapetal region are somewhat more sensitive than others. The *retinal* capillaries (see later) suggest that a horizontal strip immediately above the lower margin of the tapetum is particularly active.

The *minute stems* that connect the capillary plexus with the underlying vessels were examined in various ways, the special aim being to ascertain their number in a given area and to distinguish the arterial from the venous.

FIGS. 17 and 18 are from thin sections of the choroid perpendicular to its surface in the tapetal region near to the posterior pole. The one cuts the larger vessels transversely; the other runs parallel with them. Between the larger vessels and the capillary layer lies the transparent tapetal tissue and passing upward through it are seen many stems. The length of the part seen in each case is 1 mm.

FIG. 19 is a similar section from the same piece of membrane, but from the non-tapetal region near to the periphery. It cuts some of the larger veins transversely not far from the vein of Hovius, and the small arteries between them (compare Fig. 12).

FIG. D is from a prism-drawing of a thin section taken from the tapetal surface near to the posterior pole; it represents 1 sq. mm. Photography proved inapplicable here because of reflex from the tapetum. The plane of the section just misses the capillaries at the upper part of the picture; elsewhere it lies close beneath them cutting their stems. The lower half of the picture shows 60 stems; a whole square should, therefore, contain about 120. Many such counts were made in different parts of the tapetal area; some in sections like the present, others in pieces of the choroid from which the capillary membrane had been brushed or scraped away so as to expose the stems. Taking 18 of the satisfactory counts, I find an average of 118 stems to the square millimetre, the maximum being 132, the minimum being 104. Their distribution even in small areas is not quite uniform. They often tend to run in lines following, no doubt, the direction of the underlying vessels.

With the object of distinguishing the arterial from the venous, Mr. Lowe kindly, at my request, varied the injections in several ways: (a) Vermilion was substituted for the lead chromate, in the hope that the larger granules might be arrested in the arterial stems, leaving capillaries and venules empty. This partially succeeded. (b) Finely ground vermilion was injected through the artery, lead chromate simultaneously through a vortex vein. Both reached the capillary plexus, but in a capricious and inconclusive fashion. (c) Vermilion was injected through a vortex vein under low pressure. This gave decisive results:—

Fig. E is a prism drawing like the last. The eye was injected with vermilion through a vortex vein (the upper nasal) under a maximum pressure of 40 mm. Hg. The picture shows 1 sq. mm. of the tapetal surface (not a section) near to the posterior pole and in the area served by the injected vein. It shows 28 well injected stems of relatively large diameter, through which the vermilion has passed sparingly into the capillaries in dotted radiating lines—evidently the spokes of the wheels. These stems must be venous and are certainly the axes of the wheels. Two eyes were injected in this way and many counts were made in different parts of the tapetal area. In 9 of the most satisfactory the average number of

stems in 1 sq. mm. was 29, the maximum 33, the minimum 26. This somewhat exceeds the numbers previously found by counting the wheels themselves, but the wheels are less easily defined than their isolated stems. It is, I think, the truer estimate.

In round numbers, then, a square millimetre of the capillary network in the tapetal area is usually served by about 120 stems, of which about 30 are venous, i.e. by about 90 arterial and about 30 venous stems; a ratio of 3 arterioles to 1 venule. In each wheel the venule is at the centre, the arterioles are at or near to the periphery, and the current is centripetal. The arterioles join the plexus in such a way as to feed adjacent wheels, hence while their number in general is to that of the wheels about as 3 to 1, their number around each wheel is many more than 3.

In eyes injected through an artery, the choroidal capillaries are often found to be filled in numerous small patches not corres-

FIG. D. $\times 50$.

Fig. E. $\times 50$.

ponding with the wheels, while the central parts of the wheels are comparatively free. The mass has reached the capillaries through the arterioles and has passed along them a little in various directions, but has failed to reach the venules. The appearance produced by incomplete injection through a vein is different (compare Figs. D. and E.). Note, however, that injection through an artery may fail to reach the choroidal capillaries through the arterioles, and yet do so indirectly by passing through the ciliary capillaries into the choroidal veins, and thence backwards into the venous stems. Leber made note of this. If it be overlooked the findings may be inexplicable.

The vessels of the ciliary body are somewhat more difficult to follow.

FIGS. F. and G. are from the blood-injected eye of an albino rabbit (see p. 338). Thanks to the absence of pigment and the thinness of the membrane in this animal, the general arrangement of the larger vessels in their several layers could be seen at one

view. Fig. F. is from the horizontal meridian and shows the entrance and bifurcation of the long posterior ciliary artery—single in the rabbit. Fig. G. is from an oblique meridian near to a vortex vein. The external surface is towards the observer. At successive depths are seen the major circle (in the iris) sending branches to the processes and iris, the veins that carry blood from these structures to the vein of Hovius, and indistinctly the processes themselves attached anteriorly to the iris. The arrangement in the ox has the same general character.

FIG. 20 shows the whole ciliary circle everted; it is considerably foreshortened in the vertical meridian. The full-length processes number about 96, and between their diverging tails are many

FIG. F. $\times 10$. FIG. G. $\times 10$.

subordinate ridges—from 1 to 5 in an interspace, and in all perhaps 300. Where the major processes thicken out these minor ridges subside or join them.

The processes consist of a vascular membrane coated with epithelium and highly convoluted. The visible size of a process gives no idea of the extent of secreting surface hidden in its interior. By way of rough illustration, a sheet of paper 10 inches square may be easily crushed into the form of a ball 2 inches in diameter. A solid ball of that size has a surface of less than 7 square inches, while the crushed paper has a total surface of 200 and no part of it is cut off from the air outside. The ciliary membrane, unlike the paper, is folded in a definite way. It has an attached base and a greatly extended free border like the mesentery, and cannot be laid out flat. Mr. Lowe compares it aptly with a leaf of "curly cabbage." Besides forming the processes it lines the spaces between them and connects them by transverse folds.

FIGS. 21 to 24 show the membrane injected and denuded of its epithelium. Fig. 21 is from the lowest part of the circle, where the large vessels of the adjacent choroid are not hidden by tapetum; the

0 of the scale tells approximately the position of the ora serrata. Fig. 22 is from the temporal side and includes a little of the tapetal area. Figs. 23 and 24 are from the same preparation as Fig. 21; the picture is cut off above at 6 mm. on the scale.

There is almost no *pars plana*. Within 1 mm. of the ora serrata the membrane begins to rise in vertical planes, reminding one, by the arrangement of the vessels, of espalier fruit trees. These as they pass forward curve and fold, laterally and otherwise, with increasing intricacy, and widen out until the bodies of the processes are formed and nearly touch each other. Here there are many transverse connecting folds. Near the tips of the processes the folds take a more longitudinal direction. Seen under the microscope, and especially in relief under the binocular, these preparations are of great beauty. Photographs, however well taken and reproduced, fail to do them justice.

FIGS. 25 to 30 are from longitudinal sections through the ciliary body. The small-scale picture includes the vein of Hovius on the left and part of the iris on the right; the others show isolated parts under a uniform enlargement of 25 diameters. In FIG. 26 the section splits a process so as to expose some of the vessels that pass from the base into the free portion. It does not show the full depth of the process anteriorly. FIG. 27 shows the full depth. Near to the tip one sees a small part of the capillary network which happens to lie in the plane of the section. FIG. 28 shows a longitudinal fold from the tip of a process, flattened by the cover-glass so that the vessels are brought nearly to one plane.

In FIGS. 29 and 30 the "major circle of the iris" and some of its branches are seen cut transversely. The artery is larger in the former figure because it is seen near to the beginning of its circular course; in the latter it is nearer to its meeting place with the artery from the opposite side, and has given off many branches. FIG. 29 shows the vascular webs cut chiefly edgeways; FIG. 30 catches them more nearly on the flat. In these two pictures the processes look, of course, in opposite directions, as in the two next above them.

In FIG. 30 one sees one of the large veins that carry blood from the iris and ciliary processes to the vein of Hovius, and so to the vortex veins. The direction of these veins is at right angles with that of the artery; where they cross, the artery lies outside the veins, as in the case of the choroidal vessels.

FIGS. 31 to 37 show the ciliary body in transverse section at various points between the tips of the processes and the vein of Hovius; they are all from one series; their position in the circle corresponds with that of a vortex vein. The sections lay as follows:—FIG. 31: Near to the tips, which stand away from the iris and are more or less split into vertical folds. FIG. 32: Just before

the processes become attached to the iris; here the processes show large arteries and veins (compare FIG. 26) but the iris does not. FIG. 33: Through the region of the major circle. The tortuous artery is cut obliquely in two places; the processes are sessile and no longer contain large vessels; these latter are in the iris. FIG. 34: Through the necks of the processes. Beneath each process a vein passes backward through the ciliary muscle. Between this point and the vein of Hovius these veins become fewer and larger by coalescing, and smaller veins from the minor webs appear. FIG. 35: Through the tails of the processes, showing the major and minor webs, and the ciliary muscle. FIG. 36: Near to the vein of Hovius and the ora serrata. Here are large veins from the processes and iris, smaller vessels to and from the minor ridges, and a multitude belonging to the ciliary muscle. FIG. 37: Through large ciliary veins at their junction with the vein of Hovius, near to a vortex vein (*see* FIG. 43). There are no ridges. (In this section and in some others of the series, the membrane is abnormally curved, perhaps through swelling of the gelatin films while they lay in water. The processes stand on the inner surface; the outer surface, if discoverably curved, should appear slightly convex).

FIGS. 38 and 39, like the last, show transverse sections, but from the horizontal meridian where the long twin arteries enter, instead of from the meridian of a vortex vein. In FIG. 38 the arteries have entered the ciliary muscle but have not yet separated to take their circular course. In FIG. 39 they are passing beneath the vein of Hovius (small at this part of the circle) to reach the muscle. There are ridges even over the vein: at this part of the ciliary circle there is no *pars plana*.

FIGS. 40 and 41 show the processes sectioned in planes roughly parallel with the iris. The heads, divided longitudinally, are directed upwards; the tails, showing many lateral folds, downwards. The sections do not reach quite to either end. The second lies deeper than the first and cuts the larger vessels and the transverse webs. It will be noticed that there are more processes in a given space here, than in the previous series: they lie closer at some parts of the circle than at others. The forms here seen in the tails of the processes suggest a longitudinal rib or web throwing off lateral branches, but Mr. Lowe's comparison with the "curly cabbage,"—which is merely a membrane more and more extended and curved towards its free edge—will probably hold good. By embedding such a leaf in plaster of paris and slicing the block, I obtained forms much resembling those in question.

In man the ciliary membrane is probably less highly convoluted than in the ox; in the rabbit it certainly is so, and this, one would expect. The diameter of the ox's eye is at least twice that of the rabbit's eye; its superficies is therefore 4 times greater. If the

processes in both were built to one pattern the secreting surfaces would be roughly as 4 to 1. But this would not meet the requirements. The volume of the intraocular fluid in the two cases varies as the cubes of the diameters, viz. as 8 to 1, and if the function of the processes is the same in both, the secreting surfaces must bear the same proportion. Hence the greater complexity in the ox.

FIG. 42 is from a deeper section in the same region; it passes beneath the processes and opens the tortuous artery that feeds them, the major circle.

FIG. 43, shows a section parallel with the last but in the thinner part of the ciliary body near to the ora serrata. Here one sees several of the large veins from the processes and iris joining the vein of Hovius. The passage of the blood from the latter into the vortex veins and through the sclera has been seen already.

The vessels of the iris, apart from those which pass from the base of the iris into the ciliary body, and the other way about, are comparatively small. They have been seen already in transverse section in FIGS. 31, 32, and others.

FIG. H.

FIG. 44 is from the posterior surface of the iris freed so far as practicable from its pigment epithelium. Capillaries are seen in the pillars and in the sphincter.

The vessels of the retina can only be glanced at here. Their entrance has been seen already (FIG. 4A). Their distribution differs from that in the human eye. The chief artery and vein, close together, superimposed, or even twisted, run straight upward from the papilla giving off branches more or less horizontally on each side. Trunks somewhat smaller run horizontally from the papilla to right and left below the lower margin of the tapetum, sending branches upwards and downwards.

Fig. H, sketched from injected preparations, and from uninjected specimens where blood remained in the larger veins, gives a rough idea of the general arrangement. A fine coloured drawing by Head of the fundus oculi of the Indian ox, is to be found in Lindsay Johnson's book, Plate 12.

FIG. 45 shows the ultimate branches of three retinal arterioles, the three corresponding venules, and their capillaries. Their situation was somewhat above the posterior pole (near to 9, FIGS. C and H). The injection was made with carmine-gelatin, the photograph was taken with transmitted light (for further description see BRITISH JOURNAL OF OPHTHALMOLOGY, 1918, p. 270).

FIG. 46 was taken from an exceptionally successful vermilion-gelatin injection, under surface illumination. It shows the vessels over the lower part of the tapetal area on the nasal side of the papilla (viz., site 3, FIGS. C and H). On the temporal side the appearances were closely similar, and in no other part was so dense a capillary plexus discoverable. This remarkable capillary tract—injected, found, and photographed by Mr. Lowe—has a special interest. It doubtless indicates an area of high activity, and corroborates what Lindsay Johnson says of the Indian ox: "Just above the disc, and extending in a horizontal manner on either side, is a rose-coloured band, nearly free from large vessels. It is probably the seat of acute vision."

FIGS. 45 and 46, be it noted, are not suitable for close comparison, for not only the enlargements, but the injection-methods also, were different in the two cases: carmine-gelatin without corneal puncture in the one, vermilion-gelatin with corneal puncture in the other.

From these various preparations and from many others, numerous measurements and counts of the blood-vessels have been made, for the purpose, as already stated, of learning something of the volume, the velocity, and the lateral pressure of the blood in different parts of the eye. That purpose has not been developed in the present paper, but it is not abandoned.

In conclusion, I desire to express my gratitude to my helpers: to Mr. Lowe whose collaboration is evident on every page; to Prof. Carlier for the opportunity of working in his laboratory; to Mr. Arthur Potts (R. Bailey) who, as a scientific optician, has given me kind and prompt aid in the matter of apparatus on very many occasions; to my one-time assistant, Miss F. Warth, especially for her good work with the drawing-prism; and not least to my wife for indispensable help in the cutting and mounting of sections and in countless other ways. I am indebted to the University for a grant towards the cost of illustrating this and the preceding articles, from the Aubrey Bowen Fund for the Promotion of Ophthalmology.

REFERENCES

1. "Graefe-Saemisch Handbuch," 2nd edition, Vol. II, part 2.
2. Johnson, Lindsay.—"The Mammalian Eye, etc." *Philosophical Transactions of Royal Society*, 1901.
3. Hess, C.—"Vergleichende Physiologie des Gesichtsinnes," Jena, 1912, p. 177.

FIG. 1. X5

FIG. 2. X5

FIG. 3. X5

FIG. 4. X5

FIG. 5. X5

FIG. 6. X5

FIG. 4A. X5

FIG. 7. X5

FIG. 8. X5.

FIG. 8a. X5

FIG. 11. X5

FIG. 9. X5

FIG. 12. X5

FIG. 10. X5

FIG. 13. X50

FIG. 14. X50.

FIG. 15. X50

FIG. 16. X50

FIG. 17. X50

FIG. 18. X50.

FIG. 19. X50

FIG. 20. $\times 1.5$ FIG. 21. $\times 7$ FIG. 22. $\times 7$ FIG. 23. $\times 25$ FIG. 24. $\times 25$

FIG. 25. $\times 7$

FIG. 26. $\times 25$

FIG. 27. $\times 25$

FIG. 28. $\times 25$

FIG. 29. $\times 25$

FIG. 30. $\times 25$

FIG. 31. $\times 15$

FIG. 32. $\times 15$

FIG. 33. $\times 15$

FIG. 34. $\times 15$

FIG. 35. $\times 15$

FIG. 36. $\times 15$

FIG. 37. $\times 15$

FIG. 38. $\times 15$

FIG. 39. $\times 15$

FIG. 40. $\times 15$

FIG. 41. $\times 15$

FIG. 42. $\times 15$

FIG. 43. $\times 15$

FIG. 44. $\times 15$

FIG. 45. X30

FIG. 46. X15