THE DISTRIBUTION OF BLOOD VESSELS IN THE RETINAE OF MAMMALS.

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At a meeting[1] of the Physiological Society on February 14, 1885, I made a preliminary communication respecting the distribution of Blood vessels in Mammalian Retinae. I then demonstrated the complete penetration of the outer reticular layer of the retina of the Goat by blood vessels and believed that no vessels had previously been described as entering this layer.

A more extensive acquaintance with German technical literature has made it obvious to me that blood vessels had been previously seen in this layer of the retina of the Dog by Bruns[2] and that possibly they had been also noticed by Langenbacher in this layer of the retinae of other animals. I cannot obtain the original communication of the latter observer and can but quote an extract[3]:

"Die Lage der Gefässe ist bei allen genannten Thieren so ziemlich dieselbe wie beim Menschen, d.h. die gröberen Gefässe liegen hauptsächlich in der Sehnervenfasernschicht, die feineren Gefässe und die Capillaren dringen bis in die Zwischenkörnerschicht."

He had examined the retinae of the following animals: Man, Ox, Buffalo, Deer, Goat, Sheep, Pig, Dog, Cat, Horse, Mule, Rabbit, Guinea-pig and Rat.

Nevertheless the terms in which the relation of the vessels to the outer part of the retina is usually expressed, are so vague that I made this question the subject of a comparative anatomical study.

Method. With the kind assistance of Mr Sutton and Mr Lang of

[1] *Proc. Phys. Soc.* Feb. 1885; *This Journal.* 1885.

[2] "Vergleichend-anatomische Studien über das Blutgefässsystem der Netzhaut." *Zeitschrift für vergl. Augenh.* 1882. Heft. 2. S. 77.

[3] "Vergleichende anatomische Untersuchungen über die Blutgefässe in der Netzhaut des Auges." *Oesterr. Vierteljahrsschrift für wiss. Veterinärk.* LIII. 2. S. 121, 1880. Extracted in the *Zeitschrift für vergl. Augenh.* 1882. Heft I. s. 65.

the Middlesex Hospital I have obtained the eyes of several men and children and of many wild animals. They have been hardened or fixed in various reagents (carbolic acid, chloral hydrate, picric acid, chromic acid, bichloride of mercury) according to necessity.

From the hardened eyes sections of retina have been prepared either by the celloidin and freezing method or by the cacao butter method. The nuclear stain used has been sometimes logwood and sometimes borax carmine, whilst the diffuse stains have been either fuchsin or eosine. When the sections were prepared I examined in each case a large number of them to find out what relation the uninjected vessels bore to the internuclear layer.

To a certain extent this method is superior to that of injection, since by it vessels are seen undistended and there can be no displacement. The sections were mostly obtained from portions of the retina situated near the middle of the fundus.

It soon became evident that the term "internuclear layer" wanted precise definition. As its name implies it represents the whole space between the outer and inner nuclear layers which is free from nuclei, that is the "Zwischenkörnerschicht" of the Germans. But accepting this definition it at once becomes obvious that the "internuclear layer" of one retina is not at all equivalent to that of another.

For example, the "internuclear layer" of the human and of some monkeys' retinae consists of two portions, an inner, which probably represents what is usually called the "outer molecular layer," and an outer, made up entirely of the terminations of rod and cone fibres and of filaments derived from the Müllerian fibres. In these retinae the outer part is very broad whilst the inner part is very narrow indeed.

The division exists in most retinae of which I have been able to obtain fine specimens, but often the outer part is very narrow and quite rudimentary (for example, in the retina of the Guineapig).

It would therefore be unwise to insist on the adoption of a new terminology with respect to this layer for all mammalian retinae, but it is certainly necessary to state definitely that the internuclear layer of the human retina is not the same thing as the "outer molecular," "outer reticular," or "outer granular layer."

Making this distinction, however, is tantamount to increasing the number of the layers of the retina in description.

In those retinae in which the division was well marked, I have specified the part in which the blood vessels exist, in those in which

the distinction was not easily seen, I have used the collective term "internuclear layer."

The place of union of these two parts is marked (especially in the Guineapig) by the presence of a membranous expansion, possibly the "membrana fenestrata" of Krause[1]; this represents the place of union of the nerve and epithelial layers of the retina.

For the sake of convenience I have named the outer division of the "internuclear layer" the "fibrous layer"; the inner division, the true "outer molecular," "outer reticular" or "outer granular layer", and the intermediate membrane the "dividing membrane."

The following tabular statement of the arrangement of the layers of the retina of Man, of the Chacma Baboon, and of some other mammals, will serve to illustrate my views.

(1) Pigment layer.
(2) Rod and cone layer.
(3) External limiting membrane.
(4) Outer nuclear layer.
(5) Fibrous layer.
(6) Dividing membrane.
(7) Outer reticular, outer molecular, or outer granular layer. } = Internuclear layer.
(8) Inner nuclear layer.
(9) Inner reticular, inner molecular, or inner granular layer.
(10) Ganglion cell layer.
(11) Nerve fibre layer.
(12) Internal limiting membrane.

In a diagrammatic[2] representation of a section of the human retina Schultze did not indicate this division of the internuclear layer, but in another diagrammatic[3] section of the macula lutea (copied by Schwalbe[4]) he represented it.

He referred to the outer part as the "äussere Faserschicht," and to the inner part as the "äussere granulirte Lage." To the dividing membrane I have not seen a reference.

[1] "Die Nerven-Endigung in der Retina." *Archiv für mikro. Anat.* Bd. XII. S. 742.
[2] *Human and Comparative Histology.* Edited by S. Stricker. Vol. III. p. 219.
[3] *Ibid.* p. 285.
[4] *Handbuch der gesammten Augenheilkunde.* Von A. Graefe und T. Saemisch. Bd. I. S. 431.

The Human Retina.

This retina although tolerably vascular does not appear to be so vascular as that of the dog, or as that of some ruminants (notably the Lama). The internuclear layer is clearly divisible into a broad "fibrous layer" and a narrow "outer reticular layer." I have seen a few capillaries in the "outer reticular layer" but I have never seen them in the "fibrous layer."

His[1] published an account of the course taken by the vessels in the retina of a child aged six months. He injected the vessels; and the plate representing a section of the retina shews the most external capillaries running on the outer side of the "inner nuclear layer."

Hesse[2] made the following statement:

"Dass die Arterienästchen zahlreiche Zweige in der Tiefe senden, deren Ramification nicht über das Gebiet der Zwischenkörnerschicht hinausschreitet;" and further

"die menschliche Netzhaut besitzt zwei Capillarnetze, ein inneres, in der Nervenfaserschicht und ein äusseres, das die innere Körnerschicht einnimmt und bis zur Zwischenkörnerschicht reicht."

It seems therefore that Hesse did not see any vessels in the "internuclear layer."

Since the true "outer reticular layer" is very narrow, it is readily conceivable that the presence of an occasional capillary in it should be overlooked, and the fact that it has been customary to regard the "internuclear layer" as the "outer reticular layer," probably explains the origin of the positive statements which have been made to the effect that no vessels enter the "outer reticular layer." They certainly do not penetrate the "fibrous layer."

The Retina of the Chacma Baboon (*Cynocephalus porcarius*).

The description given of the external capillary distribution in the human retina will apply almost exactly to that in this retina.

The vascularity is not very great, the internuclear layer is divided into two parts, and the blood vessels only enter the inner part (outer reticular layer); they always lie close to the "inner nuclear layer."

[1] "Abbildungen über das Gefässsystem der menschlichen Netzhaut und derjenigen des Kaninchens." *Archiv für Anat. u. Phys.* (Anat. Abth.), S. 224. 1880.

[2] "Ueber die Vertheilung der Blutgefässe in der Netzhaut." *Archiv für Anat. u. Phys.* (Anat. Abth.), S. 219. 1880.

But the number of capillaries which so penetrate is even fewer than in the case of the human retina.

The Retina of the Bonnet Monkey (*Macacus sinicus*).

The vessels in this retina are not very numerous, and I have not seen any in the "internuclear layer."

The Retina of the Dog.

This retina appears to be more vascular than any other, not only in point of number but also with regard to the size of the vessels.

Very large capillaries (if indeed they be not small arteries or veins) not only enter the "internuclear layer" but run in it for considerable distances, often passing out so far as to rest close to the "outer nuclear layer."

My observation in this respect agrees with that of Bruns[1] who injected the vessels of the retina of the dog and made the following precise statement; "die lettzen Ausläufer der Gefässe in der äusseren granulirten Schicht, nicht wie bei allen bisher abgehandelten Thierindividuen, an der äusseren Grenze der inneren Körnerschicht flache Bogen bilden und umbiegen, sondern durch die äussere granulirte Schicht bis an den inneren Rand der äusseren Körnerschicht herantreten. Sie liegen somit der Stäbchen- und Zapfenschicht näher, als bei allen Thieren, die ich in dieser Studie bespreche."

The "fibrous layer" is usually comparatively narrow, and I cannot say that in any individual instance I have seen vessels cross the dividing membrane between this and the "outer reticular layer."

The Retina of the Cat.

This retina is not nearly so vascular as that of the dog.

The "internuclear layer" is tolerably broad, and contains a few capillaries which arise from vessels situated in the "inner nuclear layer." They run however close to the "inner nuclear layer" and I have not seen one which passed external to the middle of the "internuclear layer."

It will be seen that in this respect I am in agreement with Bruns whose precise statement has been quoted already. Yet his plate

[1] "Vergleichend-anatomische Studien über das Blutgefässsystem der Netzhaut." *Zeitschrift für vergl. Augenheilk.* 1882. Heft 2, S. 91.

representing a section of a cat's retina certainly seems to shew vessels well in the "internuclear layer."

I am inclined to think that the "internuclear retina" of the cat is divided into two parts. The outer broad part is free from vessels whilst the narrow inner division contains them occasionally.

THE RETINA OF THE LION (*Felis leo*).

In this tolerably vascular retina the "internuclear layer" is fairly broad. The capillaries run for the most part on the outer side of the "inner nuclear layer," but I cannot say that I have ever seen them fairly in the "internuclear layer;" they certainly never pass so far outwards as the middle of that layer, but lie very close to the "inner nuclear layer."

THE RETINA OF THE SEA LION (*Otaria jubata*).

The partial histological destruction of this retina which had taken place before I received it has rendered it difficult to decide whether the internuclear layer contains capillaries or not. The inner nuclear layer contains them.

THE RETINA OF THE BISON (*Bison americanus*).

The narrow "internuclear layer" of this retina is divided into two parts. Vessels enter the "outer reticular layer" and pass close to the "dividing membrane."

THE RETINA OF THE HUANACO (*Lama huanacos*).

In this retina the "internuclear layer" is narrow, and I have been unable to find in it any capillaries. The most external seem to lie in the outer part of the "inner nuclear layer."

THE RETINA OF THE WHITEFACED SHEEP.

The "internuclear layer" of this retina exhibits the division into two parts already referred to.

The "outer reticular layer" is so exceedingly narrow that it is difficult to decide whether the capillaries lie in it or in the outer part

of the "inner nuclear layer." They certainly never enter the "fibrous layer." The whole retina is vascular and the capillaries are very small.

In writing of the supply of vessels to the retina of the domestic sheep Bruns[1] states "Auch hier sind nur die äussere Körner-, die Stäbchen- und Zapfenschicht gefässfrei." His plate certainly again shews the penetration but shews no division of the "internuclear layer" into two parts.

The Retina of the Ox.

The "internuclear layer" of this very vascular retina is so narrow that the task of determining to what degree it is penetrated by capillaries is again far from easy.

For the most part the numerous capillaries confine themselves to the outer side of the "inner nuclear layer" (but not infrequently they enter the "internuclear layer").

In a section of Calves' retina represented by Bruns a capillary is so represented notwithstanding his statement (already referred to).

The Retina of Père David's Deer (*Cervus davidianus*).

The blood vessels in this retina do not appear to be so numerous as in the retinae of some other ruminants. They are very small and the fine capillaries do not appear to penetrate the very narrow "internuclear layer." The most external usually run on the outer side of the "inner nuclear layer."

The "internuclear layer" however is so very narrow that it is exceedingly difficult to make an accurate determination in every instance.

The Retina of the Goat.

The course taken by the vessels in this retina has already been described.

Sections shewing the presence of capillaries in the "outer reticular layer" were shewn at a meeting of the Physiological Society, February, 1885. Since then I have ascertained that the internuclear layer of the retina of the goat is divided into two parts. The outer "fibrous layer" is however very narrow. No vessels cross the dividing membrane.

[1] Already quoted.

THE RETINA OF THE DUYKER-BOK (*Cephalophus mergens*).

The capillaries in this retina are very small indeed and enter but rarely the "internuclear layer."

They lie always on the inner side of that layer.

THE RETINA OF THE EAST AFRICAN BUFFALO (*Bubalus aequinoctialis*).

The narrow "internuclear layer" of this vascular retina is divided into two nearly equal parts, the "fibrous" and the "reticular" layers. Capillaries frequently enter the "reticular layer" but none cross the dividing membrane.

THE RETINA OF THE TUFTED DEER (*Elaphodus Michianus*).

The "internuclear layer" is divided into two parts of which the fibrous is much the broadest.

Capillaries are plentifully supplied to the "inner nuclear layer" and some pass into the "reticular layer."

THE RETINA OF THE LAMA (*Species unknown*).

This retina as regards vascularity rivals that of the dog. The "internuclear layer" is divided into two parts of which the fibrous layer appears to be the broader.

Vessels pass into the "reticular layer" and frequently reach the "dividing membrane."

The retina of the GUINEA-PIG is absolutely, and that of the RABBIT is practically, extravascular.

Conclusion.

It seems then that the "internuclear layer" is divided into the "fibrous" and "reticular" layers in the retinae of the following animals; Man, Chacma Baboon, Dog, East African Buffalo, Tufted Deer, Lama, Whitefaced Sheep, Bison, Goat and possibly the Cat.

The division I failed to observe in the retinae of the Bonnet Monkey, Père David's Deer, Bok, Ox, Huanaco, Sea Lion and Lion.

My failure to observe a division in these retinae may be due to one of two causes—either the fibrous layer was absent or rudimentary, or there had been some histological destruction of the retina before I received it.

In the first group I saw blood vessels in the "outer reticular layer" in the retinae of Man, Chacma Baboon, East African Antelope, Dog, Tufted Deer, Lama, Bison, Goat and Cat. In the case of the White-faced Sheep I could not arrive at a decision. The penetration of the "reticular layer" in the retinae of Man, Chacma Baboon, is not so frequent as in the case of the remaining animals.

In the other group of retinae I saw vessels in the undivided "internuclear layer" in all except three, viz. those of the Sea Lion, Huanaco, and Père David's Deer, and in these cases the retinae had experienced some histological change which rendered very accurate observation difficult.

For the most part the vessels were confined to the inner part of the layer.

I have then in no case seen a vessel in the outer nuclear layer of a mammalian retina, and I have never seen a blood vessel cross the membrane dividing the nerve from the epithelial layers, and therefore so far as my observations go they tend to confirm the oft repeated statement that the epithelial layers of the retina are extravascular.

It seems that the retinae of ruminants are exceedingly vascular. Whilst I cannot make a positive statement as to the relative vascularity of different retinae since I have not made accurate quantitative comparisons, (a difficult task), yet the general impression the examination has left me is, that the retinae of the ruminants are on the whole more vascular than those of the other animals whose eyes I have examined. This statement however does not apply to the retina of the dog.

Finally I desire to acknowledge the kind assistance afforded me during the progress of my work by Mr Marcus Gunn.

LITERATURE REFERRED TO.

(1) *Manual of Human and Comparative Histology.* Edited by S. Stricker. 1873. New Sydenham Society. Vol. III. p. 218 (Schultze).

(2) *Handbuch der gesammten Augenheilkunde.* Von A. Graefe und T. Saemisch. (1874.) Band I. S. 354 (Schwalbe).

(3) W. Krause. "Die Nerven-Endigung in der Retina." *Archiv für mikro. Anat.* Bd. 12, S. 742.

(4) W. His. "Abbildungen über das Gefässsystem der menschlichen Netzhaut und derjenigen des Kaninchens." *Archiv für Anat. und Phys.* (Anat. Abth.), S. 224, 1880.

(5) F. Hesse. "Ueber die Vertheilung der Blutgefässe in der Netzhaut." *Ebenda*, S. 219.

(6) L. Bruns. "Vergleichend-anatomische Studien über das Blutgefässsystem der Netzhaut." *Zeitschrift für vergleichende Augenheilkunde*, 1882. Heft 2, S. 77.

(7) L. Langenbacher. "Vergleichende anatomische Untersuchungen über die Blutgefässe in der Netzhaut des Auges." *Oester. Vierteljahrsschrift für wiss. Veterinark.* LIII. 2, S. 121, 1880. Extracted in *Zeitschrift für vergleich. Augenh.* 1882. Heft 1, S. 65.

(8) J. W. Barrett. "The distribution of Blood vessels in the Retina." *Proc. of the Physiol. Soc. Journal of Physiology*, 1885.