On the structure and function of the rods of the cochlea in man and other mammals / by Urban Pritchard, M.D.

III.—*On the Structure and Function of the Rods of the Cochlea in Man and other Mammals.*

By Urban Pritchard, M.D., F.R.C.S., Demonstrator of Physiology, King's College, London.

(*Read before the* Medical Microscopical Society, *Feb.* 21, 1873.)

Plate XIII.

Before entering upon the description of the rods themselves, it may be well to refer briefly to the mechanism of the ear, and the method by which we are able to hear and distinguish certain sounds.

The ear itself, as is well known, is one of the most complicated organs of the body, consisting of the external, middle, and internal sections: the two former are merely concerned in collecting and conducting sounds or vibrations; while the duty of the internal portion consists in receiving, localizing, and, moreover, clearly distinguishing them. Now, it is simply with this last and most delicate function of the organ that I purpose to deal, my aim being to describe the true construction and use of the cochlea so far as its task of distinguishing the various sounds is concerned.

I may state that, for convenience sake, I shall in the course of my remarks speak of the cochlea with its apex uppermost. This cochlea, it must be borne in mind, consists of a spiral canal, in form and shape very similar to the inside of a snail-shell. From the axis, or modiolus as it is called, of this spiral, there proceeds horizontally a plate of bone, the lamina spiralis, which almost divides this canal into two. From this plate again there extend two membranes to the walls of the canal, thus separating it into three minor canals.

Of these two membranes the upper one or membrane of Reissner (Fig. II.) arises just behind the teeth of the limbus (as the peripheral end of the bony lamina is called), and passes upwards and outwards to the upper part of the ligament of the cochlea; it is exceedingly delicate, and is composed of a single layer of flattened nucleated cells, closely adhering to each other, and which are situated on a very thin membrane.

EXPLANATION OF PLATE XIII.

Fig. I.—The upper extremities of the rods (dog), showing the mode of articulation and processes. Drawn by camera, × 500 diam.; *i*, inner rod; *o*, outer rod.

„ II.—A *diagramatic* drawing of a vertical section of the central canal of the cochlea, × about 150 diam. 1. Scala vestibuli. 2. Central canal of cochlea. 3. Scala tympani. A, Membrane of Reissner; B, Membrana tectoria; C, Bony lamina spiralis; D, Membrana basilaris; E, Ligament of cochlea; F, Nerve plexus; G, Epithelium; H, Membrana reticularis; L, various cells; *i*, inner rod; *o*, outer rod.

„ III.—Three pairs of rods carefully drawn from three sections of the cochleæ of the same animal (cat), showing the mode of graduation—1, from near the apex of cochlea; 2, from about the middle; 3, from near the base, × about 250 diam.; *i*, inner rod; *o*, outer rod.

The other, the lamina spiralis membranacea, proceeds directly outwards from the limbus to the ligament of the cochlea.

This membranous lamina is composed of two horizontal membranes, having between them certain delicate structures. The upper of these (the membrane tectoria) arises from the limbus just external to the membrane of Reissner, and passes directly outwards, covering and overlapping the end of the limbus, but not actually reaching the ligament of the cochlea (Fig. II.). It may be well to state, by the way, that on this point I differ from most of the previous writers, with the exception of Böttcher. The portion which covers the limbus is moderately thin, but the outer portion which overlaps it is exceedingly thick, and the whole is marked with radiating wavy lines.

The lower, or membrana basilaris, arises from the lower lip of the limbus, while its other end is firmly attached to a well-marked ridge on the ligament of the cochlea.

Between the membrana tectoria above, and the membrana basilaris below, are situated the so-called rods of Corti.

The Rods of the Cochlea.

These interesting little bodies were first discovered and described by the Marquis of Corti, whose name they now bear, and although since then many observers have studied and written on the subject, yet scarcely two are agreed as to their exact form, while many of the later authors have gone so far as to state that their shape is of a most varied character. The greatest difference of opinion exists as to the shape of the rods at their articulation. Deiters described them very minutely in his first paper, but in a second communication he completely altered his description of them.

The following is a free translation of an extract from Deiters' first paper in Siebold and Kölliker's 'Zeitzchrift von Wissenschaft Zoologie,' vol. 10.

"The outer rods do not directly join the inner, but are connected by a curious body, which partly belongs to the true rods of Corti and partly to the lamina reticularis, and which we will call the middle union joint. These middle joints vary much in form, owing to their easy compressibility, and have not on that account been as yet properly distinguished." "This (middle joint) will best be likened to a boat which terminates at one end in a pointed keel, and at the other in a straight back or plate."

"In the natural position this back plate is turned upwards and lies parallel to the membrana basilaris; the keel, on the contrary, looks downwards and somewhat forwards. . . . . The back plate is nearly rectangular in form, but only the anterior corners are perfect, the posterior being rounded, and perhaps only appear angular on account of the plates lying side by side."

In his later work on the subject he figures these rods very differently, and much more accurately.

Kölliker, Henle, and others appear to agree with Deiters' later view of the form of the rods, and most of our text-books have copied their drawings.

Recent writers, such as Drs. A. Böttcher, Waldeyer, Göttstein, and Nuel, give varying drawings, some of which are nearer the true form of the rods than that of Deiters, while others exhibit the rods in all kinds of extraordinary shapes.

I will proceed at once to detail the results of my own observations.

In a general view of the rods from above (that is to say, looking at the lamina spiralis lying flat) they appear similar to two rows of pianoforte hammers, rather than like the keys of that instrument, to which they have been likened, the heads of the rods lying close together.

In a lateral view, these two rows of rods are seen sloping towards each other like the rafters of a gabled roof, and it is by reason of the difficulty in obtaining these side views (vertical sections) that such very different ideas exist as to the question of shape.

The rods, as before mentioned, lie between the membrana basilaris and membrana tectoria, and pass directly outwards from the lower lip of the limbus; they are both firmly attached by their lower extremities to the membrana basilaris, their upper extremities being covered by a peculiar membrane (membrana reticularis), but they are not in any way connected with the membrana tectoria. On every side they are surrounded and supported by cells of a more or less delicate structure. The rods are best described like a long bone, as consisting of a shaft, and two enlarged extremities, but the two rows differ considerably in form. The inner rods (those nearer to the bony lamina) are attached by their lower extremities to the membrana basilaris at its junction with the lower lip of the limbus and just external to the spot where the nerve filaments emerge (the habenula perforata). They are directed outwards and upwards, with a slight undulation to meet the outer rods.

The lower extremity is enlarged and rounded, gradually tapering to the shaft. The shaft is cylindrical, although Deiters, Claudius, and nearly all other observers state that they are flattened; but by referring to preparations in which the inner rods are cut through their shafts, the cut ends will be seen to be quite circular.

Curiously enough, although these very investigators say the shaft is flattened from above downwards, they give a thick lateral view of the same. The upper extremity is peculiar in form, and as I differ from all observers on this point, it requires special attention.

Its superior surface is rectangular, but longer than it is broad, as is well seen when looking from above, in flat preparations. Externally it is prolonged into a process which overlaps the superior extremity of the outer rod, and terminates somewhat abruptly. The form of this process will be better understood by looking at Fig. I. Below it is continuous with the shaft; the lateral surfaces are somewhat quadrilateral in form, with the anterior and posterior edges concave. These surfaces are divided obliquely by a curved ridge; the upper and inner is smaller, raised and marked by curved lines—the external and lower division is smooth and more transparent. The inner surface is concave from above downwards, and is continuous with the lateral surfaces.

The external surface is deeply concave, and receives the head of the outer rod very much in the same manner as the glenoid cavity receives the head of the humerus. The upper lip of this concavity is continuous with the process mentioned above, the lower one is rounded, and forms a sort of tubercle.

The outer rods are attached to about the middle of the membrana basilaris by a broad base, which is very similar to that of the inner rods, but somewhat larger, and this also gradually tapers towards the shaft. The shaft is cylindrical, and equal in diameter to that of the inner row, as may be proved by carefully measuring the two as seen in most of my preparations. The upper extremity of these outer rods is also peculiar, but very different to that of the inner. The superior surface is quadrilateral, but both broader and longer than that of the corresponding extremity of the first row. Below it is of course continuous with the shaft.

The inner surface is very convex, forming a head which articulates with the corresponding concavity of the inner rod. The outer surface is slightly concave, and from the upper part a long slender process extends outwards. This process lies at first under that of the inner rod, but is prolonged much farther outwards; it is rather more slender in form, and has a handle-like enlargement at the extremity: the whole will be better understood by referring to Fig. I. The lateral surfaces are apparently smooth, but marked by fine radiating lines.

The articulation of the two rows is not movable; there are no ligaments, unless the membrana reticularis, which is finely adherent to the upper surfaces, may be regarded as such, but the articulating surfaces may be seen to be glued together in some peculiar way.

I now come to one of the most important features with regard to these interesting little rods, namely, their relative length. Most authors state that there is very little difference in the length of the two rods; this is quite a mistake, as I am about to prove, for not only do the two sets of rods differ in this respect, but the length of each varies according to its position in the cochlea. Thus, at the

base of the cochlea, the outer rods are as nearly as possible equal in length to the inner, but as we proceed upwards, both rods increase in length with great regularity, although not in the same ratio. The outer increases with much greater rapidity, so that near the apex they are twice the length of the inner. This fact is clearly demonstrated by referring to one of my preparations, in which the various measurements were found to be as follows; beginning at the lowest section of the lamina and proceeding upwards in regular succession:—

1st Section { Inner rod measures $\frac{21}{10000}$ of an inch.
Outer rod „ as nearly as possible the same.

2nd Section { Inner rod measures $\frac{23}{10000}$ of an inch.
Outer rod „ $\frac{35}{10000}$ „

3rd Section { Unfortunately this is not sufficiently perfect to admit of measurement.

4th Section { Inner rod measures $\frac{35}{10000}$ of an inch.
Outer rod „ $\frac{45}{10000}$ „

The 5th and 6th are not sufficiently perfect to allow of measurement, although in the latter the rods may be seen to have increased in about the same ratio. Further confirmation of this statement may be obtained by comparing the rods shown in any vertical sections of the lamina.

Fig. III. represents three pairs of rods carefully drawn from three sections of the cochleæ of the same animal (cat). The uppermost taken from near the apex of the cochlea, the next from about the middle, and the lowest from near the base.

It was generally supposed *a priori* that these rods were graduated so as to distinguish the most minute variation of tone, but no one, until now, has been able to demonstrate this.

The rods, therefore, vary in length from about $\frac{1}{500}$ to $\frac{1}{200}$ of an inch. Their other measurements are as follow:—

	Inch.
Diameter of base of inner rod, about	·0006
„ „ outer rod „	·00075.
„ „ shaft inner „	·00015.
„ „ „ outer „	·00015.
Anterio-posterior measurement of upper extremity of inner rod, about	·0005.
Anterio-posterior measurement of upper extremity of outer rod, about	·0006.
Lateral posterior measurement of upper extremity of inner rod, about	·0002.
Lateral posterior measurement of upper extremity of outer rod, about	·0003.
Length of process of upper extremity of inner rod, about	·0006.
„ „ „ outer „	·00075.

The number of rods in each row is not the same, there being three of inner for every two of the outer, and, according to a rough calculation that I have made, there are about 5200 inner rods, and 3500 outer in the whole cochlea.

Deiters stated that the rods of the outer row were smaller and more numerous than those of the inner, while Claudius positively stated the reverse. Now, Deiters was undoubtedly wrong in both these statements, and Claudius not altogether correct, for although the latter was right about the inner rods being the more numerous, yet he was incorrect in stating that the inner were the smaller, there being, indeed, no difference in the diameter of the shafts, but only in the width of the upper extremities.

The rods of Corti appeared to be composed of a homogeneous substance resembling the matrix of delicate cartilage.

Numerous longitudinal and curved lines are observable, especially at the enlarged extremities, and they may readily be split up into fibres, otherwise they appear quite transparent and contain no nuclei. They evidently possess great elasticity, and are calculated in every way to receive the finest vibrations.

They are to be stained by all the various colouring fluids, as carmine, and aniline blue, magenta, &c., but they are not so deeply coloured as the nuclei of cells, &c.

Most authors, with the exception of Deiters, describe nuclei situated in various parts of these rods, principally in the lower extremities, but although at first sight, and especially when seen from above, this does appear to be the case, yet on closer observation these so-called nuclei of the rods are found to be nothing more than the nuclei of cells surrounding the bases of the rods. In my opinion there is no ground whatever for the belief expressed by some modern authors, that they are composed of fine fibres *continuous* with those of membrana basilaris, and for this reason : the bases of the rods may be easily separated from the membrana basilaris, and in this case are found to be quite rounded, and in no way jagged or uneven.

The Arrangement of the Nerves in connection with the Rods of Corti.

The cochlear nerve fibres from the portio mollis pass up the modiolus and turn off at the lamina spiralis. Just at this junction we find in the bone itself a ganglion ; the cells of this are fusiform, bipolar, with distinct nuclei. From this ganglion fibres proceed outwards, these form a close plexus, and give rise to the broad dark band seen in all transverse sections of the lamina spiralis.

Immediately before the end of the lower lip of the limbus, the nerve filaments pierce its upper surface, by a number of small foramina (habenula perforata), and appear close to the base of the inner row of rods. Concerning the termination of these nerve filaments little is really known. I have traced them on to the inner rods themselves, and to the tiny cells lying on their bases, as also to certain delicate cells between the rods, but I have good reason for believing that some of them terminate in the cells of Corti and

Deiters, on the outer rods themselves, and in the corresponding little cells on their bases.

Filaments also pass directly upwards to the inner side of the first row of rods, and on these filaments little modular enlargements may be seen.

The Function of the Rods.

Corti and most of the subsequent authors considered this system of rods to be the essential portion of the cochlea. They supposed the rods received the vibrations conducted to them, and being set in motion, so affected the nerves as to cause the brain to appreciate the various sounds.

Later German writers have, however, attributed the appreciation of the various vibrations to certain delicate cells (the cells of Corti and Deiters) which are attached to the under-surface of the membrana reticularis. From this circumstance alone, it appears evident that these investigators had not suspected, much less discovered, the fact that the rods are most exquisitely graduated, for otherwise they could surely never have doubted that so beautiful and suitable an apparatus could have any other ostensible purpose than that of appreciating the various sounds. If the rods had been found to be longer in the lower and larger portion of the canal, and shorter in the upper and smaller portion, the matter might naturally enough have been regarded as one of little importance ; but it must be remembered that quite the reverse is the case, for the rods actually increase in length as the canal becomes narrower. This uniform graduation of the rods presents to my mind so plausible and reasonable a key to their use, that there can scarcely be a doubt as to their real function. I consider, indeed, that the cochlea as a whole represents a finely-constructed musical instrument, similar in nature to a harp or musical-box, the strings of the one and the teeth of the other being represented by the rods of Corti. The spiral bony lamina is simply nothing more nor less than a natural sounding board, in connection with the end of which are arranged the rods, attached to a strong membrane (membrana basilaris) by their feet, and supported throughout by delicate cells, the whole being protected above by the thick membrana tectoria, and bathed in a special fluid secreted by the epithelial cell. This fluid, it should be mentioned (endolymph), is cut off from the other fluid (epilymph) in the general canal by the delicate membrane of Reissner. Around the rods are placed the various nerve cells and nerve fibres ; of the former, I believe the cells of Corti and Deiters to be the most important, and these being connected through the medium of the membrana reticularis to the processes (which act as levers) are, of course, suitably placed to perceive the slightest vibration of the rods.

From these cells the impressions are conveyed by the nerve fibres

to the brain itself. Thus, I think, we are in a position to trace very completely the course of sounds or vibrations from a musical instrument, or any other source, to the brain, through the medium of the ear. First, the vibrations are caught and collected by the auricle, and transmitted through the external meatus to the drum of the ear, next across the middle ear (the tympanic) cavity, principally by means of the chain of little bones, to the internal ear. Here the sound is appreciated merely as a sound by the vestibular portion of the labyrinth; the direction of the sound is probably discovered by means of the semicircular canals, but to distinguish the note of the sound it must pass on to the cochlea. The vibration then passes through the fluid of the cochlea, and probably strikes the lamina spiralis, which, acting as a sounding board, intensifies and transmits the vibration to the system of rods. There is, doubtless, a rod not only for each tone, or semitone, but even for much more minute subdivisions of the same, so that every sound causes its own particular rod to vibrate. Thus each string sounded on the primary musical instrument induces a vibration in the corresponding rod of the secondary musical instrument (the cochlea). And this rod vibrating so affects the nerve cells in connection with it as to cause them to send a nerve current through the nerve fibres to the brain, which current is no doubt modified or affected by passing through the ganglion cells, situated in the bony lamina near its junction with the modiolus, as before mentioned.

London: Printed by William Clowes & Sons, Stamford Street and Charing Cross.