ON THE NATURE OF THE TECTORIAL MEMBRANE AND
ITS PROBABLE ROLE IN THE ANATOMY
OF HEARING.

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WITH TWELVE FIGURES.

This investigation has been undertaken with the hope of contributing something to the knowledge of the shape, character and intimate structure of the mammalian tectorial membrane. Of all the organs of special sense, the ear seems to be the most complex and its functional action least understood. As voluminous as is the literature upon it, investigators, as yet, by no means wholly agree even as to the detailed anatomy of the inner division of the auditory apparatus. In running over the papers published, one is struck by the fact that they may be quite definitely separated into two classes: anatomical investigations, and physico-physiological treatises, the latter being, in most cases, purely theoretical. Quite often does it appear that the investigator in the latter class maintains that his conclusions are correct on the basis of his correct application of physics and mathematics to structures of unproven existence.

Of the four mechanisms deemed essential in the auditory apparatus, all the recent papers practically agree as to the identity and action of the transforming and regulation mechanism and the conducting mechanism, and all agree that the hair cells of the organ of Corti comprise the stimulative mechanism; but they disagree as to what comprises the vibratory or resonance mechanism. Most of the older papers attribute the faculty of selective or sympathetic vibration, in accord with the waves imparted to the endolymph in the cochlea, to the basilar membrane. Of the four more important papers of recent date, two still assume that the basilar membrane is adapted for and serves as the vibratory structure, while the other two advance the idea, but occa-

sionally held previously, that the tectorial membrane is the structure acted upon by the transferred sound waves. Either view admits that the hair cells are stimulated by impact or contact with the under surface of the tectorial membrane. The very evident disagreement of these papers in their descriptions and assumptions as to the character, form and intimate structure of the tectorial membrane, and the fact that none of the descriptions of the membrane seemed to apply correctly to some preparations of the cochlea in the possession of the author, suggested the undertaking of the study of the nature of that membrane.

MATERIALS AND METHODS.

The material used for this study has been almost wholly obtained from the pig, and all the illustrations given are made from the preparations of cochleæ of this animal. Preparations from other mammals, including man, being obtainable with less ease and abundance, have only been used for occasional comparison with the preparations from the pig.

Pig foetuses of about term, that is, from 26 to 30 centimeters, and a litter of four pigs of about two weeks after birth were used. In all cases, the heads were severed, the vault of the cranium and the encephalon removed and the cochleæ then broken out from the inside and made use of as soon as possible after obtaining the material. The entire inner ear or bony labyrinth of the pig may be shelled out from its lodgment in the temporal bone from the fact that osseous fusion with this bone is of late occurrence. Kolmer, '07, mentions that even in the adult hog the cochlea is not so firmly fused in the petrous part of the temporal bone as it is in other mammals.

All the published illustrations and all the ordinary laboratory preparations of cochleæ agree in indicating one fact, namely, that the tectorial membrane is invariably and badly shrunken and distorted by the action of the usual reagents used in fixing, dehydrating, etc. Since the chief deficiency of the papers describing the membrane appears to be failure to determine and study its normal characters, it was deemed especially necessary for the present study to obtain at least portions of it in the fresh and natural condition. Attempts toward this end were first made with frozen sections. The fresh cochleæ were oriented and frozen on the Bardeen Freezing Microtome and sections clipped into petri-dishes, some containing normal salt solution alone, others 0.1 per cent methylene

blue in normal salt. Though a few fairly satisfactory bits of the membrane were obtained from the methylene blue solution, the method had to be early discarded as being too coarse. The action of the section chisel in crashing through the bony labyrinth lacerated sorely the delicate structures within, the very action of the freezing appeared to result in distortion and dissociation, and positive orientation of the bits of membrane obtained was impossible.

Lightly crushing of the cochlea followed by gently teasing away the parts under fluid was next resorted to. A cochlea was held upon a solid surface and gently tapped around with a light hammer till the bony wall was sufficiently cracked without rupturing the wall of the membranous labyrinth and the whole placed in a petri-dish of amniotic liquor obtained from the sacs of younger fetuses. Under the dissecting microscope the bits of the crushed bone were then carefully removed with fine pointed forceps, and, with the same forceps and with teasing needles, the outer wall of the scala vestibuli gently torn away from as nearly as possible the entire length of the cochlea. Even with the greatest care, this tearing usually ruptures the vestibular (Reissner's) membrane and thus seriously disturbs the structures below it. With practice, portions of the vestibular membrane could be removed separately and the tectorial membrane identified.

The tectorial membrane floats free from its attachment upon the labium vestibulare of the spiral limbus during the disturbance necessary for the removal of the structures and the consequent agitation of the fluid in which it is immersed, but, because of the fact of its being so very delicate and flexible and so extremely subject to surface tension, only short pieces could be obtained (3 to 5 millimeters in length) undistorted and free from adhering particles of bone and other debris. It was found that these pieces had to be isolated and handled by producing currents in the fluid to waft them to desired positions, for upon touching them they would adhere to the point of the teasing needle so closely that freeing them meant distortion or destruction. These pieces were stranded upon the end of a clean slide, to which they were found to adhere less than to the ordinary section lifter, and some were mounted directly in glycerine and in glycerine jelly. Others were washed from the slide into a 0.1 per cent solution of methylene blue in normal salt and let it remain in this from 30 minutes to 2 hours. With the dish of stain over a white surface, these were again stranded upon the slide, rinsed as quickly as possible in salt solution to remove the surplus stain, and

transferred for 5 to 10 minutes to a saturated aqueous solution of ammonium picrate. From this they were mounted in equal parts of pure glycerine and ammonium picrate solution. While the methylene blue brought out the structure of the membrane quite successfully at times, it was found, by comparing with those pieces mounted direct in glycerine, that the ammonium picrate produced in places a certain amount of shrinkage and distortion. Dehydration of these pieces, however gradually and carefully undertaken, was found impossible from the fact that in the higher grades of alcohol they invariably shrunk and crumpled almost beyond recognition. In this way, especially from the unstained pieces, a fair idea was obtained of the normal contour and appearance under the compound microscope, and measurements of breadth could be made.

Owing to lack of sufficient amniotic liquor at times when material was obtained, it was found that teasing under normal salt solution gave apparently as good results, and most of the best bits of fresh tectorial membrane were obtained with its use.

In no case, however careful the procedure, could a whole or even a half of the entire length of a tectorial membrane be obtained from a fresh cochlea. This was due to some extent to the violent disturbance necessary with the crushing and removal of the bone, but largely was because of the extreme flexibility and delicacy and the remarkable adhesiveness of the fresh membrane. Of the pieces obtained with portions undistorted, many would be covered with particles of debris by the time they could be mounted. Furthermore, extreme difficulty was met in orienting these pieces with certainty as to their upper and under surfaces. Others who have attempted examination of the membrane in the fresh condition seem to have encountered similar difficulties. The descriptions of Retzius, '84, who worked in aqueous humor, of Kishi, '07, who used salt solution, and of others to be referred to, show that they obtained but small pieces of the membrane, and that these were unfortunately distorted.

Therefore, the hope of obtaining an entire membrane in the fresh and normal condition had to be abandoned, and experiments were begun for a fixing fluid whose action would result in the least possible distortion of this evidently peculiar structure. This fluid should preferably be a decalcifying fluid as well. It was already apparent that the fluid could not contain alcohol unless accompanied by some ingredient which would counteract its shrinkage effect. Van Gehuchten's (Carnoy's)

fluid was found unsuitable, though, in addition to its alcohol and chloroform, it contains acetic acid. Perenyi's fluid was found impossible, for, while it fixes with little or no shrinkage, and decalcifies well, it has a softening and macerating effect unless followed by washing in alcohol, which latter produces violent shrinkage. Depuis, '94, teased after fixing with Müller's fluid and with chromic acid, both of which decalcify and neither of which causes shrinkage, but he does not seem to have obtained whole or even long pieces of the tectorial membrane. Both of these reagents were found to act so slowly that they were deemed undesirable. Gilson's fluid fixes and decalcifies more rapidly and was found to give much better results than any of the above.

The best results were obtained with Zenker's fluid, which contains the bichromate of potassium, the bichloride of mercury and acetic acid, all of which have a decalcifying action and none of which, combined, seemed to cause shrinkage or distortion of the tectorial membrane. Furthermore, as is well known, a prolonged application of this fluid is less injurious to tissues than are most of the fixing fluids, and cochleæ immersed in it very seldom show the bubbles of gas within the membranous labyrinth, always produced by the more rapid decalcifying agents, and which disturb the arrangement of the structures within. It was found that 48 hours in this fluid resulted in good fixation and sufficient decalcification for the purpose in mind. The entire apex and the outer, thin bony wall of the entire coil were softened, while the thicker base and basal portion of the modiolus were still hard. This undecalcified base and core were found of considerable advantage in holding the specimen firmly during the careful process of teasing.

Removed from the fluid, the cochleæ were washed an hour or more in water and teased under the dissecting microscope in a petri-dish containing enough water to well cover the specimen. Holding the specimen down firmly by the semi-circular canals and vestibular portion, it was found that, with practice and the exercise of care, the outer portion of the decalcified bony wall of the coil could be stripped off in pieces, leaving the membranous labyrinth intact and not even crumpled. The next task was to remove the outer membranous wall of the scala vestibuli without injury to the structures below it. The vestibular (Reissner's) membrane was found to be fixed stiff in itself, and, being very loosely attached along its edges, it could be removed, board-like, and taken out of the way; but in doing this the tectorial membrane, easily identified below it, was necessarily disturbed and sometimes injured. Only after the

vestibular wall and membrane had been carefully removed was it found advisable to touch the tectorial membrane. This, in the meantime, could be seen, parts waving upward and downward with the agitations in the water about it, parts floating entirely free, and, at times, parts more firmly held in place. These more stationary portions were afterward found to be small areas adhering to the organ of Corti due to the coagulative action of the fixing fluid, probably upon the albumens and mucoids in the intervening endolymph.

The action of the fixing fluid results in a decrease to some extent of that remarkable adhesiveness displayed by the fresh tectorial membrane and also renders it somewhat less flexible, but, even after fixation it is so very sensitive to touch with the needles and to currents in the fluid about it that Reissner's and the basilar membrane appear as boards compared with a strip of thin silk. Fortunately, in the fixed condition, it comes away quite freely from its attachment upon the labium vestibulare ("Huschke's teeth") of the limbus spiralis. When ready to remove the membrane the water in the dish was drawn off and replaced with clean to avoid the debris resulting from the teasing. Agitations of the water and occasionally lifting it lightly with the needle where it appeared most firmly attached were found sufficient to detach it. It was best removed from the cochlea to the floor of the dish by the gentle use of a small pipette, washing it from around the coil and over the torn edges of the cochlear wall, occasionally guiding it with a needle. This removal proved the most trying part of the whole process in attempts to obtain the membrane in its entirety. It must not be allowed to adhere to structures over which it passes, it must not be straightened too much from its natural coil, and, above all, it must not be allowed to double upon itself lest it cohere and the entire region so doing be spoiled.

Orientation of the entire membrane, or of large pieces, was not found difficult, from the fact that one becomes familiar with its differences of width while working with it, and, it being in the form of a coil, it does not turn over readily or may be easily seen when doing so.

When washed out into the dish, the tectorial membrane remains for a time suspended in the water, and one has to watch it and quietly wait for it to settle to the bottom. In settling, it will return, to a certain extent, to its original coiled form.

Membranes thus obtained were stranded upon clean slides and some were mounted, unstained, in glycerine and in glycerine jelly, while

others were gently washed from the slide with and into the stain chosen. After trying several stains, including hæmatoxylin and methylene blue upon the fixed specimens, the best results were obtained with 0.1 per cent aqueous fuchsin, applied from 30 to 60 minutes. While this stains the interfibrillar matrix of the membrane, it stains the fibers more deeply, and it is both permanent and desirably transparent. From the stain solution, the specimens were carefully rinsed in water and mounted in glycerine or glycerine jelly, usually with the under surface upward. Some of the membranes removed entire were broken in handling during the staining; others were broken by the cover glass in mounting, but at these stages the pieces could be oriented with ease, and studies and measurements of them could be made with practical certainty as to locality. In all the author was able to obtain nine tectorial membranes deemed sufficiently intact and oriented for such measurements as are here given.

The study of the teased specimens was supplemented by the use of sections, some in celloidin and some in paraffin. Some cut vertical to the apex of the cochlea, some tangential and some horizontal. Certain of them were stained with the usual hæmatoxylin-Van Gieson stain; others, for microchemical studies, after being appropriately fixed and embedded, were stained, some with Meyer's muchæmatin, others with Mallory's stain for white fibrous tissue.

To study a point which arose concerning the development and later attachment of the tectorial membrane, sections were made of the cochleæ of pigs varying gradually from 3 centimeters to 18 centimeters in length. These were fixed, some in Zenker's and some in Gilson's fluid, and all were stained by the hæmatoxylin-Van Gieson method.

THE PHYSICAL CHARACTERS OF THE TECTORIAL MEMBRANE.

The investigation of the mammalian cochlea may be said to have begun in 1847 with the researches of Todd and Bowman, but Corti's "*Recherches sur l'organe de l'ouï des mammifères*," appearing in 1851, really formed the starting point of the long series of observations which have appeared about equally distributed through the years since that time. It was in this monograph that Corti not only described for the first time the organ which now bears his name, but also the structure which spans the spiral sulcus and extends above his organ. This superstructure was shortly afterwards again described by Claudius and

Henle, the former of whom discovered it independently and gave it the name, *membrana tectoria*. Embryological investigations of the structures found in the cochlea began almost simultaneously with the purely anatomical. As early as 1854 Reissner described in embryos the separate existence of the *ductus cochlearis*, discovering its limiting spiral lamella, afterwards called Reissner's membrane by Kölliker and *membrana vestibularis* by Henle. However, it was Kölliker who, in 1861, first described the formation of the ductus cochlearis from the ectodermal tube and suggested the process by which Corti's organ is elaborated and also the normal position and morphological significance of the tectorial membrane.

None of these earlier papers and but few of those following indicate satisfactory or complete observations as to either the consistency, bulk, extent, shape or actual structure of the tectorial membrane. Most of them saw in their preparations little more than an amorphous mass of very varying shape and very varying relation to the cells of the organ of Corti. Henle, in volume 2 of his *Handbuch* (1866), believed the membrane to be very delicate, yet firm and resistant, and of an especial elasticity; Böttcher, '69, also concluded that it possesses a high degree of elasticity; Nuel, '75, cited by Retzius, denied elasticity, but claimed for it a soft gelatinous nature; Gottstein, '72, considered it strongly elastic, and Lavdowsky, '77, considered it a soft, elastic mass, fragile and distensible and in large part homogeneous. Retzius, '84, examined it in aqueous humor and pronounced it transparent, soft, gelatinous, tolerably elastic, capable of some stretching, but that it would split under increased stress in the direction of evident fine fibers present in it, and found it more firm after the action of fixing fluids; Dupuis, '94, considered it not of a mucous consistency, but decidedly elastic; Van Ebner, '02, describes it as a fragile, easily distorted, fibrous structure. Kishi, '07, who examined it in salt solution as well as in the fixed condition, found it to possess a marked elastic character and to shrink when subjected to the ordinary procedures; while Shambaugh, '07, in a theoretical paper, considered it a lamellar structure of the same specific gravity as the endolymph in which it lies.

It will be noted that a majority of the authors cited above agree on one point, namely, that the tectorial membrane possesses elasticity. In my trials to obtain intact specimens of the membrane in the fresh condition, several physical characters seemed manifest. In the first place, even in proportion to its size, it is, in the fresh, most incon-

ceivably delicate and flexible. It is by far more sensitively flexible in the transverse than in the longitudinal direction and the readiness with which it bends when touched or even agitated is beyond description. Mounted bits, carefully removed, in the fresh seldom showed longitudinal folds or crumples, but it was very difficult to avoid their being bent upon themselves or sometimes tied into impossible knots and gnarls. For the greater part, the tectorial membrane is much wider and thicker than a medullated nerve fiber, for example, but the manipulation of a fresh nerve fiber, especially under fluid, is quite an easy task when compared with attempts to manipulate this membrane. Again, its quality of adhesiveness is phenomenal. It is so subject to surface tension that, it matters not how clean the needle point may be, to touch the membrane is to have it stick, and to remove it from the needle usually means totally spoiling the specimen throughout the region of contact. Scraps of debris and shreds of tissue will adhere to it, and, when bent upon itself, it will often cohere. The membrane had to be moved chiefly by carefully inducing currents in the fluid in which the work was done.

Its specific gravity is manifestly slightly greater than that of the fluid in which it normally lies. The amniotic liquor of the pig is supposedly about isotonic with the blood serum and lymph of the animal. When freed in this fluid, the membrane, or parts of it, will remain suspended and be wafted about for several seconds, moved by the slightest agitations, but gradually it comes to rest upon the bottom of the dish. Bunge's *Physiological and Pathological Chemistry* gives 0.81 per cent sodium chloride solution as isotonic or physiologically normal for the pig. In this solution the membrane finally sinks just as in the amniotic fluid. After fixation in Zenker's fluid, it sank similarly in the tap water of this laboratory.

As delicate and flexible as the membrane obviously is, the behavior of my preparations indicated that it does possess elasticity. Judging from their descriptions, and especially from their illustrations, most of the observers cited above did no more than to assume an elasticity for the membrane from its apparent consistency and the various positions and shapes it presented in their hardened preparations. Retzius and Kishi and the very few others who, in addition, observed the fresh membrane in indifferent fluids, pronounced it elastic from its behavior in these fluids, and the behavior of my preparations confirm their observations. Because of its extreme sensitiveness and flexibility, one

has to observe its behavior closely to perceive its elasticity. The elasticity apparent may be compared with that of a very thin strip of set gelatin immersed in cold water. If not injured by stretching or badly tangled, a piece of the tectorial membrane, as it floats around in a dish of unagitated salt solution, will gradually approach the coiled form similar to its natural shape when in the cochlea and thus come to rest upon the bottom of the dish. In case of whole membranes, or of longer pieces, the portion representing the upper or apical coils of the cochlea will assume the natural form more quickly than the other end or the portion from the basal coil, because of the fact that the membrane is thickest and broadest at the summit, gradually decreasing in size toward the base. Twists are far more common and more serious in the more slender region of the basal coil, and unless they disappear before the membrane reaches the bottom of the dish, the basal coil never assumes its natural form and thus pieces may come to rest with the apical coils well formed while the portion from the basal coils may be irregular or scarcely coiled at all. The more evident elasticity of the summit end of the membrane is explained as being due merely to the greater bulk of this end.

Whole membranes and pieces removed intact from the attachment upon the labium vestibulare, unless containing twists, always come to rest flat upon the bottom of the dish, the under surface either upward or downward, notwithstanding the fact that the inner zone of the membrane removed from the labium vestibulare is very thin and tapers to an edge. This behavior, coupled with the fact that the direction of its greatest flexibility is transverse to the long axis of the membrane, together with its shape in transverse section, indicates that its greatest elasticity must be in the direction opposed to longitudinal rather than transverse stress. Elasticity in this direction can be largely instrumental in inducing the membrane to resume its natural shape when in fluid, and the membrane, being laterally attached along the inner zone, elasticity in this direction must tend to maintain the outer zone in its position above the organ of Corti.

Experiments, intentional and accidental, in stretching the tectorial membrane longitudinally indicate a small amount of elasticity opposed to such force. Pieces of the fresh membrane in salt solution, if stretched very slightly indeed will return to apparently their original thickness; if stretched more strongly, they will suffer attenuation, part of which becomes permanent; if stretched further, they may be drawn

out into filaments of less than half the diameter of the original membrane and which seem to have lost all trace of elasticity. These filaments may be drawn asunder and the parts will remain with tapering and pointed ends. Pieces of membrane from cochleæ fixed in Zenker's fluid show a slight increase in rigidity and therefore greater elasticity when the slight strains are applied, but, if stretched further, they break with a transverse cleavage instead of suffering permanent attenuation. In the study of the structure of the membrane it was found that the lines of such cleavage follow the direction of the fibrous components of the membrane.

The tectorial membrane suffers severely in the presence of all reagents which are hypertonic to it. Most all the recent papers touching upon its structure admit that it undergoes shrinkage with treatment for embedding and sectioning. I made several careful attempts to prepare pieces of the membrane for mounting in balsam so as to get more permanent and probably more transparent preparations, but none were successful. However carefully the graded alcohols were applied, by the time dehydration was complete, the membrane would show shrinkage, constrictions and general distortion, and a bath in xylol would usually complete what the alcohols had begun. Results somewhat better were obtained by clearing with creosote after 95 per cent alcohol, but no preparations so made would bear comparison with the normal, mounted direct in glycerine, either as to shape, dimensions, evenness of contour or surface markings. The physical character of the membrane seems to be such that it is impenetrable to the alcohol molecule, or at least such that it cannot be dehydrated without shrinkage.

Under the dissecting microscope by reflected light it has a distinct glassy appearance and by transmitted light it is transparent. The compound microscope shows it to consist of fine colorless fibers embedded in a transparent matrix. This matrix has apparently the nature of a glutinous, collagenous semi-solid. It is hardened but slightly by fixing fluids containing no alcohol. It is about the first structure in the cochlea to be affected by maceration, for cochleæ taken from pigs not freshly obtained show evidences of liquefaction of the tectorial membrane when the organ of Corti may be practically intact. Sections of such cochleæ show above the organ merely a mass of tangled filaments resembling a coagulum. On the other hand, the membrane seems to be more readily fixed than the organ, for sections of cochlea pronounced

imperfectly fixed will often show the membrane with no sign of liquefaction when the cells of the organ are badly deranged.

It was thought that the matrix might probably have a mucous character from the fact that preparations are occasionally seen in which the membrane stains more or less deeply blue. To test this, specimens were appropriately fixed, prepared into sections and stained with Meyer's muchæmatin and mucicarmine according to the procedure followed by Bensley in his study of the glands of Brunner, but in no case did the matrix take the stain in the way considered differential for mucus. It was further found that the membrane never stains deeply blue with hæmatoxylin in preparations that have been carefully washed after fixing and decalcification. Orcein and Weigert's stain for elastic tissue likewise gave negative results. The matrix may be somewhat similar to that of certain cartilages only much softer, or, since studies of the development show the membrane to be a cuticular structure, and since it is derived from cells of ectodermal origin, the matrix may be a variety of soft keratin.

THE SHAPE AND DIMENSIONS OF THE TECTORIAL MEMBRANE.

The cochlea of the pig is of the flat type. Gray, '07, has recently divided cochleæ into two general types, the sharp pointed and the flat. The flat type is most common, being possessed by several varieties of mammals, including the primates and ungulata, to which latter the pig belongs, while the sharp pointed type is possessed by the carnivora and rodents, the Edentata having an intermediate type and the Marsupials both types.

The pig has one turn more in the coil of its cochlea than in that of the human ear. While the human cochlea is usually described as having $2\frac{1}{2}$ turns, Wiedersheim, '93, accredits it with nearly 3 turns, giving the pig 4 turns, the cat 3 turns, the rabbit $2\frac{1}{2}$, the ox $3\frac{1}{2}$, and the cetacea $1\frac{1}{2}$ turns.

The tectorial membrane of the pig extends throughout the entire length of the ductus cochlearis (scala media), and thus it is about as long as the scala vestibuli, but not quite as long as the scala tympani. Therefore, it is not quite as long as the basal side of the membranous labyrinth. This relative extent is probably true for all the mammals. Dupuis, '94, who studied teased preparations after fixation with osmic acid, Müller's fluid, etc., and decalcification with hydrochloric acid,

reports that for the cat, guinea pig, dog and rabbit the membrane extends throughout the cochlea. Measurements of the lengths of nine tectorial membranes, seven from the cochlea of pig foetuses at about term and two from pigs about two weeks old, gave an average length for the membrane of 25.5 millimeters.

In both breadth and thickness, the membrane gradually decreases from the apex of the cochlea toward the basal end (Fig. 1), and both the end at the apex and the basal end terminate bluntly, slightly tapering. The upper surface of the membrane is convex throughout its length (Figs. 2, 3, 4, 6 and 7), the height of the curvature being in the region which, in the natural condition, overlies the interclasped phalanges of the rods of Corti's organ. The under surface, or the surface next to the organ of Corti, is concave, but with a concavity of several curvatures. In the region of the apex of the cochlea, the outer edge of the membrane projects beyond the confines of the organ of Corti and here this edge bends downward slightly, resulting in an evident concavity of the under surface. The portion immediately imposed upon the surface of the organ of Corti is parallel with the surface of that organ and thus is usually plane; it may slant upward or downward from the horizontal plane of the cochlea or it may be slightly concave, depending upon the direction and the shape of the upper surface of the organ of Corti, which varies somewhat in the different regions. In the decrease in width of the tectorial membrane toward and in the basal coil, it gradually ceases to project beyond the organ of Corti, and thus finally there is no separate concavity of the outer edge to be considered (Figs. 4, 5 and 8). That zone of the under surface beginning with the inner border of the organ of Corti, spanning the spiral sulcus and including the inner, thin edge of the membrane, is, throughout, more deeply and regularly concave than any other portion. The greater concavity here is but an expression of the rapid decrease in thickness which is attained by the inner edge as it becomes attached upon the vestibular lip of the spiral limbus.

All the investigators mentioning it describe the inner edge as extending to the insertion of the vestibular (Reissner's) membrane. In the main, this has been found to be true in my preparations of the pig. Occasionally, observation and comparative measurements from the free membrane and of the width of the labium vestibulare have indicated that the inner edge does not necessarily in all regions extend quite to the vestibular membrane. Hensen, '63; Retzius, '84; Barth, '89;

Dupuis, '94, and others have described the inner edge as sometimes notched. Notches were frequently seen in my preparations, but they were always angular and could be explained as breaks suffered in freeing the membrane from its attachment.

The outer edge of the tectorial membrane in all my preparations is rounded and terminates brusquely. In discussing observations made by Kölliker in 1859 which denied an attachment of the outer edge of the membrane to the lamina reticularis and the cells of Hensen of the organ of Corti, Lowenburg, '64, described a delicate, almost invisible, seemingly frayed-out reticulum along the outer edge. Others have since mentioned this appearance, giving it the name, *Lowenberg's border plexus*. Dupuis, while admitting that it is very irregular, usually appearing in fragments, and not always present, referred to it as a third and outermost zone of the tectorial membrane, while Von Ebner, '02, among others, refers to it as a filamentous structure, adhering to and collapsed upon the outer zone of the membrane and representing its original connection with the lamina reticularis.

The existence of this border plexus as a normal appearance of the tectorial membrane is here denied.

Though the appearance observed may be seen at times in the preparations used here, there is evidence that it may be due to three causes, separately or in conjunction: First, it has always been observed in fixed preparations, and the fixing fluids and especially the alcohol produce coagulation of the albumens and globulins in the endolymph. Coagulum filaments, in forming, always appear most abundant on surfaces, and especially between surfaces which are close together. The places on the tectorial membrane where these filaments are most apt to be noticed are its outer edge and that portion of its under surface which is imposed upon the organ of Corti. Second, evidences of beginning liquefaction of the matrix of the membrane are, in the preparations used here, always most apparent along its outer edge and under surface. Portions of the fibers in the membrane, set free along the edge by the dissolution of the matrix, may produce a delicate, tangled, filamentous appearance which is no doubt augmented by coagulum filaments produced by the reagents. Third, in the study of the removed pieces of the tectorial membrane, I have now and then seen what appeared to be parts of Lowenberg's border plexus, but these appearances proved to be displaced portions of the accessory tectorial membrane described below (Figs. 3 and 5). In the region of the basal

coil, the outer edge of this accessory membrane nearly coincides with the outer edge of the main body of the tectorial membrane, and but slight displacements will result in its projecting far enough to be separately distinguished.

Corti, in first describing the tectorial membrane, expressed the belief that the outer edge was normally attached to the structures below it and located this attachment as far over as the epithelium upon the spiral ligament. Coyne and Cannieu, '85, agreed with Corti in so far as to place the attachment upon the cells of Claudius, and ever since Corti, investigators have looked for and claimed an attachment of the outer edge, though seldom agreeing as to the locality, and they have explained Lowenberg's border plexus as the outer edge of the membrane frayed by having been torn from its attachment. Quite recently, Kishi, '07, who seems to believe that the membrane is normally attached to the organ of Corti, states that the border plexus, or third zone, is only an artifact which results from the tearing of the membrane from the organ of Corti, and which consists either of the frayed edge of the membrane alone, or of this edge together with a portion of the lamina reticularis removed with it. On the other hand, beginning with Hensen, '63, and Böttcher, '72, the outer attachment has been frequently denied. Kölliker and Von Ebner admit, from the study of its development, that at one time the tectorial membrane is of necessity attached along its under surface, but that early, during the differentiation and elaboration of the organ of Corti, and the resultant displacement and adjustment, the attachment of the outer edge at least becomes obliterated. Ferré, '85, described the outer edge as bluntly rounded, and so it appears in the large majority of preparations, in both sections of fixed cochleæ, always allowing for shrinkage, and also in the fresh condition in teased preparations.

Measurements of the width of the tectorial membrane of the pig were carefully taken at the different turns of the coil of the nine teased preparations obtained. These measurements were transversely across each tip or extremity and across the intervening portions at intervals of each half turn of the coil. Now and then partial breaks or slight distortions appeared in short portions of a specimen, and if these appeared in the particular portion of the turn to be measured and seemed sufficiently serious to invalidate the measurement, the measurement for that interval had to be omitted. However, these injured places were not very numerous, and, from the nine specimens, enough trustworthy measure-

ments at the different turns were obtained from which to compute very fair averages. Fortunately, one of the membranes from the pigs two weeks old was more successfully manipulated, and, after mounting, was so nearly intact and uninjured that a complete set of measurements was obtained from it alone. The measurements of the membrane from the foetuses at term averaged throughout so nearly identical with those from the pigs of two weeks that one could infer no essential dimensional differences between them. These transverse measurements were made with an ocular micrometer whose spaces were standardized in terms of microns. The measurements obtained from all the specimens gave the following averages for the total width of the tectorial membrane in the regions specified:

	tip of basal end	near basal tip	7th half- turn	6th half- turn	5th half- turn	4th half- turn	3d half- turn	2d half- turn	1st half- turn	width near tip at apex	tip of end at apex
microns	58.1	107.9	124.5	149.4	170.2	190.9	207.5	257.3	307.1	215.8	166.0

The measurements of the tip at the apex were taken transversely through the point at which the inner edge terminates, and those of the basal tip, transversely through the point at which the outer edge terminates (see Fig. 1).

What is very apparent in the actual specimen may be perceived from these figures, namely, that the tectorial membrane of the pig varies widely in breadth, but varies gradually and somewhat progressively from the basal end toward the apex. Each end terminates bluntly, the widths of the tips taken at similar levels being much less than the widths possessed by the half-turns to which they belong. The width of the tip at the apex of the cochlea is nearly three times that of the basal tip. At the apex the membrane rapidly increases to its greatest width, which is attained in the first half-turn. From the basal end, it increases in width gradually till the width in the first half-turn is 2.8 times greater than that of the last.

Almost the entire variation of the tectorial membrane occurs in its outer, free, portion, or that strip spreading from the outer edge of the labium vestibulare (Huschke's auditory teeth) over the spiral sulcus and the organ of Corti. That portion, or inner zone, which lies upon and adherent to the labium vestibulare varies relatively little in width.

However, like the total width of the membrane, this inner, attached, strip is narrowest in the basal turn and increases gradually, though slightly, toward the apex to attain its greatest width in the first turn. Owing to the extent and shape of the labium vestibulare at the ends of the coil, this attached strip terminates in a point, and is the first zone to terminate at the apex, while at the base it terminates bluntly rounded and is the zone which persists farthest, wholly constituting the basal tip of the membrane.

Dupuis and others to be mentioned below, who studied the markings on the under surface of the membrane, distinguished a boundary line representing the outer extent of the labium vestibulare, or the boundary of the zone of attachment upon it. Barth and Böttcher considered this line an artifact. In all my teased preparations, but especially those fixed in Zenker's fluid, this line was distinguishable and, from further study, it is evident that Barth and Böttcher were correct in considering it an artifact in so far that it only represents the impress of the edge of the labium vestibulare, and has nothing further to do with the structure of the membrane. Measurements of the attached zone taken transversely to the inner edge of the membrane showed it to vary gradually from 62.3 microns in the last half-turn to 87.2 microns in the first half-turn.

These measurements subtracted from the total width of the membrane at the same regions, give the free, outspanning portion of the membrane a width of only 45.6 microns near the basal end, while the free portion of the first half-turn attains a width of 219.9 microns. Kishi, '07, who studied the human tectorial membrane and that of a number of common mammals, states that this outer portion (second zones he calls it) is at least three times broader at the apex of the cochlea than it is in the basal coil. He does not give measurements. In Kölliker's *Gewebelchre*, Bd. 3, Second Half, Von Ebner states that the tectorial, like the basilar membrane, is widest toward the apex of the cochlea, and that, in man, the free portion has a width of 240 microns at the apex, and 120 microns in the basal region. These figures indicate that the free portion of the apical turn in man is only 2 times as wide as that of the basal region, while the above figures for the pig show the free portion in the first half turn to be 4.8 times as wide as it is in the last. However, Von Eben does not state at what particular portion of the coil the measurements were taken nor whether they were made from fresh or fixed specimens or from sections. Kishi, though he only

publishes some very misleading photographs of vertical sections of the cochlea, made some of his observations from isolated bits of the membrane teased free in fluid, and probably these bits suggested to him the greater difference in the width of the outer portion in the two regions. Obviously, measurements of the membrane from sections, necessarily treated with alcohol, etc., and therefore shrunken, would average less and be less regular than if taken from teased and unshrunken specimens, and, as may be seen from Fig. 1, such results depend materially upon the particular localities at which measurements of the free zone are taken. None of the literature I have consulted indicates the successful isolation of appreciable lengths of the tectorial membrane of any animal.

Fig. 1 illustrates the shape of the pig's tectorial membrane as seen from the under surface and with the coil slightly opened, and it is an attempt to indicate its appearance under low magnification. In its natural position in the cochlea, it is more closely coiled, and, especially in the apical turns, the outer edge of one turn appreciably overlaps the inner edge of the turn below it. Thus it was necessary to draw it less closely coiled in order to show it entire. When mounted in glycerine, the cover-glass presses the apical coils of the membrane together and radially outward from the center. The basal coils could not be induced to retain their corresponding curvature with the application of the cover glass, though carefully arranged in the glycerine beforehand. Therefore, it should be stated that none of the preparations obtained showed the membrane as evenly coiled as it is shown in Fig. 1. In making this drawing, the character and extent of the coil was taken from the labium vestibulare laid bare under the dissecting microscope, after the removal of the membrane, and from the appearance of the membrane resting upon the bottom of the dish in fluid. A coiled line was drawn representing the inner edge of the membrane and imitating the character of the coil of the cochlea, but opened sufficiently to avoid overlapping of the edges of the membrane. Then radially from this line, the width of the membrane at each half turn, obtained by measurement of the actual specimen, was indicated by dots. The character and dimensions of the ends and the lines of demarkation of the under surface were likewise sketched in from measurements and from the study of mounted specimens. The scale decided upon gave each space of the ocular micrometer the value of one millimeter. The outline being made, the width and variations of the different zones were determined and other

peculiarities of the difficult regions sketched in. The sketch was then transferred to a sheet of Ross-board, upon which it was thought advisable to make the attempt to represent the glassy, delicately fibrous character of the membrane as it appears over a black surface. Figs. 2, 3, 4 and 5 were outlined in the same way, but under higher magnification, and are intended to show greater structural detail.

Measurements of the thickness of the membrane could be obtained only from vertical sections of cochleæ made after the usual fixing, dehydrating and embedding. After getting some idea of the character of the membrane, a few specimens, carefully treated and embedded in celloidin, gave sections which showed considerably less shrinkage and distortion than is usually evident. Figs. 6, 7 and 8 were outlined from photographs of and drawn from a section of one of these specimens.

All the membranes showed some distortion and shrinkage. The latter especially is evident in a denser and more amorphous shell-like thickening about the entire periphery, which suggests a primary condensation due to the first attack of the shrinking agent, and which, once formed on the periphery may be less permeable and may result in the interior portion being subsequently more gradually and therefore less violently acted upon by the reagents. Fig. 8, from the seventh half-turn or basal coil, shows decided distortion and displacement due to shrinkage. This is from the more slender portion of the membrane, and, if the above suggestion is true, would necessarily be affected most by the reagents.

Measurements of the thickness taken from these specimens and corrected with the study of the isolated and supposedly unshrunk pieces indicate two relations:

(1) That, like the width, the thickness of the membrane begins with that of the outer zone in the rounded end at the apex (see Fig. 1), rapidly increases to its maximum in the apical region and thence gradually decreases toward the basal coil, in the end of which the minimum thickness occurs.

(2) That, throughout, the line of the greatest thickness, in the different transverse sections, runs approximately parallel to the edge of the labium vestibulare and approximately over or slightly to the inner side of the line of the enclaspèd phalanges of the rods of Corti.

The measurements of thickness were all taken from sections of the cochleæ of pigs at or very near term. They gave the following average thicknesses for the regions specified:

	tip at apex	1st half- turn	2d half- turn	3d half- turn	4th half- turn	5th half- turn	6th half- turn	7th half- turn
microns	49.8	74.7	70.5	62.3	53.9	42.4	31.1	13.4

These averages are obtained from vertical, axial sections from each of four cochleæ. The thickness of the tip at the apex is computed from one measurement, for, unfortunately, the plane of only one of the sections was such as to pass transversely through the tip. Further, it is uncertain how far from the basal tip the measurements designated "seventh half-turn" were taken. Evidently they passed varying distances from it, for the measurements varied from 12.4 microns to 24.9 microns. The other regions did not vary so widely. All the measurements were made and recorded before the averages were computed and converted into the terms of microns.

It is seen from these figures that the greatest thickness of the membrane occurs in the first half-turn, and thence the thickness decreases gradually and somewhat progressively toward the basal end. A comparison of Figs. 6 and 7 indicates that in this cochlea the greatest thickness occurred in the third half-turn instead of in the first. The shrinkage here seems to have resulted in a lateral crumpling and probable increase of thickness in the third half-turn. The drawings of this specimen were made before the average thickness was ascertained; otherwise a more average specimen might have been used. This specimen was among those measured. The first and second turns all showed much smaller differences than any other adjacent half-turns. That the differences between adjacent basal half-turns are greater than those between the half-turns of the apex is due to the fact that the basal turns are longer, the basal coil of the cochlea being several times longer than the apical, and thus longer strips of membrane intervened between the measurements in the basal half-turns. The lack of greater uniformity in progressiveness of decrease is probably due both to irregularities in the shrinkage effects of the reagents and to lack of identical orientation of the plane of section of the different cochleæ, the plane passing nearer to the ends, especially the basal end, of some membranes than of others.

Von Ebner quotes Retzius for the statement that the thickest part of the human tectorial membrane measures from 24 to 25 microns. The particular turn from which this observation was made is not stated. The

figures seem rather low when compared with the 74 microns obtained here for the first half-turn of the membrane of the pig.

THE STRUCTURE OF THE TECTORIAL MEMBRANE.

Surface markings. Since the beginning of its study, the natural tendency has been to divide the membrane into zones. These zones vary in the different descriptions both as to their number and their boundaries, as is to be expected from the fact that some investigators have dealt wholly with appearances seen in vertical sections of the cochlea, others with the surfaces of isolated pieces of the membrane, and the majority with preparations more or less distorted by the action of reagents. Gottstein, '72; Coyne and Cannieu, '85; Barth, '89; Dupuis, '94, and others made three zones: (1) The inner zone, comprising the thin, attached strip spreading from the inner edge, at the insertion of the vestibular membrane, and terminating with Huschke's teeth or the edge of the labium vestibulare; (2) the middle or second zone, comprising the body of the membrane which spreads from Huschke's teeth to the outer, bruskiy rounded border; and (3), believing Lowenberg's border plexus to be a part of the membrane, they called this the outer or third zone.

In 1863, Hensen, examining the surface of the membrane, observed a line running along the middle of the main body, approximately parallel with the edge of the labium vestibulare and apparently constant in occurrence. Later, this line was farther observed by Retzius and Schwalbe who described it as a transparent, glittering strand on the under surface of the membrane, having the appearance of a hyaline thickening along the middle zone. By both of these investigators it was given the name "*Hensen's stripe*." This stripe or streak, while it has been reported absent in some animals (the rabbit, for example), has been used as a boundary line by those who have chosen to divide the membrane into three zones, exclusive of Lowenberg's border plexus whether admitted or denied. Divided in this way, the first zone comprises the strip attached upon the labium vestibulare; the second or the middle is the strip between the labium vestibulare and Hensen's stripe, while the third or outer zone comprises the balance of the width from Hensen's stripe and including the outer edge of the membrane. Most of the more recent papers divide the membrane into zones in this way, though some, for example, Rickenbacher, '01, divide it into two zones: an inner, as

above; and an outer, comprising all of the outspanning portion and thus including Hensen's stripe.

Also, throughout the literature, occur descriptions of various lines and markings of the under surface in addition to Hensen's stripe and the line of impress of the labium vestibulare. Hensen's stripe has even been given various appearances, various widths and varied occurrence. Dupuis, '94, working with the tectorial membranes from the dog, cat, rabbit and guinea pig, found Hensen's stripe apparently absent in some cases, while in others it seemed to be represented by three lines, which, however, he thought might have been due to optical defects produced by the variations in the thickness of the membrane compressed under the cover glass. Various extra lines have been described upon the under surface of the membrane, some running longitudinally, others transversely or obliquely. Only recently, Kolmer, '07, working with various mammals, including the pig and man, describes a small piece of the membrane, giving it longitudinal lines upon its under surface which he interprets as bundles of longitudinally running fibers. In all of my preparations which proved to be shrunken, extra lines were always apparent. The prevailing direction of these was always longitudinal, and most of them appeared on the under surface. Especially, in all those pieces which I attempted to dehydrate and clear in oil, numerous lines were apparent, some of which ran obliquely and many of which anastomosed. Comparison with the fresh preparations and with those fixed with apparently little or no shrinkage made it very evident that these extra lines were due to the shrinkage effect of the reagents, and they were explained as crumplings and crimps of the shell-like peripheral condensation which is seen in all sections of embedded material and is probably produced in the first attack of the reagents upon the matrix of the membrane. Further shrinkage or extraction of water from the interior can but result in crimps of this outer, already condensed layer. As Kolmer says, such lines always seem to stain more deeply than the adjacent material, but this must be due to their greater condensation, and therefore greater capacity for holding stain. Though seeming more or less amorphous, as do all condensations of the membrane, a fibrous structure may be detected in them; but neither in these lines nor in any parts of the tectorial membrane of the pig have I been able to distinguish any longitudinally running fibers.

The normal markings readily detected on the under surface of the tectorial membrane of the pig when removed intact and unshrunken,

and viewed under surface upward, are four only: (1) The fine fibers of which the membrane consists, the prevailing course of which is obliquely transverse and which are embedded in the transparent, collagenous matrix; (2) the line of impress, the boundary of the zone of attachment, left by the edge of the labium vestibulare; (3) Hensen's stripe, always present, whose variations and significance will be mentioned below; (4) a line on the outer zone which, in passing from the apical to the basal end, gradually approaches and comes to coincide with the outer edge of the membrane, and which constitutes the outer edge or back of the *accessory tectorial membrane* to be described below, and from which may usually be detected short fibers extending obliquely towards Hensen's stripe. Some of the descriptions for Lowenberg's border plexus, some of the claims of attachment of the outer zone of the tectorial membrane to the cells of the organ of Corti, and some of the descriptions of extra lines on the surface were very probably dealing with this accessory membrane, for it seems to be easily displaced, and, in shrunken preparations, is diminished and distorted beyond recognition.

All the papers dealing with the appearance of detached pieces, seem to agree that the upper surface of the membrane is smooth and more or less evenly convex. Beyond the effect given by the component, obliquely transverse fibers of the membrane, the upper surfaces of my preparations showed no markings that could not be interpreted as due either to injuries from manipulation, adherent debris or coagulum filaments. The highest point in the convexity of this surface remains throughout in about the same relation to the organ of Corti.

The fibrous structure of the tectorial membrane is very evident in teased preparations, though the exact internal arrangement of the fibers is somewhat difficult to determine. As mentioned above, the fibers are imbedded, or distributed throughout, in a transparent matrix, seemingly having the character of a glutinous or collagenous semi-solid. It is the nature of this matrix that allows of that most remarkable flexibility and sensitiveness possessed by the membrane and probably determines its low specific gravity. The matrix is stiffened but slightly by fixing agents, shrinks severely in dehydration and stain tests indicate that it is not of a mucous nature. It is due to its shrinkage that the membrane so often appears in sections as an irregularly shaped, deeply staining, amorphous mass lying in various positions above the organ of Corti, and it is with this appearance the investigators have had frequently to deal.

Lowenberg, '64, thought that the membrane consisted of layers, one above the other; Göttstein, '72, pictured it as structureless, and many others after these failed to comprehend its character. Most of the physiological and theoretical papers giving it any attention assume rather than study its anatomy. All the more recent anatomical studies admit the membrane to be fibrous. Shambaugh, '07, assumed the membrane to be constructed of an immense number of delicate lamellæ, and on the basis of this, propounds a very interesting theory of tone perception. Coyne and Cannieu, '85, were, I think, the first to make tangential sections of the cochlea, passing through the membrane transverse to its fibers, and to picture the transverse sections of the fibers as fine dots, as shown here also in Fig. 9. They also tried to analyze the course and arrangement of the fibers, and, with Barth, '89; Dupuis, '94, and Kishi, '07, made, I think, a mistake in describing the fibers as coursing from the labium vestibulare in two layers, one on the upper surface and one on the under, with a less compactly assembled layer of fibers between the two. They probably mistook the peripheral condensation, explained above, as due to the action of the reagents, as special upper and lower layers of fibers.

Seen from the *upper surface*, the fibers appear to course from the attached or inner zone outward, but, instead of coursing radially, they always slant from the labium vestibulare toward the apex of the cochlea. This slant is greater in the region of the inner zone, and deviates slightly toward the radius in the outer zone as shown in Fig. 4, the general course showing a slight tendency toward the shape of the letter *S*. This general course was also noted by Dupuis, '94, in his preparations. Kishi notes an oblique direction tending toward the apex in the animals he studied, and Von Ebner states that the inclination is about 45° from the radius.

Kishi claims to have noted fibers of varying size and length, and Kolmer, '07, states that the fibers have a thickness of $\frac{1}{4}$ micron. From casual observation the impression is very readily obtained that the fibers course individually across the entire width of the membrane, but closer study of the membrane of the pig under higher power convinces that they are far more numerous than first supposed, and that they are too fine to be followed individually or to be measured by the ordinary means.

Comparing the surface view with the *transverse section* (Figs. 2, 6 and 4) shows that, instead of all the fibers extending from the labium

vestibulare across to the outer edge of the membrane, the greater number of them at least course varying distances across, then curve downward and, still curving, reach the under surface, where they terminate, many running a short distance parallel to the under surface, prior to termination. The shape of the bluntly rounded, outer edge of the membrane is determined by the curvature downward of the outermost of the fibers. The outline of this edge is never perfectly even, but always appears finely and irregularly scalloped, as shown in Fig. 3, suggesting that the fibers may have a tendency to course and curve around the edge in bundles. In some of my preparations the under surface of the outer edge of the sections at the apex (similar to Fig. 6) appeared thickly studded with the down-hanging ends of fibers as though the under surface had been frayed either by the tearing away of the peripheral condensation or by partial liquefaction of the matrix. Along the inner edge, the sections show that all the fibers by no means are continuous from the inner, attached zone, but that the rapid increase in the thickness of the free portion results from an enormous increase in the number of fibers concerned. The interior fibers of this region course and curve parallel in the main with those of the upper surface, till those nearer the under surface gradually come to sweep downward and then outward and parallel for short distances with the under surface which they form and in which they terminate.

Fig. 9 is made from a horizontal section of the cochlea, and represents a tangential section of the tectorial membrane passing about parallel with the surface of the labium vestibulare and splitting Huschke's teeth. It is taken from the neighborhood of the third half-turn, and a comparison of it with a line drawn in the same plane through Fig. 7 will make clear the relations and appearances shown by it. The plane passes through the dorsal aspect of the membrane, and, as is to be expected from the evident course of the fibers shown in Fig. 7, near Huschke's teeth (Ht) the fibers are cut transversely and obliquely in the zone indicated by *a*, while the fibers in the outer zone, indicated by *b*, course more nearly in the plane of the section. In this section the fibers do not appear to run wholly parallel with each other. Apparently they even anastomose, and where they are cut transversely, they appear to be connected with each other by fine collateral filaments. How much this specimen was shrunk and how much this appearance is due to the reagents cannot be determined. The tangled appearance is no doubt due largely to shrinkage and coagulation effects. The fine filaments

may represent the individual fibers, while the heavier lines and dots may consist of agglutinated bundles of them.

The *under surface* of the main body of the membrane is thus given a transversely fibrous appearance when viewed on the flat, not by continuous fibers coursing across it individually, but by the general direction of the curved ends of many fibers. Beginning on the under surface, the fibers first lie parallel with this surface and form it, and then curving outward, upward and then inward, contribute to the upper surface. The summation of the course of these ends gives to the under surface the appearance of being striated in a direction oblique from the radial and, like the upper surface, the slant is from the labium vestibulare toward the apex of the cochlea. But the direction on the under surface is more nearly radial than that on the upper, as may be seen by comparing Fig. 4 with Figs. 2 and 3. On both surfaces, the direction of the fibers in the inner or attached zone of the membrane is inclined more toward the apex than that of the fibers in the main body and especially the outer edge. An examination of the under surface showed that the most nearly radial direction of the fibers occurs in the second and third turns, and an attempt is made to show this in Fig. 1.

Fig. 4 represents a drawing of the broken end of a piece of membrane from a cochlea fixed in Zenker's fluid. The preparation showed that the fixed specimen, at least, in breaking, has a tendency to break parallel with the direction of the fibers, and it suggests that the difference in the course of the fibers above and below may contribute to the strength and elasticity of the membrane by a sort of interlocking arrangement. In a break like this, the portion of the fibers intervening between the under and upper surfaces must of necessity be broken across. In the break pictured, there were evident clumps of fibers which seemed to have been partly split off from the remainder before breaking, and which appeared something as slivers, each a mass of fibers held in a corresponding amount of the glassy matrix (Fig. 4, S).

From a careful comparison of the surface views with the sections one may conclude that the fibers contributing to the under surface of the tectorial membrane make their immediate approach (or, rather, considered from the standpoint of their origin, they leave this surface) from two general directions: (1) Most of those on the outer side of Hensen's stripe contribute first to the striation of the upper surface, then curve downward and then inward to contribute to the striation of the

under surface; (2) most of those on the inner side of Hensen's stripe curve from the inner zone, first slightly outwards, then sharply downwards, and finally inwards to contribute to the striation of the under surface, thus following an S-shaped course. Apparently, these two general directions would result in a midregion either free from fibers, or, in which the general direction would be neither the one nor the other; but, in the sections, the transitions of curvature seem to be so gradual that this region is never definitely marked. Further, the two directions should result in a zone of the under surface in which the ends of the fibers from the two directions intercross. The sections show this intercrossing, and that, while it occurs to some extent in the body of the membrane, the greater part of it, as to be expected, occurs in the immediate under surface, and by no means all in one line (see Fig. 7).

The cut ends of the segments of the membrane represented in Figs. 2, 3, 4 and 5 were, of course, not possessed by those segments, but were outlined upon them and the arrangement of the fibers drawn in accordance with the arrangement apparent from the study of the sections, in order to illustrate the relation between the fibers of the upper and under surfaces. The intercrossing of the ends of the fibers in the under surface is seldom apparent in the ordinary sections because such sections are usually more shrunken than those represented in Figs. 6, 7 and 8, and the intercrossing, and indeed the whole parallel arrangement, is involved in the more deeply staining peripheral condensation of the substance produced by the reagents. In Fig. 7, Pc, for some reason or other during the manipulation, probably in the sectioning, this peripheral condensation seems to have partially peeled off from the under surface of the inner side of the membrane and the strip to have become stuck to the inner supporting cells of the organ of Corti.

Looking down upon and into the under surface of the freed membrane, with the compound microscope and with transmitted light, this surface, and all focal planes near it, appear studded with numerous fine dots which manipulation of the focus shows to be the ends of fibers. These ends are most numerous in and along either side of Hensen's stripe.

Hensen's stripe, or streak, in my preparations has a structure, and, I think, a significance. Hensen, who discovered it, and Retzius and Schwalbe, who named it and described it as a hyaline, transparent strand on the under surface of the "middle zone," probably had to do with preparations shrunken at the periphery at least. Transparent

preparations examined from the ventral surface, by transmitted light, show it to be fibrous and to be largely composed of a dense linear series of the intercrossing ends of the fibers approaching each other in the ventral surface from the two directions. In fact, the stripe occupies approximately the position of the dividing line between the fibers coursing in this surface from the two directions. It is most probably distinguishable because it is a linear accumulation of these intercrossing ends which, as such, behave toward the light differently from the other regions. For the same reason, it was distinguishable in my preparations by reflected light, that is, when viewed over a black surface, as well as by transmitted light. It is strong enough to appear quite distinctly through the membrane when studied from the upper surface.

Von Ebner, '02, notes that Hensen's stripe may show from the upper surface, and thinks that it is produced by a thickening or bunching of the substance of the membrane, and he accepts the statements of others that it lies over the line of the inner hair cells of the organ of Corti. He, Coyne and Cannieu, '85, and Dupuis, '94, state that it is absent in some animals. The latter notes that it varies in different species, and that it may be modified by pressure of the cover glass, not leaving one to feel positive that the stripe is ever normally absent. Hensen himself thought the stripe a line of connection with the inner hair cells, and Shambaugh, '07, describes it as "a sort of fascet where, normally, the membrane is attached to the supporting cells just internal to the inner row of hair cells." The latter description is based upon the appearance of the membrane in sections, largely one section, manifestly distorted. In none of the sections of the pig's cochlea used here was it possible to locate Hensen's stripe by any means as positively as Dr. Shambaugh was able to do with his sections. It is of necessity always involved in the peripheral condensation. Denser, or more condensed, spots were often seen cut across in the under surface, but these were too numerous and too variously placed to be interpreted as other than sections of crimps in the peripheral condensation produced by the further shrinkage of the membrane during the preparation for sectioning.

In removing two of the preparations used here from cochleæ fixed and decalcified in Zenker's fluid, the tectorial membrane was found to be stuck down to the organ of Corti in the regions of the first and second turns of the spiral. By careful use of the needle one of these was freed, and, though finally broken, the pieces were stained in fuchsin and mounted, under surface upward. Though disappointing and practi-

cally useless for the purpose in mind, this preparation was of interest with reference to the position of Hensen's stripe. Cells and portions of cells of the organ of Corti were adhering to the region involved, and, in one place, nearly the whole organ, including both rods, for a stretch of several cells. The ends of the hair cells could be distinguished as such by means of the crescentic lines of the exit of their hairs, and it could be seen that the outer and inner rows of hair cells extended one on each side of Hensen's stripe. In other words, both by actually distinguishing it at times in their midst and by tracing it from the clean regions into the region involved, it was evident that, in preparations of the pig fixed in Zenker's fluid at least, Hensen's stripe lies between the inner and outer rows of hair cells, and therefore over the relatively smooth line occupied by the enclasped phalanges of the rods of Corti.

It is difficult to say whether or not Hensen's stripe exists as a ridge projecting beyond the general level of the under surface. A number of investigators have described it as such; others, less definite, mention it as a thickening or bunching of the material, and I remember none to have specifically denied its being ridge-like. Sections should be practically the only means by which this can be determined, but sections have proved very untrustworthy, because, even if a ridge is indicated in them, one is never sure it is not due to inequalities of surface shrinkage, and also because Hensen's stripe cannot be positively located among the variable thickenings and markings that different sections show. When viewed from the under surface, one gets a very decided impression of a ridge, but, under magnification, allowing the whole width of the membrane in the field, the greater part of the under surface appears roof-like with Hensen's stripe as the highest part. Careful focussing up and down under high power shows that the stripe is higher than the adjacent surface, but much less so than was to be expected, and that the roof-like appearance under low power was an optical effect, explained as due to the ends of the fibers converging, in the glassy matrix, from the two directions toward and into Hensen's stripe.

If the stripe runs along between the inner and outer rows of hair cells, one might infer that it is a ridge which represents a strip of the membrane never in contact with the projecting hairs, but which fits into the groove walled on either side by the hairs, and that it should have a width throughout corresponding to the width of the line of the exposed surfaces of the phalanges of the rods of Corti. The exposed

surface of the phalanges is widest at the apex of the cochlea and grows narrower towards the base of the coil, just as the rods and the angle they form decrease in size, and it was found that the stripe is somewhat wider at the apex and decreases in width toward the base, but at no level was it found to be as wide as the groove floored by the phalanges, nor does it vary in width as much as the groove. The only inference drawn from this study is that Hensen's stripe probably has the form of a low ridge the existence of which may be protected by the groove over which it lies.

In looking over papers dealing with the development of the tectorial membrane and the sections from pig foetuses prepared here for the purpose, the possibility was suggested that Hensen's stripe may have an embryonic significance; namely, that it represents that area or line on the under surface which is last to become detached from the cells which give origin to the membrane.

ON THE DEVELOPMENT OF THE MEMBRANE.

It is not the object of this paper to describe in detail the development of the tectorial membrane. All the essential stages of the process have already been worked out quite thoroughly. Kölliker, '61, Middendorf, Rosenberg, Göttstein, Nuel, Retzius, Schwalbe, Böttcher, Hensen, Prichard, Exner and Rickenbacher, '01, all agree that, in vertebrates, the membrane is a cuticular structure arising from the thickened epithelium of the inner side of the floor of the embryonic cochlear canal, and Kuhn and Hasse have described a similar origin for invertebrates. I find that in pigs of 2.5 cm. there has begun the marked thickening of the epithelium of that side of the cochlear canal which will become the portion to line the spiral sulcus and overlie the inner portion of the basilar membrane. At 3 cm. the thickening of the epithelium has increased and there appears above the entire thickening a cuticular film of quite appreciable thickness and decided fibrous character. The later stages, up to about 12 cm., show increase in the width of the epithelial thickening corresponding to the increase in the diameter of the cochlear canal, consequent increase in the width of the developing tectorial membrane and marked increase in the thickness of the epithelium concerned. At 12 cm., or shortly before, there is differentiated a second and much smaller epithelial thickening along the immediate outer edge of the first one, thus giving the greater and the lesser epithelial thicken-

ings, "pads," noted by Kölliker, '61, and more fully described by Böttcher, '69, and Rickenbacher, '01. The lesser thickening is the first indication of the differentiation of the organ of Corti, while the cells of the greater give origin to the tectorial membrane and later gradually retract and sink back into the low, indifferent cells lining the spiral sulcus. Böttcher thought that the tectorial membrane takes origin from both the greater and the lesser thickenings. This can hardly be claimed, for the pig, for while the edges of the two thickenings are, of course, quite close together, the early membrane does not begin to extend over the lesser till there are evidences of the beginning of retraction on the part of the greater thickening. Evidences to the contrary of this are sometimes seen in the form of a thin, frayed reticulum sticking to the inner edge of the lesser thickening and continuous with the membrane, but serial study suggests that such appearances are due to distortion and to coagulum films produced by the reagents. Two years after its publication, Hensen showed that Böttcher's conclusion was based in part upon artifacts.

As Rickenbacher pointed out, the membrane, throughout its elaboration, undergoes no active growth whatever, but is purely a passive product of the continued activity of the epithelial cells below it. Not till pigs of about 14 cm. do my preparations show evidences of differentiation of the cells of the lesser thickening into what will become the different cells of the organ of Corti (Fig. 10), and at that stage none of the cells of the organ are in the least recognizable until traced backward from the more advanced stages. The contention of Ayres, '91 and '98, partially supported by Czinner and Hammerschlag, '97, that the tectorial membrane consists of a segregation of continuations of the hairs of the hair cells of the organ of Corti, is shown in my preparations to be fully met by the statement of Rickenbacher, namely, that the tectorial membrane is considerably developed some time before the hair cells are differentiated as such. Rickenbacher showed further that much of the findings of Czinner and Hammerschlag in this relation were artifacts, and cites Hensen in suggesting the same to have been true with Böttcher.

By a process of retrogression and displacement, first suggested by Kölliker and described later by Exner, '97, the tectorial membrane developed wholly from cells at the inner side of the organ of Corti, finally becomes so left that its outer part extends over the organ. At first, when the lesser epithelial thickening is not apparent in the prepa-

rations used here, a thin fibrous film may be discovered overlying the entire surface of the greater thickening and inward upon what will become the labium vestibulare. At the very beginning, the then very short fibers stand vertical to the epithelium and are even then agglutinated by a seemingly fluid-like stage of the transparent matrix. From pigs of 3 cm. up to 15 cm. the more important changes taking place in the floor of the cochlear canal are a marked increase in both the thickness and the width of the greater epithelial thickening and the appearance and differentiation of the lesser thickening.

At the stage when the labium vestibulare is evident, the greater thickening wholly occupies the area of the future spinal sulcus and consists of a high, pseudostratified epithelium whose surface is level with the upward pointing tip of the labium itself (Fig. 10). As to be inferred from this condition, the continuation of the epithelium upon the labium is very much lower than that of the thickening proper. In fact, this portion comprises the inner, tapering edge of the thickening at the stage before occurs the differentiation of the mesodermal tissue into the limbus spirale and its labium vestibulare and when the whole is covered by the delicate beginning of the tectorial membrane. The epithelium upon the labium is thus thin from the first, remains so throughout, and takes part in the production of only the thin, tapering, permanently attached, inner zone of the tectorial membrane. In reality, it ceases as an epithelium, and probably altogether, in the adult cochlea, for then the only superficial cells of the labium are those which are situated between and level with the horizontal connective tissue bundles comprising the auditory (Huschke's) teeth (see Fig. 9). Probably it ceases quite early to produce tectorial membrane, for, from pigs of 12 and 14 cm. upward, the inner, attached zone of the membrane gains apparently very little in thickness.

As the greater epithelial thickening increases in width during the earlier stages of the development, the fibers of the tectorial membrane, standing vertical to the epithelium at the very first, are gradually drawn outward from the more firmly attached inner zone, so that, by the time a membrane has gained a more appreciable thickness, 10 cm. pigs, the first formed portions of the fibers come to lie horizontal or nearly parallel to the surface of the epithelium while their continuations curve downward till the growing ends of the fibers only are vertical to the cells of the parent epithelium. In this way is produced the transverse striations apparent in the upper surface of the adult membrane and

the curved course of the fibers apparent in sections of it. All sections of foetuses show that the stages of development advance from the basal coil toward the apical, and so in the increase in thickness and width of the greater epithelial thickening, beginning at the base and advancing toward the apex of the cochlea, must lie the explanation of the fact that the outer direction of the fibers is inclined from the radial toward apex. Measurements from my preparations show that between 10 cm. and 15 cm., the width of the greater epithelial thickening increases from 124 microns to 174 microns. This increase consists of a very evident increase in the number of the epithelial cells concerned.

At about 14 cm., the lesser epithelial thickening, the future organ of Corti, has considerably advanced in form and appears as if it acts as a block to the further increase in width of the greater thickening, for, at that stage, the outer edge of the latter becomes bluntly rounded and bows upward (Fig. 10) with the result that in this edge, adjacent to the lesser thickening, there is formed the thickest part of the greater thickening. The outer edge of the developing tectorial membrane necessarily bends downward around this bluntly rounded edge of its parent epithelium. Up to this stage, the membrane never overlaps the lesser thickening and in confirmation of the statement of Rickenbacher, it must be said that at no stage is there good reason to assume that the cells giving rise to the organ of Corti ever have any thing to do with its development.

The order of the development of the membrane seems to be, first, the fibers and then the matrix, both being subadded gradually at the under surface. In all stages, from the very first, there always exists upon the immediate surface of the epithelium a thin, clear, parallel layer in which the matrix is either in a soluble stage of its development or wholly absent, and across which course the ends of the fibers from the epithelial cells into the body of the membrane above. In sections the thus unembedded ends of the fibers appear exceedingly tender, are often broken free and usually appear in agglutinated bundles (Fig. 10).

The stage of retrogression of the greater epithelial thickening, and the resultant displacement of the parts, begins with a cessation of growth of the epithelial cells, followed by their exhaustion and finally by a liquefaction of their remains, till, in the adult cochlea, the cells of the greater thickening are represented by the very low, indifferent epithelium which lines the spiral sulcus from the inner supporting

cells of the organ of Corti to the edge of the labium vestibulare. The exhaustion begins along the inner side of the greater epithelial thickening, at the edge of the labium vestibulare and gradually proceeds outward. Thus the first portion of the tectorial membrane to become free from its parent epithelium, that is, to cease growing, is the strip adjacent to the labium vestibulare. Sections from pigs of 15 and 17 cm. usually show a beginning recession of the epithelium in this region, and it is probably indicated in Fig. 10. (More strictly speaking, the portion of the membrane which first ceases to increase in thickness is, as mentioned above, the inner zone, attached upon the surface of the labium vestibulare.) The exhaustion of the epithelial thickening gradually passes outward till the last region of it that is active and attached to the tectorial membrane is its outer edge, or the region adjacent to the organ of Corti, which region, in the previous growth changes as noted above, became its thickest region. Finally this region recedes, the remains of the cells liquefy and the tectorial membrane is left entirely free from the cells which give rise to it. Transverse sections of the cochlear duct of pigs from 20 to 25 cm. often show a mass of disintegrating epithelial cells lying against the inner supporting cells of the organ of Corti, which mass represents the vestige of the greater epithelial thickening.

By the above processes of increase, recession and disintegration, the disposition of the fibers within and in the under surface of the tectorial membrane may be explained as well as the position which the membrane finally attains with reference to the organ of Corti (the lesser epithelial thickening).

The retrogression of the epithelial cells undoubtedly results in a decrease in the width of the space occupied by the greater thickening (the space which becomes the floor of the spiral sulcus), and this decrease results in the inward displacement of the organ of Corti to its final position under the outer zone of the tectorial membrane. Counts of the cells comprising the greater epithelial thickening in the third half-turn of several cochleæ from pigs of 14 to 15 cm. gave an average of 93 cells per transverse section. Counts of the cells lining the spiral sulcus, up to the inner supporting cells of the organ, in the same region of several fully developed cochleæ gave an average of only 21 cells, the averages showing that the space in the foetal cochlea contains four times as many cells as the developed. Measurements of the width of the floor of the spiral sulcus of the developed cochlea gave

an average of only 75 microns, while measurements of the width of the greater epithelial thickening in the 15 cm. pig gave an average of 174 microns, showing the space in the foetal to be more than twice as wide as in the developed cochlea. (The measurements indicate, further, what is shown in the specimens, that the epithelial cells of the foetal cochlea, though much higher, are thinner than those of the developed.)

The direction of the fibers of the inner region of the body of the membrane is outward and almost parallel throughout. In this region multitudes of fibers are added to the body of the membrane, contributing to its sudden increase in thickness. The practically uniform outward direction here is due to the fact that these fibers were produced before the epithelium began to recede and the width of the thickening to decrease. Further outward, as far as Hensen's stripe, the fibers are directed outward, then downward, but still outward. At the region of Hensen's stripe, many fibers curve downward from their outward direction above and approach the under surface vertically. In fact, Hensen's stripe seems to be an expression of the period at which the retrogression of the epithelial thickening began. It also represents the line along which the thick, outer edge of the thickening was last attached and along which growth was last contributed to the membrane.

With the exhaustion and retrogression of the cells of the inner portion of the thickening began the decrease in the width of the space occupied by it. Consequently, the portions of fibers produced by it after the decrease in width began were no longer directed outward or vertically, but inward, drawn inward, as it were, by the now receding outer edge of the thickening. As a result, there is in Hensen's stripe a crossing of the ends of fibers approaching it from the two directions, as noted above, in describing Hensen's stripe.

And also as a result, the fibers coursing in the membrane on the outer side of Hensen's stripe are directed outward in the upper surface (the portions earlier formed), then curve downward (as do those on the inner side) and finally curve inward to approach the under surface at acute angles or to run short distances parallel with it. The tectorial membrane, firmly attached along its inner zone and sustained by its semi-solid matrix and its consequent elasticity, holds the position and shape in which it was molded; while the organ of Corti, during its elaboration, appears to follow the receding greater epithelial thickening and finally comes to be situated under the outer zone of the tectorial

membrane in such a position that the line of the phalanges of the rods of Corti about coincide with Hensen's stripe.

The greater width and thickness acquired by the tectorial membrane as its apical end is approached may be explained as due to the longer persistence and greater width attained by the apical portion of the greater epithelial thickening, noticeable in sections of foetal cochleæ. All signs of the thickening may have disappeared in the basal coil when the coil of the apex may show considerable of the epithelium, and, in the adult, the floor of the spiral sulcus, as well as the entire spiral lamina, is left considerably wider in the apical than in the basal coils.

AN ACCESSORY TECTORIAL MEMBRANE.

Though this structure as I shall describe it is undoubtedly present in my preparations, its description is entered into with some hesitancy because of the fact that in none of the papers I have been able to examine is such a structure noted for either the pig or other animals. The only explanation of why it has not been described before now is offered in the fact that it is so thin and fragile and so susceptible to the action of reagents that, with its existence not realized, it is impossible to distinguish in the ordinary preparations anything suggesting such a structure. Even after noting it in the unshrunk teased preparations, in only two of my transverse sections of the tectorial membrane, the best I have been able to get, could there be distinguished anything which might be interpreted as sections of this structure, however distorted. It was not evident on some of the broken teased preparations, because of the fact, soon learned, that it is apparently but very slightly attached to the main body of the tectorial membrane and is easily displaced or lost in the removal from the cochlea. In the teased preparations after reagents found to produce shrinkage, the "accessory membrane" was usually unrecognizable, appearing, from the under surface, as an irregular belt of very delicate zig-zag lines which might be interpreted equally well as crumplings and shrinkage disarrangements of the surface and fibers of the main body.

The structure was first noted in a piece of tectorial membrane removed after Zenker's fluid and broken on the slide while mounting it in glycerine. Under low light, it appeared as an exceedingly thin transparent ribbon extending far beyond the broken end of the main body, in places slightly twisted, but for the most part flat and showing

parallel edges. Traced to the main body, it was found to be lifted off for some distance and to lie upon the main body much as a ribbon would appear if lifted by the end from slight adherence to a surface. Fig. 3 is an attempt to imitate this appearance of the structure, as seen in the preparation, the end of the main body, however, not being shown as broken, but being utilized to show the arrangement and relations of the fibers of the body. When viewed in its undisturbed position, it appears lying upon the under surface, as shown in Figs. 1 to 5, Ac, and so delicate it is, that one unaware of its presence, especially upon unstained or darkly stained pieces of the membrane, might consider the appearance produced by it as due to mere disturbances in the arrangement of the fibers of the under surface of the main body. That it lies practically free or, at least, very lightly adherent to the under surface of the main body is indicated by the apparent ease with which it comes away and by its occasional total absence from broken pieces. During its further study upon various preparations, short extents of it were at times seen crumpled away and free from the under surface, and at times deviating inward or outward from its general alignment. In several cases the deviation outward was sufficient for a small portion of its outer edge to project beyond the outer edge of the main body. Because it seemed to have a practically separate existence, it is referred to here as an Accessory Tectorial Membrane. Its structure, its delicacy, and its position explain the difficulty with which it is distinguishable and suggest that the probable reason it has not been noted before is because none of the investigators using teased preparations happened to obtain pieces of it isolated, extending free and undistorted, in the field of the microscope.

In *shape and structure* this accessory membrane somewhat resembles a long comb, the tapering teeth of which, however, are in the form of a net consisting of two sets of parallel fibers all continuous into the "back of the comb" which is the outer edge of the membrane. The direction of one set of the fibers coincides with the direction of the fibers in that zone of the under surface of the tectorial membrane over which they lie. Thus, this set of the fibers cannot be distinguished when the accessory membrane is in position (Fig. 3). The other set of fibers crosses the first set obliquely, arising at acute angles to outer edge of the membrane and coursing in a decided slant pointing toward the apex of the cochlea. The fibers are embedded in a thin film of transparent matrix of the same character as that supporting those of the

tectorial membrane proper, and it is this matrix that maintains the shape of the accessory membrane and holds the two sets of fibers, and the fibers of each set, in their relative positions.

The inner edge of this membrane consists of nothing but the crossing inner ends of the fibers and is so exceedingly thin that it could not be distinguished at all when lying in position but for the optical effect produced by the obliquely coursing set of fibers. The outer edge (the back of the comb) is thicker than the inner, apparently resulting from a gradual increase in the amount of the supporting matrix. In the outer edge, the fibers of both sets seem to curl upward so as to produce a short abrupt curl in this edge of the membrane with the convex side toward the under surface of the tectorial membrane proper, as indicated in the drawing of the end in Fig. 3.

The question of the *attachment* of the accessory to the main body of the tectorial membrane could not be definitely settled. The accessory membrane was found so delicate that it would not stand manipulation; in more deeply stained preparations it could not be studied in its relations to the main body because of the light being obscured in passing through the whole structure; transverse sections, necessarily from dehydrated and embedded specimens, were entirely impossible, and, in the unstained and lightly stained mounts, if attaching fibers exist, they could not be distinguished in the maze of other fibers present on both sides of their probable locality. From the study made here, only this can be said: If the accessory membrane is attached other than by light surface cohesion to the main body, it is most probably attached along its outer, and thicker, edge. In several of my mounts, the inner edge appeared folded over for short distances as though it had been waving free in the fluids preliminary to the cover glass, while the outer edge retained its normal position as though it had behaved as a hinge. Further, the curled disposition of the fibers in the outer edge suggest that their ends may be continuous into the under surface of the tectorial membrane and that they may be broken, ripped asunder, in cases in which portions of the accessory membrane appear entirely free.

As to its *position*, the accessory membrane lies under the outer zone of the under surface of the tectorial membrane proper and to the outer side of Hensen's stripe. It exists throughout the length of the tectorial membrane.

Like the tectorial membrane proper, it is widest at the apical end and decreases in width toward the end of the basal coil. The decrease

in the width of the tectorial membrane proper occurs chiefly in the decrease in the width of the zone or strip on the outer side of Hensen's stripe. The decrease in the width of the accessory membrane is relatively much more gradual than that of this zone under which it lies. At its greatest width, in the apical turn (Figs. 1 and 2), its outer edge is considerably within the outer edge of the tectorial membrane proper, but its decrease is so much more gradual that by the time the seventh half-turn is reached, the outer edges of the two membranes coincide (Figs. 1 to 5). Also, at the apical end, its inner edge extends not quite to Hensen's stripe, but below, this edge comes to coincide with Hensen's stripe, and, at the basal end, the tips of its fibers may occasionally overlap the stripe. If Hensen's stripe coincides throughout with the line of the enclasp'd phalanges of the rods of Corti, then the accessory membrane can only come in contact with the hairs of the outer series of the hair cells.

Of the illustrations given of transverse sections, Fig. 7 alone shows a structure whose position warrants its being interpreted as a section of the accessory membrane. The structure is naturally attacked severely by the reagents, being very thin and fragile, and distortion renders it unrecognizable and often invisible in sections. One unaware of its existence would never discover it in even the best of sections.

Some of the observations recorded in the literature of the tectorial membrane may refer to this accessory membrane. It is somewhat probable that the irregular, transparent, reticular fringe described by Lowenberg, '64, as existing along the outer edge, and since referred to by some as "Lowenberg's border plexus" and by others as the third or outer zone of the tectorial membrane, may have been nothing more than the displaced outer edge of the accessory membrane projecting irregularly beyond the outer edge of the tectorial membrane proper. Coyne and Cannieu, '85, may have used this in their claim that the tectorial membrane is attached as far over as the cells of Claudius; Dupuis, '94, notes that Lowenberg's border plexus is very irregular and not always present; Von Ebner, '02, in Kölliker's *Gewebelehre*, notes and illustrates it as filamentous; Kishi, '07, considers it an artifact. Hensen, '63; Böttcher, '72; Ferré, '85, and several others since them deny the existence of the border plexus. The latter may have been dealing with more nearly normal conditions. Further, several observers, to be mentioned below, claim filamentous attachments between the under surface of the tectorial membrane and the hairs of the hair cells and

various other elements of the organ of Corti. It is probable that some of these attachments consist of crumpled bits of the distorted accessory membrane, augmented by coagulum filaments. Also some of the descriptions of various lines and markings on the under surface of the tectorial membrane, noted above, may have been dealing with appearances produced by the distorted accessory membrane as well as with crumplings of the peripheral condensation of the main body.

The processes by which the accessory tectorial membrane is developed from the greater epithelial thickening have yet to be worked out. Evidently it is one of the last structures formed, and probably its individual character may be due to its being formed during a period of rapid displacement of the parts.

THE ATTACHMENT OF THE TECTORIAL MEMBRANE.

All the observers invariably agree that the tectorial membrane is attached along its inner thin zone upon the surface of the labium vestibulare. This attachment is developed early in the development and is the line of fixation instrumental in the final course and arrangement of the fibers of the membrane resulting from, first the widening of the greater epithelial thickening and then followed by its retrogression and decrease in width.

Numerous investigators claim other attachments, but there is lack of agreement as to their location. There are to be found in the literature claims for attachment of the under surface of the membrane varying from attachment to the epithelium of the spiral ligament (Corti) and the cells of Claudius (Coyne and Cannieu), all the way across the lamina to attachment upon the inner supporting cells of the organ of Corti (Shambaugh). The majority of the claims are for attachment to the structural elements comprising the organ of Corti alone, especially to the hairs of either the inner or outer hair cells or both. Of the more recent papers, Kishi, '07, agreeing with Böttcher, '69, states that the membrane is connected with the lamina reticularis and with the hairs of both the inner and outer series. Siebenmann, '00, denies connection with the lamina reticularis in either the embryo or the adult. Von Ebner, '02, holds the membrane was attached to the lamina during development, but, in the adult, after the displacement of the parts, this attachment is necessarily lost and the membrane extends free over the spiral sulcus and organ of Corti. Rickenbacher, '01,

thinks, from his studies of the development of the membrane, that it is improbable, *à priori*, for the membrane to float freely in the cochlear duct. He did not carry his studies through the processes of the displacement. Shambaugh, '07, assumes that the membrane is attached to the inner supporting cells and that Hensen's stripe serves as a fascet for this attachment. Kolmer, '07, often found the membrane attached to various of the cells of the organ of Corti, but thinks these attachments were artifacts. As early as 1872 Göttstein described "transparent filaments" extending between the membrane and the inner supporting cells of the organ of Corti of foetal cochleæ, but considered these as remnants of liquefying processes. Hensen, '07, in elaborating a theory for tone perception, assumes and pictures the tectorial membrane as extending free over the organ of Corti so that the hairs may brush against it during the agitations of the endolymph, resulting in auditory stimuli. The hairs have been described as sticking into the under surface of the tectorial membrane.

All the claims for the attachments of the membrane to any portion of the epithelium of the spiral lamina (including the organ of Corti) are based upon appearances presented in sections, and all describe the connections as filamentous. The studies made here tend strongly to the view that the membrane is attached only along its inner side and only upon the labium vestibulare.

(1) During the teasing away of the upper wall of the membranous labyrinth to expose the membrane preparatory to its removal, the outer portion could at times be easily seen under the dissecting microscope to wave upward and downward in response to agitations produced in the fluid with which it was covered during teasing. These movements seemed to occur along its entire course. They occurred within very small arcs and were suggestive of a certain amount of elasticity in the membrane, causing it to retain its horizontal position because of the attachment along its inner zone. If attached to the elements of the organ of Corti, or even to the hairs alone, while individually such attachments would be delicate and easily broken, it is hardly probable that the necessarily great multitude of such attachments would so readily disappear and allow the movements.

(2) Sections of fixed and dehydrated material are but little more suggestive of attachment of the membrane than they are of its being free from the organ of Corti in the adult condition. The membrane is always more or less shrunken and distorted, and these effects of the

manipulation may result either in its being drawn in contact with the organ below or in its being lifted well away from the organ. Sections often show it even pressed upon the organ, but the *majority* of sections show it directed in various angles, entirely free from the organ, and many of the older pictures of it are thus drawn. When caught more nearly in its normal position with its under surface parallel with and near the surface of the organ of Corti, delicate filamentous connections are often apparent, but such connections can be justly explained as brought about by crumplings or abrasions of the fibers in the under surface, or by bits of the very thin accessory membrane coming in contact with the auditory hairs or other elements, the appearance of continuity being accentuated by adhering coagulum filaments precipitated from the albumins and globulins of the endolymph.

(3) From the process of its development, it seem probable, contrary to Rickenbacher, but in accord with Von Ebner, that, *à priori*, the membrane is free from the underlying epithelial structures. During its development it is attached only to the epithelial cells giving origin to it, and since its outer zone acquires its adult position over the organ of Corti only by the recession of the parent epithelium and the consequent displacement of the organ, one must at least assume that, if attachment to the organ exists, it must be developed after the development of both the organ and the membrane. This is hardly probable and, moreover, it is hardly necessary to an explanation of the rôle of the organ in the phenomena of hearing.

ON THE ANATOMY OF HEARING.

It may be said that the tectorial membrane is comparable and analogous to the otolithic membranes of the cristæ and maculæ acusticæ, except that it is neither developed by nor upon cells belonging in the group of special sensory cells with whose stimulation it is concerned, and except, further, that in the higher animals it is not beset with calcareous products.

Lavdowsky, '77, and others, including Ayers, '91, have called attention to the fact that, from the nature of the stimuli, the function of hearing must require three mechanisms: (1) A vibratory mechanism; (2) a regulation mechanism, and (3) a mechanism for the perception of sound stimuli.

Hensen, '63, was the first to advance the idea of the hairs of the hair cells being brushed against the tectorial membrane for the origin

of the stimuli in the perception mechanism. Lavdowsky, Hensen, Nuel and others describe the basilar membrane, in the spiral lamina, as being composed of independent, radially disposed fibers. This and the further observations that the basilar membrane is considerably wider (and therefore its fibers longer) at the apex than in the basilar coils of the cochlea, led Helmholtz to advance the theory of hearing which bears his name. This theory involves the sympathetic vibration of the different "fibers" of the basilar membrane in resonance with the atmospheric waves as transmitted to the endolymph by the tympanic membrane and auditory ossicles, and it assumes that the vibrations of those fibers involved by a given stimulus cause the hairs of the hair cells overlying the fibers to rub upward against the tectorial membrane. It thus assumes, further, that the cochlea has the power of analysis of sound or that the perception of tone is mediated by different parts of the cochlea. Ter Kuile, '00, in a purely theoretical paper dealing with the transmission to the hair cells of energy from the supposedly vibratory basilar membrane, shows that the hairs do not rub against the tectorial membrane, but strike its under surface vertically. Ewald, '99 and '06, accepts the idea of the basilar membrane and experiments with thin rubber membranes placed under fluid, finding that vibrations may be induced in them in response to atmospheric waves. In fact, with but two exceptions that I know of, all of the investigators of physiological acoustics since Helmholtz have accepted the assumption that the basilar membrane is the vibratory mechanism, and in their writings have merely put forth various modifications of the original conception. The two exceptions are Kishi, '07, and Shambaugh, '07, both of whom assume that the tectorial membrane is the vibratory mechanism, both claiming the power of resonance in it, as will be mentioned below.

As noted by Gray, '00, the explanations of hearing as now offered may be divided into two general theories: (1) The Resonance Theory, suggested by the work of Hensen, Nuel and others, propounded and elaborated by Helmholtz and variously modified ever since in its application to the cochlea by different investigators, and (2) The Telephone Theory.

The latter theory was suggested by Rinne in 1865, supported by Voltolini in 1885, more fully elaborated by Rutherford in 1886, modified by Waller in 1891, and further modified by Max Meyer in 1898. It assumes that the transformed sound waves as imparted to the endolymph affect the structures of the cochlea as a whole.

Rutherford first advocated that all the hairs of the hair cells vibrate equally to every note and that the nerve impulses thus aroused are mere vibrations similar in frequency, amplitude (intensity), and character (quality) to the sound vibrations, and that, therefore, sound analysis is wholly cerebral.

Waller and Meyer assumed that the transformed sound vibrations in the endolymph act upon the basilar membrane as a whole, repeating the vibrations of the tympanic membrane. Meyer supposes that each wave, as it passes up the scala vestibuli, presses the basilar membrane downwards and does this just in the proportion in which amplitude of the wave is not decreased by the resistance it meets in passing upward toward the apex. Thus each wave will produce irritation of a certain number of hairs and the intensity of the irritation will diminish as the amplitude of vibration is diminished by resistance; and therefore a wave of greater amplitude will involve a greater extent of the basilar membrane, and of auditory hairs, than a wave of lesser amplitude. Certain waves, sooner than others, in passing up the scala will become too faint to sufficiently press down the basilar membrane. According to this view, pitch depends upon vibration frequency or the number of stimuli per second, while intensity depends upon the total number of nerve endings irritated. It allows a certain amount of analysis in the cochlea.

The telephone theory differs from that of Helmholtz in that it assumes that the basilar membrane, instead of certain of its fibers vibrating in sympathy with given notes, vibrates as a whole to every note in so far as the original amplitude of the wave and resistance to propagation will allow, and that the auditory nerve fibers transmit to the brain stimuli of frequencies and intensities of the note or notes concerned. The resonance theory supposes analysis of sound by the cochlea; while the telephone theory supposes distinctions of sound, perception of tone, etc., to be accomplished by the brain, made possible of course by the varying quality of the stimuli in the peripheral organ, the cochlea. The resonance theory of necessity requires that each fiber of the basilar membrane and each arch, or pair of rods, of the organ of Corti be able to vibrate or move upward and downward independently.

Numerous objections to the resonance theory have been made, both physiological and anatomical. Of the physiological objections, two may be cited as examples of those the obviation of which has been recently undertaken by adherents of the resonance theory.

(1) A mixture of notes of closely approximate beats, even having varying intensity, cannot be analyzed by the auditory apparatus; rather, only the maximum stimulus in the mixture is perceived. Gray, '00, attempts to obviate this with a modification of the resonance theory, in which he compares the sense of hearing with that of touch. He supposes that the basilar membrane does not vibrate as to its individual fibers, each in response to a given note, but rather in areas of its extent for each note, and thus he assumes that the mixture of approximate notes involves a given small area of the basilar membrane from which only the maximum stimulus is appreciated by the brain, all others of the mixture being neglected, just as when a small area of the skin is stimulated by a very bluntly pointed instrument and the "mind only pays attention" to the point of maximum stimulation; or, just as when two points on the skin, close enough together, cannot be distinguished from a single point when stimulated simultaneously. Evidently this modification also obviates the requirement of the resonance theory that each arch or pair of rods of the organ of Corti, as well as each fiber of the basilar membrane, must be able to move or vibrate independently.

(2) It is generally conceded that sensations of "noise" as distinguished from the perception and analysis of tones cannot be adequately explained by the resonance theory. Hensen, '07, has recently put forth an elaborate modification of this theory in which he tries, among other things, to account for this inadequacy. It is unnecessary here to discuss his ingenious paper further than merely to state that he retains the assumption that the basilar membrane is composed of fibers with the power to vibrate individually, allowing that probably several adjacent fibers, being of approximately the same length, may vibrate together with the respective note. To do this, he finds it necessary to add the assumption that the cochlea mediates only musical tones, and he calls it the "musical organ." This makes it needful for some other structure to mediate sensations of noise, etc., and for this he finds the *cristæ* of the semi-circular canals and the *maculæ acusticæ* adequate.

While, strictly speaking, the two objections or inadequacies cited are anatomical as well as physiological, there are some which may be considered more purely anatomical, and therefore physical, objections to the resonance theory.

From the nature of available information, the intangibility of the apparatus, it has been the rather common custom in discussing the physiology of hearing, to first assume the existence of anatomical

characters and then to base explanations of the phenomena, many of which may be largely psychic, upon the results of the application of excellent mathematics and physics to the structures assumed. The resonance theory must depend essentially upon the character it assumes for its vibratory mechanism. Therefore the anatomical objections to it must deal with these assumed characters. Among these objections may be enumerated the following:

(1) Supposing the basilar membrane to be composed of individual fibers capable of vibrating independently, its environment in the lamina spiralis is such that its vibration in response to many of the transferred sound waves, and certainly with any degree of sensitiveness, seems very improbable. The basilar membrane, the fibrous portion of the spiral lamina, is closely invested by two continuous layers of tissue on each of its sides. On its tympanic side, there is first the layer of endothelium lining the scala tympani (see Fig. 7), and second, the much thicker layer of epithelioid cells which contains further, that anastomosing plexus of blood vessels known as the vas spirale, which is only approximately a single vessel in the end of the basal coil, but which elaborates with increasing complexity toward the apex of the cochlea. On its vestibular side, it is covered first by a "homogeneous" and well developed membrana propria of the neuro-epithelium (see Von Ebner, loc. cit., page 927, Fig. 1450), and lastly, the whole is covered by, or supported by, the neuro-epithelium including that comprising the thick organ of Corti. Outside the animal body, structures of such relative thickness adhering throughout to a system of strings would effectually damp at least their resonant vibration. Further, if the basilar membrane were vibratory in the degree supposed by the theory, the circulatory pulsations in the vas spirale would very probably tend to at least confuse agitations produced by resonant vibrations of its directly overlying fibers, even with the habitual neglect by the auditory apparatus of the blood pulsations themselves.

(2) The resonance theory requires, and, truly, the earlier pictures of it assume (Neuel, '72, for example), that the basilar membrane be composed of a single set of radially disposed fibers. Ayers, '91, describes it in man as composed of four layers of fibers, three of which run radially from the lamina spiralis ossea into the ligamentum spirale to terminate at the base of the stria vascularis, and the fourth, a thin layer, running at right angles to the other three. If these four layers exist, there is nothing to be observed in either sections or teased prepa-

rations, indicating that they do not lie in direct contact and probably adhere to each other, and such an arrangement must tend to interfere with sensitive resonant vibration.

(3) Assuming that any or all parts of the basilar membrane proper consist of independent fibers, the question may be asked whether the membrane is capable of being thrown into vibration at all by sound waves. Ewald, '99, constructed a model in which he was able to so stretch a very thin rubber membrane that he succeeded in getting pieces as small as 0.5 mm. broad to vibrate when suspended in water by sound waves in the air. The recent measurements of the assumed vibratory width of the basilar membrane by Kolmer, '07, show this width to vary from only about 0.2 mm. (168 microns) in the basal turns to only 0.3 mm. (304 microns) in the apical turns. Shambaugh, '07, thinks that Ewald's model falls far short of proving that the basilar membrane, which he describes as being "much shorter, thicker and more rigid" than Ewald's rubber membrane, vibrates in response to sound waves transferred to the endolymph, and he mentions the fact that Helmholtz himself appreciated the doubt as to whether fibers so short as the width of the basilar membrane can be thrown into vibration by sound waves. Certainly its relative width and thickness, coupled with objections 1 and 2 above, make its vibration reasonably doubtful. Shambaugh describes the basilar membrane, in his preparations of the cochlea of the pig, as becoming so thick and rigid in the basal coil, "a considerable distance" from its basal termination, as to preclude the idea of its being a vibratory structure. In one specimen he found complete absence of the basilar membrane in the basal end of the coil, but instead the perfectly formed organ of Corti, with its tectorial membrane, rested upon a direct junction of the crista of the spiral ligament with the labium tympanicum of the spiral limbus. In another specimen, he found the perfectly formed organ of Corti resting upon a solid bony plate bridging the width between the lamina spiralis ossea and the outer wall of the cochlea. Such absences of the basilar membrane under a completely formed organ of Corti, suggest that it is not essential to the sense of hearing either as a structure vibrating in accordance with the resonance theory or in accordance with the telephone theory.

(4) To the above anatomical objections to the resonance theory may be added evidence that the basilar membrane is not composed of individual and independent fibers at all. The idea of resonant vibration as implied in the theory demands the existence of such. Some of the

older papers illustrate the fibers as separately distinct, and even counts of them are claimed, varying from 15,000 to 25,000. And measurements of their thickness have been given, varying from 1.5 to 2.3 microns. One of the most recent modifications of the theory, that of Hensen, is founded wholly upon the existence of separate fibers.

After becoming convinced by micro-chemical tests that the basilar membrane consists of white fibrous connective tissue, some horizontal sections of pig cochleæ were prepared here and stained by Mallory's method for white fibrous tissue. The sections were necessarily cut quite thin in order to get areas containing the basilar membrane alone, exclusive of its coverings, so that its actual construction might be studied. Fig. 11 is an attempt to show the appearance of flat sections of the membrane as brought out by Mallory's method. From these preparations, and afterwards even from the pieces obtained from the teased cochleæ stained with fuchsin, it became evident that the basilar membrane is nothing more nor less than a thin flat tendon, and that its so-called "fibers" correspond exactly to the well known fiber-bundles in tendon fasciculi, being by no means independent of each other even as bundles. Each bundle is, of course, composed of multitudes of fibers so fine that, even under oil immersion, one can never separate them with certainty as to the divisional units of the structure, much less measure them. The bundles (fibers of the basilar membrane), just as the bundles in a tendon fasciculus, are abundantly connected or continuous with each other by myriads of fine, silver-like collateral fibers inserted at all conceivable angles, the majority slanting in the direction of the bundles. In other words, the basilar membrane, instead of being formed of independent fibers, is a sort of a feltwork or modified reticulum of interwoven fibers, the general direction of most of which is radial to the axis of the cochlea, but withal, the resulting structure is such as to wholly preclude the idea of the independent vibration of adjacent fibers. True, in itself, it does not preclude the telephone theory of hearing. This radial or parallel tendency is no doubt due to the fact that, as the cochlea grows, the basilar membrane is developed from the mesenchyme under tension, just as tendons are, and thus it becomes stretched taut as the floor of the ductus cochlearis and merely serves for the support of the neuro-epithelium in the position for its functioning. The membrane differs from an ordinary flat tendon in the distribution of its nuclei. These, instead of being arranged throughout in the varying columns of tendon cells, are absent under the region of the organ of Corti. As

shown in Fig. 11, they appear between the bundles, in a belt near the beginning of the spiral ligament in the outer edge, and, in the inner edge, the nuclei of the labium tympanicum encroach but little further than the foramina nervosa of the habenula perforata. The membrane no doubt grows at the edges, and the midregion being oldest, its cells are probably exhausted.

(5) The resonance theory, with its assumption of individual fibers in the basilar membrane, as mentioned above, carries with it the idea that the different elements of the organ of Corti, including the arches, or pairs of rods of Corti, must be capable of moving separately. Not only do anatomists agree that the neuro-epithelium forms a continuous membrane throughout the cochlea, but the component cells of the organ of Corti are easily seen to be intertwined and interwedged among themselves. Further, the rods of Corti's organ are probably more firmly adherent to each other in their series than are any other elements of the organ. This may certainly be said of the series of outer rods. In teasing the cochlea for the tectorial membrane, I found in several preparations when mounted, considerable extents of the outer rods adhering to each other, appearing on the flat as a grill-work, and wholly free from other elements of the organ. From one specimen, fixed and decalcified with Perenyi's fluid, which has a macerating effect upon tissues unless followed by washing in alcohol, I succeeded in obtaining a tier of the outer rods more than 5 mm. long and so firmly coherent that it floated about in the teasing fluid and withstood manipulation sufficient to mount it entire. Occasionally short tiers were found in the mounts of the tectorial membrane, sometimes adhering to its edge and lying out flat and otherwise free so as to be easily studied. Fig. 12 represents an end of one of the latter, and was chosen because it had been torn from the series in such a way that it afforded an excellent illustration of the shape, interrelations and character of the outer rods. This preparation was fixed in Zenker's fluid. The inner rods are manifestly not so resistant as the outer, for, while distorted scraps and fragments from their dissolution were found in the mounts, tiers of them alone were never found intact. The ends of the phalanges of the outer rods often showed frayed bits of the phalanges of the inner adhering to them. All appearances indicated, however, that the rods of Corti, both inner and outer, must be quite firmly coherent both the inner to the outer and to each other in their series.

(6) The resonance theory applied, as it has been from the beginning, to the basilar membrane, requires not only that the rods (and the other

elements) of the organ of Corti resting upon the vibratory fibers should be able to move up and down independently, but it is usually inferred that both rods of the arch must rest upon the basilar membrane throughout the extent of the cochlea. In all of my vertical sections of the cochlea of the pig, and Shambaugh notes the same in his preparations, usually throughout the basal coil the feet of the inner rods of Corti do not rest upon the supposedly vibrating basilar membrane, but reach over to stand upon the thicker edge of the labium tympanicum. Ter Kuile, '00, recognized this, but made use of it to assume that contact of the hairs of the hair cells against the tectorial membrane during stimulation is not in a vertical direction, but occurs as a lateral, inward brushing motion, the outer rods alone being moved by the vibrations of the membrane while the inner rods merely act as fulcrum in producing the brushing motion. This assumption gains nothing but an increase in the complexity of the resonance theory, since, above the basal coil, the feet of both rods do rest upon the supposedly vibrating portion of the basilar membrane. It is fairly well indicated from clinical evidence that the nerve fibers from the basal coil mediate sensations of notes having the higher pitch, and ter Kuile's assumption merely adds the anatomically improbable condition that the neuro-epithelium is agitated by these higher notes in a different way than it is by the lower notes supposedly affecting the coils toward the apex.

(7) To the anatomist, given structures in a given species of animal are strikingly identical in character. For example, all cochleæ of normal individuals of a given species are strikingly alike in all details.

The power of tone perception and tone distinction by different individuals is not as constant and uniform as would be expected with the apparently constant anatomical mechanism for the mediation of sound. Individuals without special training (habits) differ markedly, and it is well known that the "trained ear" in any special direction shows a far greater power of analysis of sound and distinction of smaller differences of tone than the untrained. Most of the investigators of the physiology of hearing, including Helmholtz, recognize this and usually try to obviate it by assuming modifications in the mechanism of the cochlea.

More probably, as in all the other senses, the whole question of analysis of stimuli and the power of finer perception, inherent or acquired by education, must be transferred from the peripheral or receptive mechanism to the central nervous organ. Just as in touch or smell, or sight, so in hearing, all being physiologically similar, the variety of

the sensation experienced depends only upon the quality and intensity of stimulus applied to the peripheral nerve endings. The specialization of sensation is doubtless with reference to general groups only, and this specialization dependent upon the locality of the cerebrum to which the impulses aroused by external stimuli are borne. The optic nerve, stimulated by touch (pressure) conveys impulses which are interpreted as sensations of light; the acoustic nerve, stimulated by touch (tumors, etc.) gives rise to sensations of sound. And it is very probable that within the general groups, most manifest in touch, identical nerve terminations acted upon by external stimuli varying in quality, give rise to sensations varying according to the quality of the stimuli.

It is considered neither possible nor necessary in this paper to consider fully the numerous modifications and additions to the resonance theory. Many of the papers are merely attempts to explain away the physiological (and psychological) difficulties and anatomical objections to the theory as applied to the basilar membrane and the action of the organ of Corti. It seems to the author that these objections, taken collectively, are such that neither the resonance theory nor the telephone theory as applied to the basilar membrane are any longer tenable.

The fact has been frequently noted, and especially by ter Kuile, that the tectorial membrane, in all species, is always entirely coextensive with the organ of Corti, and is always sufficiently wide to cover the hair cells, whether these are in linear series on either side of the rods, as in mammals, or whether they are scattered throughout the entire epithelium of the organ of Corti, as in birds and reptiles. Since the same cannot be said of the basilar membrane, it seems very probable that the tectorial membrane is more essential to the sense of hearing. Further, because of its shape, its more logical position, above the auditory hairs, and its far more delicate sensitiveness, the tectorial membrane seems much better qualified to serve as the vibrating mechanism than the basilar membrane.

Siebenmann, '00, seems to have been the first to suggest that the tectorial membrane is the structure agitated by sound waves, though the inference drawn by Ayers, '91, amounted to something similar. Quite recently Kishi and Shambaugh, realizing the anatomical disqualifications of the basilar membrane, have attributed the power of resonance to the tectorial membrane.

Kishi, '07, after citing four anatomical objections, concludes that the basilar membrane is not qualified for the vibrating mechanism of either

the resonance theory or of any other theory of hearing. He substitutes the tectorial membrane as being more suited to the purpose, and then, from some rather distorted sections of the cochlea (illustrated with photographs), he assumes that the tectorial membrane is attached along its outer edge to the lamina reticularis of the outer supporting (Hensen's) cells of the organ of Corti, and thus claims that it is held down firmly upon the organ and always at right angles to the auditory hairs. Being also firmly attached along its inner edge, as all admit, Kishi describes and diagrams it as a membrane stretched tautly over the organ from the labium vestibulare of the spiral limbus to the lamina reticularis of Hensen's cells. He then assumes that the length of the fibers composing the membrane corresponds throughout to the breadth of the membrane in the respective turns of the coil. Admitting that his assumed absolute length of the fibers (the breadth of the membrane) cannot be determined because of shrinkage and distortion produced by the technique, he finds, from measurements of the width of the membrane in his sections, that the relative length of the fibers in the apical region is at least three times greater than those of the basal coil. Therefore he assumes that the fibers have different spans, vibrating lengths, in the different regions of the cochlea with all conceivable variations between the longest in the apex and the shortest in the basal end, and thus it is to be inferred that the tectorial membrane is a resonant structure composed of fibers capable of sympathetic vibration to all sound waves of lengths between and including those which may affect its longest and shortest fibers. He realizes that the fibers course obliquely across the membrane, slanting toward the apex, and that, therefore, their actual lengths are greater, especially in the apical region than the width of the membrane as seen in radial sections.

Against Kishi's conception of the tectorial membrane, three objections may be urged:

- (1) From the processes of development of the membranes, it is very improbable, if not impossible, that any of its fibers in any region extend across the entire breadth of the membrane.

- (2) From the processes of its development, it is probable if not certain that the great majority of the fibers are attached at neither of their ends, but merely lie embedded in the transparent matrix.

- (3) From the studies made here and by others mentioned of preparations as nearly normal as possible, it is concluded that the tectorial membrane has but one attachment in life, namely, its inner edge upon the

labium vestibulare of the spiral limbus. In the apical turn, at least, its outer edge cannot be attached to the lamina reticularis, for this edge in the first half-turn (Fig. 6) may extend into the space of the ductus cochlearis a distance of nearly half its width beyond the organ of Corti.

Shambaugh, '07, urges the objections, accredited to him above, against the possibility of the basilar membrane being a resonance mechanism, and, from appearances in some of his sections, concludes (1) that the tectorial membrane does not lie free in the endolymph over the organ of Corti, but is attached along Hensen's stripe to the inner supporting cells of the organ; (2) that "the hairs of the hair cells project normally into the under surface of the tectorial membrane"; (3) that "the size of the membrana tectoria near the apex of the cochlea is many hundred times its size near the beginning of the basal coil"; and (4) he concludes further that, in structure, the tectorial membrane consists of "an immense number of delicate lamellæ taking their origin from the portion of the membrane which rests upon the labium vestibulare." From these conclusions and the conclusions generally accepted as to the relation of the tectorial membrane and the hair cells to stimulation of the acoustic nerve terminations, he advances a theory that the tectorial membrane consists of a series of resonators (the lamellæ) which are capable of responding to the most delicate impulses passing through the endolymph, claiming that the great variation in size of the membrane from one end to the other, suggests the possibility that, by acting the part of a resonator, it is capable of responding in different parts to impulses (tones) of different pitch. Shambaugh, in applying his theory, claims with reason that all the observations by Helmholtz and his followers supporting their resonance theory apply more readily to the tectorial membrane as a resonator than to the basilar membrane, and proceeds to explain the pathological phenomena of "*tone islands*," "*diplacousus binauralis dysharmonica*" and "*tinnitus aurium*" on the basis of a resonating tectorial membrane.

Some of the observations both made and cited in this paper are not in accord with the premises from which Shambaugh's theory follows. In the first place, it is considered probable that the tectorial membrane does lie free over the organ of Corti and that the auditory hairs do not project into it. In the second place, it is not a lamellated structure. Ever since 1869, when Böttcher teased portions of it and found them to contain fibers, the fibrous structure of the membrane has been conceded by all who have studied it with reference to its structure. Sections in

different planes, as made by Coyne and Cannieu, '85, and here (Fig. 9), indicate clearly its fibrous nature.

It is not the intention of the paper to elaborate another theory of hearing and to enter into a necessarily prolonged application and defense of it. Leave is asked to merely suggest a modification of a theory already advanced, namely an application to the tectorial membrane of the telephone theory, heretofore applied exclusively to the basilar membrane. Some of the considerations upon which this suggestion is based are the following:

(1) The prevailing acceptation is that the cochlea is the peripheral organ of the auditory apparatus, and that the construction of this organ is such as to be especially capable of serving, in conjunction with the central nervous system, in the analysis of sound.

(2) From their anatomical relationship, it is conceded that auditory impulses are aroused in the acoustic nerve through the mediation of the hair cells of the organ of Corti about which they terminate.

(3) It is usually conceded and here accepted that the hair cells are stimulated through the agitation of their hairs, but that the hairs are neither suitably constructed, long enough, nor vary sufficiently in length to be themselves acted upon selectively by the sound waves as transferred to the endolymph.

(4) All the recent conceptions of the process of hearing accept the idea that the hairs of the hair cells are agitated by contact with the under surface of the tectorial membrane, either by brushing against it or by perpendicular impingement, produced either by vibrations of the basilar membrane below or movements of the tectorial membrane above.

(5) The numerous physiological and anatomical objections to it are considered sufficient to render untenable the idea that the basilar membrane is the vibrating mechanism either of the kind demanded by the resonance theory or in accord with the telephone theory.

(6) While experimental investigation has not yet been able to ascertain the exact form of the wave motion in the endolymph of the cochlea, it has been determined by observation of the action of the tympanic membrane and auditory ossicles that the force of the motion produced in the tympanic membrane by the atmospheric sound waves may be increased thirty times in the transformation and transference of the motion to the basis of the stapes and the membrane of the fenestra vestibuli, and that the amplitude of the atmospheric waves may be reduced as much as seventy-six times (or more). In this transference

of the energy to the endolymph, the reduction of amplitude, as well as the increase of the force, depends not only upon the lever arrangement of the ossicles, but upon the tensility of the tympanic muscles and the pressure of the air in the tympanic cavity. Therefore, the wave motions imparted to the endolymph by the basis of the stapes *correspond* to the atmospheric sound waves, of which they are transformations, but *resemble* them only in frequency of vibration. The quality of the motion imparted to the endolymph depends of course upon the quality or form of the atmospheric waves acting upon the tympanic membrane, but the quality of the two may not be identical in detail. While the canals of the cochlea are probably entirely filled with endolymph normally, and under a pressure which depends largely upon the blood pressure of the different conditions of the body, the membrane over the fenestra cochleæ (rotunda) and the direct continuation of the endolymph of the cochlea with that of the vestibule are considered sufficient to allow compensation for the incompressibility of the fluid and to allow propagation of the motion in the form of true compression waves. Pressure applied by the stapes to the endolymph in the cochlea may not only be compensated or relieved by the membrane below and by the ductus reuniens connecting it with the sacculus, utriculus and semi-circular canals, but, by way of the sacculus, such periodic pressure may be compensated through the ductus endolymphaticus into the cranial cavity. Furthermore, the layer of softer tissue between the epithelium lining the scalæ and the solid walls of the bony labyrinth may aid in maintaining the form of the wave motion. Therefore there is reason to conclude that the motions imparted by the stapes at the basal end of the cochlear coil are propagated in the endolymph toward the apex of the cochlea in the form of compression waves, however short, with longitudinal direction and transverse vibration. The waves are very probably similar in many respects to pulse waves.

(7) That the agitation of the hairs of the hair cells is brought about through the activity or actual movements of the tectorial membrane induced by the wave motion transferred to the endolymph is suggested by the peculiarities of that membrane.

(a) It is in the logical position for such action. It lies above the hair cells adjacent to the portion of the endolymph to which the waves are first imparted by the basis of the stapes. The basilar membrane is situated below the tectorial and is both covered and obstructed.

(b) In the mammalia and in all animals possessing it, the tectorial

membrane is entirely coextensive with the organ of Corti. The basilar membrane as such is not entirely coextensive.

(c) From its specific gravity, its evident lateral elasticity and from its most remarkable transverse flexibility and sensitiveness to agitations in a fluid surrounding it, the tectorial membrane appears to be far more admirably qualified to serve as the vibrating mechanism than does the basilar membrane.

(d) From the evidence that the tectorial membrane ~~is~~ attached along but one of its sides; from the fact that, even if it were attached along both sides, none of its fibers are coextensive with its width; from the fact that it is so constructed that relatively very few of the fibers, even if vibrating, can in any way come in contact with the hairs of the hair cells, and from the fact that the great majority of its fibers are evidently attached at neither of their ends, it is very improbable that the membrane is capable of acting as a sympathetic resonator.

(e) In addition to its suggestive consistency and structure, the tectorial membrane is so shaped and proportioned as to suggest that it may act with reference to vibrations in the endolymph in a way by which the peripheral components of the phenomena of hearing may be explained; namely, the membrane may be acted upon as a whole, the extent, region, amplitude and quality of its vibrations depending upon the force, frequency, amplitude and quality of the vibrations acting upon it.

From the various pathological phenomena, observation of which have been followed by post-mortem examinations of the cochlea, it is quite generally accepted that sensations of the higher pitches are mediated by the structures of the basal coil of the cochlea, and from this it has been assumed, naturally, that the sensations of lower pitch are mediated by the apical coil.

The tectorial membrane is narrowest and thinnest in the basal coil and gradually increases in both width and thickness to acquire its greatest proportions in its apical end. Being attached along its inner edge throughout, it must be affected by sound waves in the endolymph very much as a very flexible ribbon so attached would be by agitations running parallel with its length in a fluid in which it floats.

The extent to which the tectorial membrane can be agitated must depend (1) upon the energy of the wave motion, or upon the extent and point at which the wave motion in the endolymph is neutralized by overcoming the inertia of the fluid and by the resistance offered by the

walls of the cochlea, and (2) upon the breadth and thickness of the membrane and thus upon the extent to which the wave energy is exhausted in overcoming the inertia of the membrane itself.

That notes of higher pitch or greater vibration frequency are more apt to produce vibrations in the thin, narrow, basal coil of sufficient amplitude to stimulate the auditory hairs than they are to produce such vibrations in the apical coil is considered probable for the following reasons:

(1) The thin, basal end of the membrane lies nearer the fenestra vestibuli (ovalis) or the point at which the waves are imparted to the endolymph. Of sounds of equal intensity, or amplitude of vibration, but of different pitch, those of higher pitch or greater vibration frequency are sooner overcome by the resistance of the medium (do not travel so far) as those of lower vibration frequency. In the atmosphere, sound waves of high frequency are damped out before those of low frequency and their speed of transmission continuously decreases as they become fainter. This damping out must occur much more quickly in a medium like the much more viscous endolymph. Therefore it is possible that sound waves of the highest perceivable pitch may affect only the end of the basal coil of the tectorial membrane and be damped out wholly before reaching the upper coils, or at least to such an extent as not to agitate the upper portions of the membrane sufficiently for stimulation of the hair cells.

(2) The natural vibration period of the thin, narrow strip is of greater frequency than that of the thicker wider strip. It is possible to subject a strip of material to vibrations of such frequency, either above or below its natural vibration period, that it will not vibrate at all or vibrate weakly or irregularly. It is probable that no portions of the tectorial membrane, when subjected to sound waves transferred to the endolymph, will undergo vibrations of sufficient excursion to impinge upon the auditory hairs except those portions whose natural periods correspond to the vibration frequencies of the waves affecting the endolymph. Portions adjacent to these, having approximately the same natural periods (thickness and width), would of course be also affected, but to a degree decreasing as the distance from the portion most affected increases. Or, again, the effect of loading a vibrating body is to lower its vibration frequency or pitch. If the body be of uniform proportions and the load be distributed uniformly, the vibration frequency of all its components will be lowered; if the load be placed at one part of the

body, one of the resulting complications will be a lowering of the vibration frequency of that part. Should the tectorial membrane be considered a vibrating body carrying a load so distributed as to gradually increase toward its apical end, then its vibration period or frequency must decrease as this end is approached. Therefore, it is possible that the thin, narrow basal coil of the tectorial membrane may be sufficiently affected by waves of high frequency to stimulate the auditory hairs when other portions of the membrane are not. Several waves, of course, may pass in a medium simultaneously in the same direction.

This idea suggests a sort of resonance quality in the tectorial membrane when the latter is considered as a whole, and thus it is not fully in accord with the idea originally suggested in applying the telephone theory to the basilar membrane. It is slightly analogous to some of the features of Waller's and Meyer's modification of the telephone theory.

(3) The natural consistency of a strip attached along one edge determines in considerable measure the extent and form of movements induced in it by wave motion in the medium surrounding it. The basal end of the tectorial membrane, being narrower and thinner, though of the same material, is more flexible than the end at the apex. Therefore, it must offer less resistance to waves of high frequency (is more easily crumpled into abrupt and frequent folds) than the thick apical end. The viscosity of a vibrating body, while it may affect the vibration frequency (pitch) but little, aids materially in causing the amplitude of vibration, the excursion or intensity of movement of the body, to gradually decrease and dwindle away as the waves pass along the body. It is therefore possible that waves of high frequency are capable of throwing the thin basal coil of the tectorial membrane into waves of considerable excursion or amplitude, while, as they pass along toward its apical end, they may be gradually absorbed in overcoming the inertia of the membrane; first, becoming too faint to throw it into vibrations, or folds, of their frequency and of sufficient amplitude to agitate the auditory hairs below, and finally, as the broad, thick end is approached, a region is reached in which the waves of high frequency wholly dwindle away.

In the same way, for the above reasons, it may be suggested that waves of lower frequency than those which sufficiently agitate the basal end of the membrane only, can, according to their frequency or length, affect respectively the remaining regions sufficiently to stimulate the auditory hairs, because such longer waves travel farther in the given medium, are less rapidly overcome by friction of the walls of the scala

of the cochlea, and because the broader and thicker portions of the membrane probably can be thrown into vibrations by the waves of lower frequency. In other words, the vibrations of higher frequency are more rapidly absorbed and dwindle away in passing along the membrane, while waves of greater length or lower frequency may throw the thicker portions of the membrane into undulations of sufficient amplitude for impingement upon the auditory hairs. Thus the first half-turn of the cochlea would be a portion of the peripheral organ of the auditory apparatus which is thrown into activity only by sound waves of the lowest frequency to which the mechanism is capable of reacting.

Aside from the possibility that the different widths of the tectorial membrane possess different natural vibration periods and therefore may exercise a sort of synchronous selection or resonance with reference to the waves passing in the endolymph, there is nothing in the above suggestions to claim it improbable that the thin, basal coil is not made to undulate by waves of low frequency also. It very probably is, and under the following conditions:

There is little information available as to the properties of sound waves traveling in a substance whose elasticity is not the same in all directions. It is known that in strips of wood the waves travel more rapidly, are less impeded, in the direction of the fibers than across them. The tectorial membrane is most elastic in the direction of its fibers, that is, it is more resistant to stress applied transversely to them. It is exceedingly flexible and sensitive to motion applied transversely to its long axis. Such motions are, in the main, parallel to the direction of its fibers and thus can meet less resistance from them. Since, as shown above, the fibers are not so arranged nor so attached as to act as a system of resonators, and since the membrane is attached only along one side instead of at each end or along both sides, it is very probable that it is largely a passive structure. Attached along its inner edge and held in its position over the organ of Corti by its elasticity, it extends, suspended in the endolymph and subject to be acted upon by whatever motion may be imparted to the latter. Sound waves transferred to the endolymph by the stapes at the fenestra vestibuli must travel along the membrane from basal end to apex with excursions of amplitude transverse to its long axis and thus in the direction which may bring into play its remarkable flexibility. Waves of a given frequency of vibration will affect corresponding vibrations in the membrane to just that extent and amplitude to which they are not damped

out by the endolymph and resistance of the walls, and not absorbed in overcoming the viscosity and bulk of the membrane itself. The waves of lowest frequency, or greatest length, may produce corresponding undulations in the *entire* membrane; waves of the highest frequency may produce in the thinner, and therefore most flexible, end of the membrane *alone* corresponding undulations of sufficient excursions for the necessary impingement upon the auditory hairs. Undulations of high frequency would result in a greater number of impingements per unit of length of the organ of Corti than would waves of low frequency, and thus both the nature and the locality of such stimulation would be different. Waves of higher amplitude, or intensity, would produce impingements of greater intensity and thus give sensations interpreted in degrees of intensity.

Functioning in this way, the peripheral organ of the apparatus is functionally as well as morphologically comparable to the so-called otolithic organs, the *cristæ* and *maculæ acusticæ*. And, further, it is comparable with the other organs of special sense. The varieties of optic sensations, for example, depend upon the intensity and quality of the stimuli, that is, upon the number and variety of waves of light impinging upon a unit area of the retina. The various sensations obtained by touch depend upon the number, intensity and quality of the stimuli applied to the skin. Differences in quality of stimuli at the periphery are perceived and interpreted as differences by the central nervous organ. A number of stimuli applied to a unit area of the skin gives rise, within the possibilities of skin-innervation, to a different sensation or interpretation than does a single stimulus applied to that area. The same stimuli applied with different intensity give rise to interpretations of different intensity. So, in general, for taste and smell, all being dependent upon contact, whether the energy applied be simply mechanical or more strictly chemical.

In the auditory organ the stimuli arousing the sensations are thought to be mechanical. The greater numbers of stimuli applied to unit areas of the organ of Corti result from waves of high frequency and give rise to a sensation interpreted and named by the central nervous organ as high pitch. It happens that the region of the cochlea anatomically adapted for mediating sensations of highest pitch is its basal coil. Conversely, smaller numbers of stimuli applied to the unit area are interpreted as low pitch, the stimuli from waves of the lowest frequency being distributed most sparingly, but throughout the extent of the cochlea,

including the basal coil. Greater amplitude would mean intensity of impingement and interpretations of intensity of sound. Physical reinforcement of wave motions would mean reinforcement of tones; quality of impingement upon the auditory hairs would mean quality in the sensations as interpreted; the number of a given variety of stimuli applied to the unit area of hair cells would determine the predominant variety of the sensations resulting.

If the *accessory tectorial membrane* described in previous pages of this paper should prove to be a true and constant structure, it would be considered capable of separate vibration. Varying slightly in width, being narrowest at the basal end, this membrane suggests a considerable increase in the possibilities of function of the cochlea. It would undulate in accord with waves in the endolymph too faint to agitate the main body of the membrane at all, while its vibrations would be subject to the same conditions and would vary much as those of the main body. With waves of greatest amplitude it would act in conjunction with the main body. It is interesting to note that from its position it would act alone, only upon the outer and wider series of the auditory hairs.

In all the preparations showing the coherent series of the outer rods of Corti's organ, an interesting interrelationship of the rods was suggested. As seen on the flat, the shafts or slender mid-portions of the rods invariably showed a tendency to be grouped (Fig. 12). From those preparations in which the locality of the coil could be determined, this grouping seemed to be different in different regions. In the first turn of the organ of Corti, the shafts were grouped in twos and threes; in the second turn (Fig. 12) they were grouped in threes and fours; in a longer strip of them, fully five millimeters, which, during the teasing process, was seen to float out from the region of the fifth turn, the shafts were arranged in groups of from five to eight. None were obtained as coming from the basal coil.

We have no information as to whether or not the rods stand in this relation during life. They possibly stand straight and equidistant and cohere into groups during the manipulation before and during the mounting on the slide. In forming the arch bounding the tunnel of Corti, the shafts of the rods stand approximately straight in profile view, while the portions braced by the foot-cells always curve as they approach their rest upon the basilar membrane (Fig. 12). It was thought possible, then, that the grouped appearance of the shafts on the slide might result from the straightening of the curved foot-portion

when the series comes to lie flat on the slide. However, if this were true, one would expect all of the shafts to be curved, whereas those in the middle of each group are usually straight. Again, if the shafts stand straight and equidistant during life, noticeable depressions in the surface of the phalanges opposite the spaces between the groups would probably result from the bending of the shafts in forming the grouping. In all the preparations, the outline formed by the cohering phalanges appeared straight. Further, in the grouped conditions shown in the preparations, the granular protoplasm dispersed between the rods appeared continuous throughout the smaller spaces between the rods of each group, but in the spaces between groups it appeared above and below with a thin film along the sides of the bounding rods, leaving a definitely bounded vacant space in the center (p., Fig. 12). In the split shown in Fig. 12, the upper area of this protoplasm appeared split also. Since this preparation came from a cochlea fixed in Zenker's fluid, the protoplasm must have been hardened while in position in the cochlea and therefore was firm enough to be broken, as shown when the rod-series was split by the teasing process.

Whether equidistant or grouped in life, the preparations suggest an anatomical arrangement which may increase the functional possibilities of the organ. As shown by Joseph, '00, and by Held, '02, and as shown in Fig. 12, the rods proper consist of bundles of longitudinally placed fibers held together by a seemingly hyaline matrix, and therefore may be distinguished from the granular protoplasm distributed between the rods and forming the foot cells. From all appearances, the rods are relatively rigid, the outer more so than the inner series, and their presence is generally conceded as serving for the support of the neuro-epithelium at each side. If they are grouped during life, then the two phalanges which come together opposite the larger spaces between the groups (a., Fig. 12), might be less resistant to vertically applied force than would the phalanges of the rods of the middle of the groups, b, and thus, also, would the hair cells immediately supported by these phalanges be held in varying degrees of rigidity against the impact of the tectorial membrane. On the other hand, a separation of the rods, as shown in the groups, into straight and equidistant relations would produce slight bulges in the outline of the coherent phalanges, and thus, if the rods are straight and equidistant during life, this condition probably results in hair cells at intervals standing higher than others and more apt to be stimulated by slight undulations of the tec-

torial membrane, and to be stimulated more strongly by undulations of greater amplitude. Either relation (that is, if the hair cells do not lie in the same plane), would be a factor in determining the number (and also the intensity) of the stimuli applied to a unit area of the organ of Corti. Such conditions are merely suggested by the slides. Though constant in my preparations, the grouping may be artifact and may mean nothing at all.

As evident in the above pages, I have entered very lightly into an application of the laws of physics to the anatomical rôle suggested for the tectorial membrane. Many features must be subjected to further anatomical investigation and must receive further substantiation before a wise application of the known can be made. For the same reason, the physiological phase of the question, which, based upon the many auditory phenomena, could be prolonged indefinitely, is touched upon but little. Just how far the cochlea, in itself, takes part in the analysis of sound is the difficult question. In the physiological literature the cochlea is spoken of as *analyzing, noticing, appreciating phase, distinguishing and perceiving tones, etc.* It is well known that several waves may pass, in the same direction, simultaneously through a medium. In the cochlea, acting as above suggested, their resulting stimulation of the auditory hairs would be somewhat segregated as to pitch. A mixture of sounds of different qualities but of approximate pitch would act upon approximately the same area of the organ of Corti, complicate the process and probably be interpreted as "*noise.*" The matter of the finer analysis of sound is no doubt almost wholly cerebral. It certainly is largely a matter of education. It is of course probable that cochleae, as other organs of the body, may differ as to their anatomical excellence in different individuals. I wish to suggest that most of the phenomena of hearing which are actually peripheral may be explained on the basis of the relationships suggested.

Impulses borne by the cochlear division of the acoustic nerves are conveyed to given localities of the cerebrum. Probably any stimulus aroused in these fibers gives rise to sensations of sound. Gray, '00, reports a case of deafness and "singing noise in the ear" in which the post-mortem examination showed all the divisions of the ear to be in perfect condition, but, on further search, a tumor was found in the medulla oblongata encroaching upon the entering trunk of the acoustic nerve. *Tinnitus aurium* could be produced not only in this way, but, if produced temporarily, or permanently as sometimes happens, by a

violent auditory stimulation (explosions, etc.), it might result from the tectorial membrane being thrown by the excessive amplitude of the vibrations so violently upon the auditory hairs that it becomes stuck to them for a while by means of its glutinous matrix and thus would give rise to continuous stimulation. When teased out in the fresh condition, the membrane adheres to the needle point with a readiness very embarrassing to the operator, and sections often show it adhering to the hair cells upon which it has evidently been crumpled by the manipulation.

Calcareous deposits in the matrix of the membrane would not be surprising, considering the developmental analogy it bears to the otolithic membranes. If uniformly distributed, these would produce a stiffening of the membrane and a general impairment of the hearing; if localized they would result in "*tone islands*." Calcification may be the cause of some of the peculiarities of the "failing ears" of old age.

Hensen, '07, in his recent paper upholding the resonance theory as applied to the basilar membrane, claims that the tectorial membrane, considered free by him, cannot be made to impinge upon the auditory hairs by wave motion in the scala vestibuli, assuming that waves in this canal would produce simultaneous depressions of the whole spiral lamina below and thus of the hair cells, so that the usual space separating them from the tectorial membrane when the cochlea is at rest would be maintained. And he thinks, therefore, that sensations of sound do not arise till the wave motions have passed through the scala vestibuli and, therefore, only on their return in the scala tympani below does the resonance action of the fibers of the basilar membrane force the hair cells upward to impinge upon the under surface of the membrane. This idea seems to me subject to the following suggestions:

(1) It seems probable that confusion would result from the anatomical necessity, involved in his idea, that the two sides of his resonant membrane would be subjected simultaneously to different sets of waves, those passing above and those below a given point.

(2) Or, if the basilar membrane is capable of undulating so freely to the waves in the scala vestibuli, these waves would be imparted through it to the endolymph in the scala tympani below, and the same waves passing in the same direction in both canals would meet at the helicotrema and would either be reflected there by the wall of the labyrinth and return towards the middle ear, meeting other waves traveling in the opposite direction, or they would be damped out in the confusion at the helicotrema.

(3) The scala tympani increases in diameter in passing from the helicotrema to the fenestra cochleæ (rotunda). Therefore, supposing that the sound waves passing in the scala vestibuli return without interference in the scala tympani, they would not only be fainter because of the resistance of the endolymph and walls of canal through which they have passed, but their amplitude would be further decreased because of their being dispersed over the increasing space of the scala tympani. So, Hensen's idea must assume that the stimulating resonant action of the basilar membrane is accomplished with waves of less amplitude than when entering the cochlea.

(4) Anatomical studies of the basilar membrane suggest that it is wholly incapable of moving as sensitively as the tectorial membrane to waves in the scala vestibuli. Not only is the basilar membrane firmly continuous along its either edge with the walls of the labyrinth and invested above and below by layers of other tissue, but even when torn away as a free strip, it is far more stiff than the tectorial membrane. When teased free in fresh preparations it is rigid enough to more than retain its shape, and its flexibility, compared with that of the tectorial membrane, is as a wooden board compared with a strip of tissue paper. It must at least resist wave motion in the endolymph far more than the tectorial membrane which lies suspended in the endolymph, one edge free, and by position is the first to receive the impact of the waves.

To these objections to Hensen's idea may be added the objections enumerated on another page against the idea that the basilar membrane is a resonance mechanism at all.

From the anatomical standpoint, the basilar membrane may be considered as nothing more than a thin, flat tendon, thicker along its edges, whose purpose is to so strengthen the floor of the cochlear duct that it may firmly support the organ of Corti and at the same time be thin enough to allow the presence and necessary caliber of the scala tympani below it.

The *vestibular* (Reissner's) *membrane* is considered as having little to do with the function of the organ of Corti. By development, it is the remains of the outer wall of the embryonic cochlear canal, after the liquefactions of the mesenchymal tissue resulting in the scala vestibuli. It may serve as a protection to the organ below, damping violent agitations in the scala vestibuli and preventing upward displacement of the tectorial membrane. It is weakest along its edges, which condition gives, in teased cochlea, somewhat the impression of its being hinged to

the walls of the labyrinth. Grasped in the forceps, long strips of it can be removed intact, so easily does it come away. Therefore, sound waves passing in the scala vestibuli may be readily imparted to the endolymph in the cochlear duct.

SUMMARY.

(1) The tectorial membrane of the pig, occupying a cochlea of about four turns, has an average length of 25.5 millimeters. It is about three times as broad and five times as thick in the apical half-turn as it is in the last half-turn, its dimensions decrease gradually from its apical toward its basal end, and its ends terminate bluntly.

(2) Its specific gravity is but little greater than that of the fluid in which it lies.

(3) It possesses a small amount of elasticity, barely sufficient to cause the thicker, apical region to resume its normal coils while the membrane is suspended in fluid after being freed from its attachment. Its greater elasticity is in the direction opposed to stress applied longitudinally. It is remarkably flexible to stress applied transverse to its long axis.

(4) Its structure consists of multitudes of delicate fibers of unequal length embedded in a transparent matrix of a soft, collagenous, semi-solid character with marked adhesiveness. The general transverse direction of the fibers inclines from the radius of the cochlea toward the apex, which inclination is greater in the upper than in the under surface. Most of the fibers, by coursing and curving through the membrane, take part in producing the fibrous appearance of both the upper and under surfaces.

(5) From the study of both its adult structure and the processes by which it is developed, it is concluded that none of its fibers extend the entire width of the membrane, none are attached at both ends, and the greater number of them are attached at neither of their ends.

(6) Hensen's stripe is explained as a line of the intercrossing ends of the fibers of the under surface resulting from the processes by which the growth of the membrane terminates.

(7) From its study in both the fresh condition and in preparations considered least shrunk and distorted, it is concluded that the tectorial membrane projects free over the organ of Corti and is attached only along its inner zone upon the labium vestibulare of the spiral limbus.

(8) A thin, exceedingly delicate, accessory tectorial membrane is described lying along the under surface of the outer zone of the main body to which its outer edge is lightly attached. It varies in width somewhat as does the main body and its fibers extend inward toward Hensen's stripe, but only extend over the outer series of hair cells.

(9) To the several objections advanced by others to the assumption that the basilar membrane performs resonant vibration, there is added evidence that the basilar membrane is nothing more than a flat tendon composed of a lamina of interconnected bundles of white fibrous connective tissue whose purpose is merely to strengthen the floor of the ductus cochlearis and the position of the organ of Corti, and which are too rigid and firmly associated to allow of resonant vibration. And, further, even if resonance were anatomically possible in the membrane, the two layers of tissue on each of its sides would be sufficient to damp such action.

(10) To the evidence adduced that the different elements of the organ of Corti are incapable of being moved separately by vibrations in the basilar membrane, there is added evidence that the outer series of the rods of Corti are especially so associated as to be incapable of separate motion. The outer rods are more resistant to maceration than the inner rods.

(11) The theories in which the basilar membrane is considered the vibrating mechanism in the cochlea are considered untenable, and an application of the telephone theory to the tectorial membrane as the vibrating mechanism is suggested on the basis of its logical position, its extent, shape, proportions, consistency and structure, and the probable character of the transformed and transferred sound waves in the endolymph of the cochlea.

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EXPLANATION OF FIGURES.

Abbreviations in common.

- Ac.*, accessory tectorial membrane.
Hs., Hensen's stripe.
Iz., inner zone of tectorial membrane.
Lv., Labium vestibulare.
Mb., Basilar membrane.
Mv., Vestibular (Reissner's) membrane.
St., Scala tympani.

FIG. 1.—Representing unshrunk appearance of an entire tectorial membrane teased from the cochlea of a pig two weeks old. Under surface upward. Shape constructed from measurements from several specimens and from study of specimen represented. Drawn with coil more open than normally to avoid overlapping of edges in apical turns. Arrangement of fibers drawn in from specimen.

FIG. 2.—Block from first half-turn of whole specimen. Viewed from under surface. Cut end showing course of fibers is added from study of sections of other membranes. *Li.*, line of impression of edge of labium vestibulare.

FIG. 3.—Block from third half-turn of whole specimen, under surface upward, showing course of fibers and appearance of accessory membrane as torn loose from main body. *Li.*, line of impression of edge of labium vestibulare; *Lr.*, portion of lamina reticularis removed from labium with inner zone of tectorial membrane.

FIG. 4.—Block from fifth half-turn of whole specimen, showing the general course of the fibers as viewed from the upper surface, and indicating the character of cleavage in a broken end of the membrane. *S.*, slivers of fibers and matrix formed in the breaking.

FIG. 5.—The end of the basal coil of the tectorial membrane, showing the outer edge of the accessory membrane coinciding with the outer edge of the main body, and showing how the inner zone (*Iz.*) or the attached portion of the membrane curves so as to constitute the tip of the termination.

FIG. 6.—Vertical section of the tectorial membrane in position and through the first half-turn of its coil, showing the extent to which its outer edge projects beyond the organ of Corti and the course and arrangement of its fibers. *Pc*, peripheral condensation interpreted as produced by the shrinkage action of the reagents; *Vs.*, vas spirale, here a plexus instead of a single vessel; *Ss.*, spiral sulcus.

FIG. 7.—Vertical section from third half-turn of same cochlea as Fig. 6, with the organ of Corti represented entire and showing the character of the epithelium of the spiral sulcus (*Ss.*) and an appearance on the under

surface of the outer zone of the tectorial membrane, *Ac.*, which is interpreted as representing the much shrunken accessory membrane in section. *Pč.*, below, shows what seems in the section to be a strip of the peripheral condensation torn off in the manipulation and adhering to the inner supporting cells of the organ of Corti. *E.*, endothelium lining scala tympani, *St.*; *Vs.*, vas (plexus) spirale. The curved shape of the section of the tectorial membrane is due to shrinkage.

FIG. 8.—Vertical section from seventh half-turn of same cochlea as Fig. 7. The curve in the upper surface of the outer zone of the tectorial membrane is explained as due to shrinkage produced by the technique as well as the fact that the membrane does not appear to extend entirely over the organ of Corti. From the size of the tectorial membrane, as compared with Figs. 6 and 7, it is assumed that the section passes some distance from the basal end. Lettering same as in Figs. 6 and 7.

FIG. 9.—Horizontal section of tectorial membrane at region of second turn of coil, showing appearance and arrangement of fibers as cut transversely, obliquely and longitudinally. Irregularities of course of fibers explained as due largely to collapsed condition produced by reagents. *a.*, region of transversely cut fibers; *b.*, longitudinally cut fibers; *Ep.*, "Epithelial cells" inserted between the white fibrous tissue bundles; *Ht.* (Huschke's teeth) of the labium vestibulare.

FIG. 10.—Vertical section from the third half-turn of a cochlea from a foetal pig of 14 centimeters, showing a stage in the development of the tectorial membrane just before the beginning, along the inner edge, of the retrogressive changes of the greater epithelial thickening, *Get.* *Let.*, lesser epithelial thickening, enlarging to form organ of Corti; *Mt.*, tectorial membrane; *Ss.*, cells in region of what will become spiral sulcus; other lettering same as in Figs. 6 and 7.

FIG. 11.—From thin horizontal section of basilar membrane, stained by Mallory's method for white fibrous tissue, showing the structure to be composed of bundles of white fibers, *Fb.*, connected with each other by numerous fibers less compactly arranged. *Ls.*, side toward spiral ligament; *Lt.*, side toward labium tympanicum of spiral limbus; *Fn.*, foramina nervosa in habenula perforata.

FIG. 12.—Portion of a line of the outer rods of Corti, adhering together and showing grouping as appeared in teased specimen from second turn of cochlea. *a.*, phalanges assumed to be less resistant to downward pressure than those designated by *b.*; *f.*, fibrous portion of curved foot of rod which rests over basilar membrane; *Ir.*, fragments of inner rods left in their separation from the outer; *P.*, granular protoplasm between rods and probably continuous with that forming the foot cells.

Fig. 1

THE NATURE OF THE TECTORIAL MEMBRANE

IRVING HARDESTY

FIG. 2

THE NATURE OF THE TECTORIAL MEMBRANE
IRVING HARDESTY

FIG. 3

THE NATURE OF THE TECTORIAL MEMBRANE

IRVING HARDESTY

FIG. 4

THE NATURE OF THE TECTORIAL MEMBRANE

IRVING HARDESTY

FIG. 5

FIG. 6

THE NATURE OF THE TECTORIAL MEMBRANE
IRVING HARDESTY

FIG. 7

FIG. 8

THE NATURE OF THE TECTORIAL MEMBRANE

IRVING HARDESTY

FIG. 9

FIG. 10

FIG. 11

THE NATURE OF THE TECTORIAL MEMBRANE
IRVING HARDESTY

FIG. 12