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COCHLEAR RESONANCE

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THE following account of the movements of the basilar membrane and the generation of nerve impulses by the hair cells, though partly supplementary to that given in my little book, *Hearing and Equilibrium*, is sufficiently comprehensive in itself. When that book was written I regarded the length of the hair cells as incidental, and the filaments of the cells of Deiter as morphological curiosities, probably perpetuated because of the general support which they afforded to the hair cells and the phalanges. In the present account they become interesting features. Also I accepted a description of successive changes in the membrana tectoria given in a standard physiology, and they now appear to have been singularly erroneous. There are other structures rather casually mentioned in textbooks, which physiological discoveries invest with special interest. The ear, in fact, becomes the most beautiful example of these modern conceptions. The physiological principles specially relevant to hearing are briefly described in advance, and the structures to which reference has been made will be described when describing the functions attributed to them.

Firstly the sensation of touch depends on the distortion of the touch receptors produced by pressure, and not on the direct pressure. The classical proof is that when a finger is immersed in mercury the sensation of touch is experienced only

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at the surface where there is distortion. The obvious effect of distortion is to produce a degree of compression many times greater than would result from the direct pressure, as when a strip of metal is bent; but distortion implies extension as well as compression, and an alteration in the relative positions of different parts, and these changes within a cell wall may be partly or wholly responsible for the stimulus. A very interesting experiment can quite conveniently be conducted by any reader. (1) Hold a pen holder lightly near the centre and allow the nib to fall gently on the palm of the other hand, just proximal to the fingers, and draw it across the palm a few times. (2) Place a coin at the temperature of the body in a similar position on the palm of the hand which had held the pen, with the fingers fully extended so as to avoid pressure by the edges of the coin, and apply moderate pressure on its centre. Note the almost complete absence of sensation. (3) Close the fingers gently on it and observe that the sensation is almost confined to the edges. (4) Place a coin on the table and examine it with the finger-tips, as if ascertaining its nature with eyes shut. This would be described as examination by touch; yet the sensation produced by the nib is as different from this, as from those sensations produced by the other methods. It is produced by the most delicate mechanical stimulus, and it will be found to closely resemble that produced by deflection of sensitive hairs.

Secondly, there is no relation between the magnitude of a stimulus and that of the nerve impulse which it excites. The weakest stimulus which will excite a nerve impulse will excite an impulse indistinguishable, either instrumentally or by the physiological response which it evokes, from that excited by the strongest. It has been demonstrated conclusively that it is the increase in frequency, and not in strength, which is responsible for an increase in the sensory effect.*

It is often found that the duration of the stimulating current is a more important factor than its intensity in determining whether excitation does or does not occur. Also a number of sensory impulses, individually inadequate to excite a nerve

* "All or none nature of conduction. . . . This means that if a fibre conducts an impulse at all it will be of the maximum strength possible for the conduction of the nerve at that time."—Prof. Bard in Macleod's *Physiology*, 1941, p. 47.

"While the intensity of any kind of sensation certainly depends on the number of impulses reaching the central nervous system over one group of sensory fibres per unit of time."—*Ibid.*, p. 69.

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impulse, if repeated at sufficiently short intervals, becomes summated and excite it.*

As the minimum stimulus which will excite a nerve impulse is termed a threshold stimulus, the distortion of the cell necessary to evoke it may be termed threshold distortion, and the necessary displacement of fibres of the membrane threshold displacement.

According to the theory being submitted a number of fibres undergo inadequate displacement in every degree of resonance. As resonance increases the number of fibres being displaced remains substantially the same, but an increasing number undergo threshold displacement, while the centre of the resonating region remains constant and is associated with pitch. If the pitch rises the longer fibres at the upper end remain quiescent while those below the lower end commence to vibrate, and *vice versa*. It will become evident that as the amplitude of displacement increases it does so most rapidly in those fibres which have reached, or are reaching, threshold degree. There is, therefore, a fairly well defined limit to the differentiation in the volume of sound reaching the ear by varying the number of fibres reaching threshold displacement. Yet one of the most vital, as well as remarkable, features of hearing is the faculty of detecting almost incredibly small differences. If, however, serial rows of cells are provided which reach threshold distortion *seriatim* as the displacement increases, any necessary degree of perfection in differentiation can be obtained: and it can be definitely shown that the membrana tectoria subjects the rows of hair cells from within out to threshold distortion as the amplitude of displacement increases.

Anatomical considerations render it evident that the hair cells are the specialized auditory receptors, and that auditory impulses are generated in the nerve endings with which they form synapses. The upper surfaces of the cells are cuticular and the hairs are not part of, nor have they any direct communication with, the nervous system, and deflection of them must result in distortion of the cell by movement of its upper surface as a whole. The concept, however, that the number of tones is limited by the number of hairs or, in fact, has any relation to it is, in my view, quite erroneous. Various instruments vary by small fractions of a vibration while being

* Macleod's *Physiology*, 1938, pp. 10, 40, 120.

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played, and yet the ear responds to every shade of tone equally well. There is another theory on which this is explicable, and as an example of the principle the stimulation of three adjacent cells will be given.

The central cell will be referred to as " C " and the cells on its apical and basal sides, respectively, as " A " and " B ". Assuming that all three are involved in a resonant curve of the basilar membrane and that " C " is at the dead centre of the curve, it will undergo the most rapid and extensive distortion. " A " and " B " will reach threshold distortion subsequently to "C", but simultaneously with each other, and the interval of time which has elapsed since the excitation of " C " indicates the rapidity and the ultimate extent of the movement of the fibres. If the centre of the curve had been situated between " C " and " A ", the cells on the " A " side would have reached threshold degree before those towards " B " and the time elapsing between the excitation of " A " and " B " would indicate the exact position of the summit of the curve.

In relation to sound time, in great measure, takes the place of space. The actual sequence in which the hair cells are excited gives the sensation of pitch, and the rapidity of the sequence, as well as the number of cells involved, gives an accurate conception of the extent of the movement. The principle has been applied to the cells on the apical and basal sides ; but it probably applies still more to the rapidity with which the successive rows of cells are stimulated. Those on the apical and basal sides may be involved in other movements ; but the rapidity with which the successive rows are stimulated can have but one interpretation.

In this concept the brain forms the chronogram of a natural chronograph on which every pitch is automatically and accurately recorded and transmuted into sensation ; but the permanence of the records, and the psychological power of discriminating between those closely akin, is limited and varies in different individuals.

The mechanism emphasizes the curious reflection that we are never in touch with the absolute present. Our conception of the present is the sum of the records of the immediate past. The difference is relative, not absolute, between our deduction that the earth is beneath our feet or the sun overhead and that stars are present, though the light reaching us was emitted some hundreds of thousands of years ago from where stars were,

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now seems to be, and was emitted to reach an abyss towards which our system moved or fell. Since the arrival of the impulses owing to which we see the stars, millions of others have reached us, each was of itself a present and has produced changes which have subsequently affected our consciousness. But during evolution our perception of our surroundings has been rendered sufficiently immediate, and our perception of changes in tone sufficiently acute to satisfy our requirements.

To fully appreciate the reasoning which follows it is necessary to have in mind a fundamental proposition detailed in the number of the Journal for June 1941. Briefly, the proposition is that pressure of the magnitude of a sound wave produces two synchronized movements, namely, an *outward* movement of the stapes and an *inward* movement of the membrane closing the fenestra rotunda ; the result being a simultaneous decrease in pressure on the upper, and an increase on the lower surface of the basilar membrane, and *vice versa*.

The question of the number of cells involved in each movement can be profitably prefaced by a review of the theory that a fibre, or set of fibres, owing to a specific length and tension, vibrates in resonance with sound of a specific frequency, and that the movement leads to the stimulation of a cell and the sensation of a corresponding tone.

The inward movement of the secondary membrane reduces the capacity at that end of the scala tympani, raises the pressure and produces a movement of the fluid along the length of the scala. If the scala were straight, as in Fig. 1, and movement were restricted to a single fibre, or to a set of fibres corresponding to a single cell, momentum would carry almost the entire fluid past the narrow band of fibres, and almost the entire momentum, into which the energy of the wave has been converted, would be lost. Also, apart from this consideration, there are about 24,000 fibres and the pressure sustained by such a band would be a negligible fraction of the whole. The essential requisite is the utilization of practically the entire pressure and momentum, with correspondingly rapid development of resonance.

Throughout this paper the terms up and down, and, above and below, will be limited to transverse movements and positions related to each other as the scala vestibuli is to the scala tympani. The terms forward and backward, or in front and behind, will refer to movements or positions in reference

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to the long axis of the scalae ; and all pressures, unless otherwise stated, refer to those in the scala tympani.

If a considerable area, such as that between C″ and C, Fig. 1, were to vibrate in resonance with a tone, a force in proportion to the number of fibres resonating would be utilized. The movement from the fenestra, represented by the arrows F B, F′ B′, would nevertheless be divided into two parts, one T A towards the apex and the second T M towards the membrane. The latter would increase as resonance developed, but the process would be prolonged and in the cochlea never quite complete : and it is not the final result, but the rapidity with which resonance develops, which is the vital consideration.

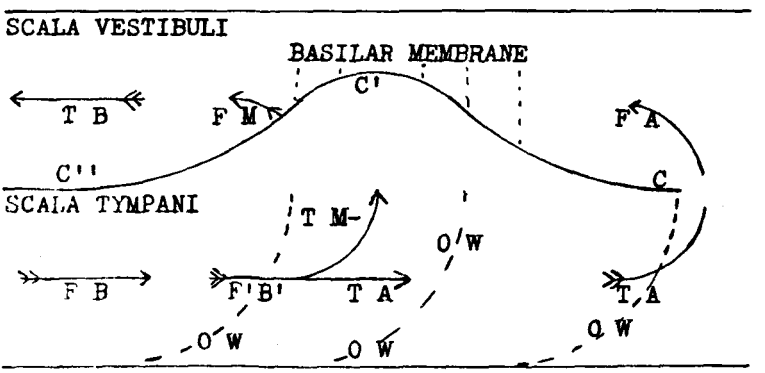


FIG. 1.

Vertical section through a resonating segment of the cochlea, representing the scalae as straight canals. The arrows in the scala vestibuli are marked as follows : F M from the membrane, F A from the apex, T B to the base. The markings in the scala tympani are F B and F′ B′ from the base, T M to the membrane, T A to the apex. The outer wall is indicated by three interrupted lines O W. The interrupted curved lines on either side of T M should be conceived as curving up and away from the observer, in a plane at right angles to that of the paper. In the cochlea in the corresponding position the movement of fluid would be towards and through the plane of the paper and up the wall on the opposite side.

In the diagram the outer wall is represented by three interrupted lines marked O W ; because in the cochlea the movement would not be in a plane corresponding to that of the paper : it would correspond to a movement from the observer through the plane of the paper to the outer wall on the other side, up which it would move directly on to the basilar membrane. The effect of the curved shape of the cochlea is, therefore, that almost the entire momentum of the first

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vibration, as well as all which follow, is utilized in the generation of resonance.

It is necessary to recapitulate certain constructive criticisms which I urged in my book, because they form essential parts of the arguments which I am advancing in favour of the theory, and the reader may not be familiar with them. (1) I submitted that the curve of the cochlea would aggravate the effects of gravity rather than eliminate them, and that the purpose of the curve was that just given. In the case of the scala vestibuli the entire fluid from the posterior end of the posterior canal to the anterior end of the first quadrant of the cochlea would operate under gravity in both directions, and was probably of service in the case of the canal. There was no compensatory column of fluid. In the case of blows on the back of the head, which would cause a sudden movement forward of the head, the fluid would be left to some extent behind, and this, creating a partial vacuum, might incidentally account for the capillary hæmorrhages which are distinctive of blows on the head. (2) I maintained that " Its function (that of the cochlea) as a resonator must be explained without attributing various degrees of tension to the resting membrane, which has been a serious flaw in previous explanations. The tension of one part has been estimated to be several thousand times greater than that of another, and evidence has been adduced to show that living tissue would stand the strain. This is not the principal difficulty in accepting the suggestion. Living tissue, a few centimetres long, would have to acquire and retain unaltered throughout life this diversity of tension. . . . There is no difficulty in furnishing stringed instruments with strings made of a variety of materials which will stand the strain for sufficiently long to enable the instrument to be used for a reasonable time, but there is no material, metallic or non-metallic, which would stand the strain throughout a life time, with such perfection . . . without readjustment."

Other structures in virtue of their resilient nature, which remains unaltered, fulfil the function attributed to the differentiated tension of the basilar membrane.

Certain of the premises on which the theory of resonance rests are so well established that they must be taken as facts. An inward movement of the structures closing either of the fenestrae must be associated with a movement of fluid along the corresponding scala ; but I am confining my remarks to

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movements in the scala tympani. Pressure must rise in any section of the scala into which additional fluid has been forced. The basilar membrane, being elastic, must yield ; and the fluid forcing, and consequently following it upwards must be replaced, and the fluid replacing it must in turn be replaced ; and this process constitutes a movement of fluid towards the membrane. There are thus two movements, one towards the membrane and a second along the long axis of the scala. Fig. 2, which will be immediately described, illustrates graphically the manner in which the recoil of the membrane converts any movement towards itself into one along the scala until the resonating segment is reached. There is nothing more abstruse, or less inevitable, in this explanation, than the expansion of an artery by the action of the heart. Both render possible the presence of an increase of fluid and its transmission, without loss of energy, to the region in which its function is fulfilled. In Fig. 2 a concrete example is illustrated, because it facilitates the representation of the generation of resonance, the conservation of energy till the resonating segment is reached, and its complete utilization in that segment, and the assessment of the number of fibres participating in a single vibratory movement. The central C of the piano and the octave above and below it have been chosen because, without serious error, their respective periods may be represented as 2, 4, and 86 microseconds (σ).

In the acceleration of any body, as for example a motor car, there are two primary factors—namely, the weight of the body and the accelerating force. Any vibratory movement consists of a period of acceleration and of retardation, and the duration and the degree of force producing each are equal, and the duration determines the frequency. In the cochlea, excluding extraneous force, the weight of the fluid represents that of the car and the resistance and recoil of the membrane the retarding and accelerating forces, and without affecting the issue retardation may be substituted for both. The weight increases from base to apex and the resistance of the membrane to displacement, which is the retarding force, diminishes. The retardation, therefore, occupies progressively longer and the resonating segment is the first segment in which it occupies 2σ and in which, consequently the movement upwards continues *during the fall to neutral* as well as during the rise to maximum pressure and until the pressure at the fenestrae is changing.

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The figures in Fig. 2 represent the duration in micro-seconds (σ) of one-half of the total cycle, that is the time in which the membrane in that situation would make one complete movement upwards *were it in resonance* with wave motion. At C″ the movement occupies 1 σ, therefore the membrane returns to and reaches the middle line while that at C′ is still moving to and reaches the extreme. At C″ it reaches the neutral plane when pressure is neutral and the fluid is at rest, and it would, itself, be free from tension. It would, therefore, remain at rest were it not for the ensuing negative pressure, during which it moves downwards and returns in a similar way and with a similar result. In each case the recoil is opposed by a force virtually the equivalent of the force which produced the displacement, and the energy is restored. The same reasoning equally applies to the membrane between C″ and the fenestra rotunda.

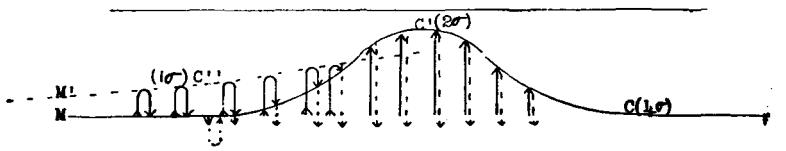


FIG. 2.

Vertical section through the basilar membrane similar to that represented in Fig. 1. M the basilar membrane at the end of the positive phase. M′ its position in the middle of the phase, when pressure is at its maximum. The displacement is, of course, much exaggerated for diagrammatical purposes. The solid arrows represent the movements of the membrane during the positive phase, and those in interrupted outline its movements during the negative phase.

Between C″ and C′ and, as a corollary, the resistance to displacement frequency progressively decrease, the upward and return movements take progressively longer and the membrane reaches the neutral plane correspondingly later than 1 σ, when minus pressure supervenes, and during the additional time the minus pressure supplements, instead of opposing, the recoil. Finally at C′ it supplements the recoil throughout.

Had C been the centre of the resonating segment, C′ would have been at its basal end, and the same reasoning would have applied to the membrane between it and C.

The movement of fluid from the fenestra, as far forward as the resonating segment, is constrained to a circular path by

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the basilar membrane, which only permits a movement of fluid up the wall by an upward movement of the membrane comparable to the outward movement of the wall of an artery under blood pressure. This movement is represented in Fig. 3 by the arrows B, B.

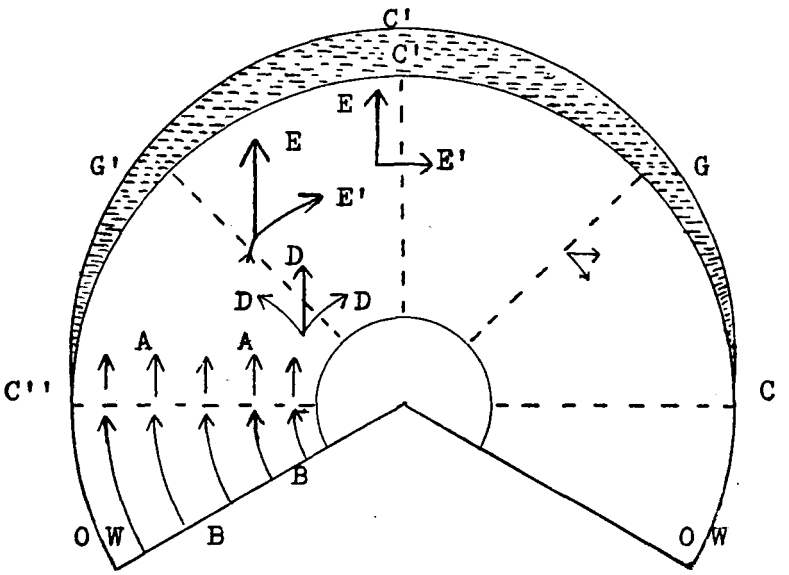


FIG. 3.

Representing a horizontal section through the scala tympani immediately below the basilar membrane. The shaded crescent represents the height of the basilar membrane at corresponding levels, when in resonance with a particular frequency. O W, the outer wall; A A, arrows indicating the immediate direction of the movement of fluid along the scala at any level of the cochlea; B B, indicating its constant constraint to a circular path along the outer wall, in situations in which the development of resistance by the basilar membrane is sufficiently rapid to prevent its movement changing from one resembling that of the wall of an artery into one of resonance; C″ the commencement of the resonating segment, that is, the level at which the resistance* of the membrane falls sufficiently to permit a gradual change in the movement of fluid from that of a circular path, parallel to the long axis, to one towards the outer wall; D D D, divergent movement of fluid towards the outer wall in inverse proportion to the resistance of the membrane; E E, the essential movement due to the momentum; E′ E′, the direction of principal deviation due to the comparatively low resistance of the membrane in the quadrant terminating at C.

* It would be more accurate to speak of a reduction in the rapidity with which resistance develops than of a reduction in resistance.

The transverse line at C″ may be taken to represent the basal end of the resonating segment. At any such line the immediate direction of the movement of fluid is towards the

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outer wall of the quadrant in front, as represented by the arrows A A. Being subject to pressure the fluid would tend to move in diverse directions as indicated by the arrows D D; the movement being towards the different regions of the basilar membrane in inverse proportion to its resistance to displacement. The essential movement of the fluid, however, would continue to be that due to momentum, represented by the arrow E; and the essential modification of it would be due to the great difference in resistance of the membrane in the quadrants on either side of C′, the effect of which is represented by the arrows E′ E′. The difference in resistance by the membrane immediately behind and in front of the line C″, however, would be slight and, although the movement would no longer be constrained to a circular path, there would be considerable rotation so that the direction of movement would be towards the quadrant of which C′ is at the centre. The diminishing resistance of the membrane from C″ to C′ would lead to a proportionate increase in its movement upwards, as represented by the shaded crescent shown in the figure.

The resistance of the membrane on the right (apical) side of C′, is less, and its movements *when in resonance with a wave* are more prolonged than those on the left (basal) side and it might appear that the upward movement of the membrane, in the present instance, would be greater and more prolonged. This is not so. There is a fundamental difference between the basilar membrane and the strings of musical instruments or other vibrating bodies. In the case of these bodies mass and elasticity are both either attributes of the body or are inseparably associated with it. Momentum is imparted to the mass and becomes converted into stress, which in turn becomes reconverted into momentum; and the repetition of the alternate change constitutes the vibratory movement. It is clear that if the momentum is expended or is curtailed its conversion into stress must simultaneously cease. In ordinary vibratory bodies momentum can only be nullified by applying extrinsic force to the string or other body, and the relation of cause and effect are obvious; but in the cochlea the mass is a separate entity and its movement is both curtailed and arrested without the application of force to the membrane. The resonating movements at C are twice the duration of those at C′ when the pressure takes 2σ, to reach its maximum, and

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materially increase its range. An additional quadrant, making $2\frac{3}{4}$ turns, would increase it from 20,000 to 40,000.

The shape of the cochlea is ideal for the generation and localization of resonance and the complete utilization of the energy of a wave; and it becomes not a series of resonators but a single resonator of infinite gradation. The mechanism for the reception of sound is perfect, and the limits to its differentiation are psychological.

There is another fundamental difference between the movements of the basilar membrane and those of any other resonator or vibratory body; namely that the neutral plane is decentralized. "In order that a segment of the basilar membrane may move, or participate in generating fluid movements, in resonance with sound waves, it is not necessary that its excursions to each side of the position of equilibrium should be equal. The oscillation might resemble that of a highly resilient ball which was set, and maintained, bouncing by an accelerating impulse in both directions." The ball would pass through the neutral plane as it reached and left the ground. "This is not the usual conception of a vibratory movement; but it gives a mental picture of a movement which could with advantage be substituted in the cochlea."

In order to fully appreciate the advantages of decentralization it is necessary to recall certain physiological principles which have already been quoted: namely, that it requires a stimulus of a definite strength, for a time varying with the strength of the stimulus, to excite a nerve impulse and that the time factor is often as important as the strength of the stimulus in determining whether a nerve impulse is or is not excited.

In Fig. 4 the advantage of decentralization is graphically illustrated. Graphs representing the movements when the neutral plane is central and when decentralized are superimposed. In both instances the distance between the extremes is 10 μ and the time occupied in traversing it is 10 σ: but when the neutral plane is centrally situated the maximum displacement is 5 μ and is reached only at the extremes, whereas when the plane is decentralized the same degree of displacement is reached early in the movement, and is both increased in extent, and prolonged in duration, and the prolongation is as important as the increase.

It may be feared that such an unfamiliar form of resonant

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movement renders the organ complicated and its movements difficult to comprehend; on the contrary every structure will be seen to fall into its place as an essential part of a perfect mechanism and every movement to form part of a harmonious whole, and visualization of the organ and its movements will be found to be facilitated.

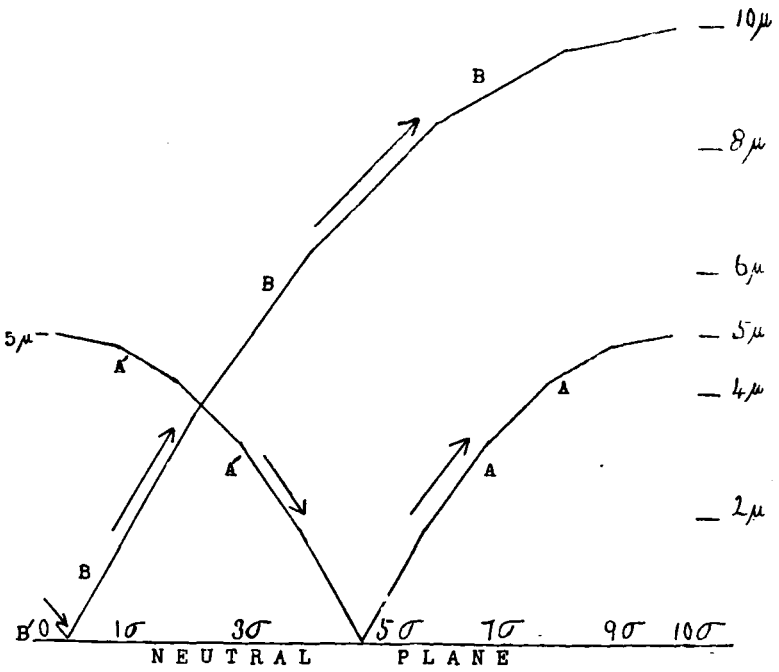


FIG. 4.

The rebound of a perfectly elastic ball is contrasted with an ordinary vibratory movement. The figures represent the time in microsecs, and the displacement in microns, of one complete movement from extreme to extreme including, in both instances, a movement to and from the neutral plane. A′ and A indicate, respectively, the ordinary vibratory movements to and from the neutral plane; B′ and B the corresponding movements of the ball. A A is intended to represent a continuation of A′ A′, on the other side of the neutral plane, the movement being in the same direction. B B is also a continuation of B′, across the neutral plane.

The group of cells on the outer side of the outer rods contain two different types of cells arranged in alternate rows, namely receptors or hair cells and phalangeal or supporting cells—the cells of Deiter (Fig. 5*d*). Each cell of Deiter contains a filament, which rather resembles a very delicate rod of Corti. It consists of a slender column of closely apposed fibres which

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extend throughout its entire length. Their lower ends expand into a somewhat conical base, which is attached by a relatively broad surface to the basilar membrane. At its upper end the fibrils also diverge to form the margins of an elongated octalateral disc or phalanx with its long axis radially directed (Figs. 5 and 6). The phalanges, which form the lamina reticularis,

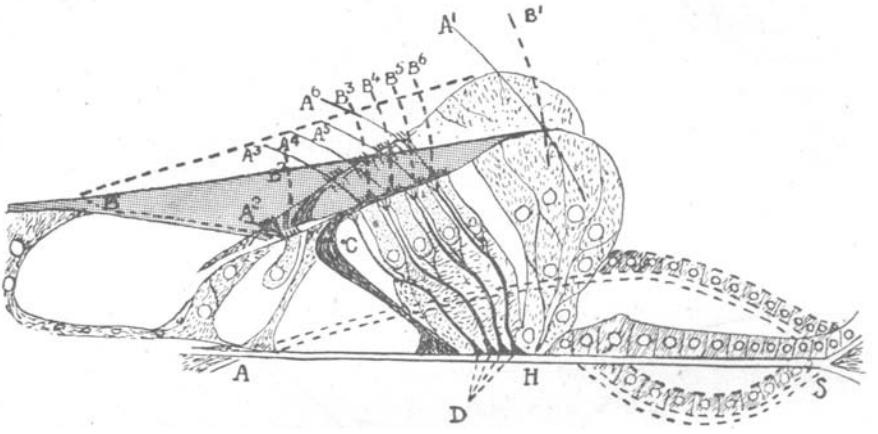


FIG. 5.

Transverse section of the basilar membrane. The portion on which the cells of Deiter (D) and Hensen (H) rest is referred to in the text as the central zone. The upper surface of the membrana tectoria is represented as straight for diagramatical purposes. It is, in fact, materially convex. It will be observed that the only part of the upper surface of the basilar membrane subject to fluid pressure, such as would produce uniform curvature, is the outer zone. A, the point round which the inner rods rotate. Circles are drawn in continuous outline with A as centre, and the summit of the cells of Hensen (A1) and the upper ends of the hair cells (A2, A3, A4, A5 and A6) at the circumference. Arcs are also drawn in interrupted outline (B1, B2, etc.) with B, the limbus, as centre, and the circumference at points corresponding with those marked A1, A2, etc. The distances between the lines A and B indicate the extent of the movements towards the limbus. The filaments are shown giving off wisps of fibrils to form nests for the hair cells and the remaining fibrils are seen forming terminals expanding at their upper ends. The terminals as actually seen under the microscope appear to be fragmentary, because each leaves the plane of section, bending towards the apex, to reach a phalanx two or more cells further forward, and filaments from cells behind cross the section and appear as fragments.

are arranged sufficiently regularly that each may be regarded as simultaneously entering into the formation of two flexible bands, one of which is radial and the other coincident with the long axis of the cochlear canal. The margins of the phalanges are sufficiently thickened to prevent overlapping, while the remaining central portions are sufficiently thin to be almost

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invisible when seen from above. They are relatively incompressible and are retained in the same plane by the filaments and, therefore, permit of thrust as well as traction. They thus constitute a light flexible surface permitting of curvature or undulatory movement in any direction, but which resists compression. It completely co-relates, whether the co-relation

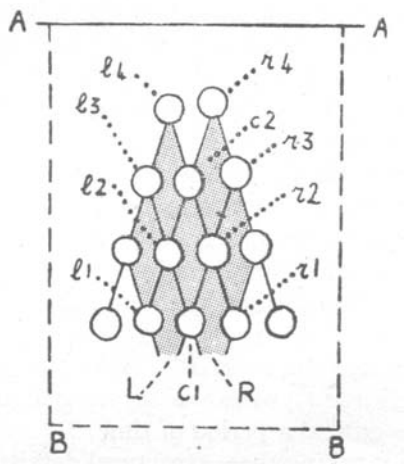


FIG. 6.

The lamina reticularis seen from above. Two phalangeal processes are represented: L (left) and R (right) with their connections. A movement of either R or L in either direction would necessitate a movement of the cells marked C and also of either those marked l or r. If, however, the lamina were covered by a membrane such as A B B A, one border (the outer) of which was attached at A A, while the other border (the inner) at B, B was free: and if the membrane underwent shrinkage, or contraction, or compression, it is obvious that the rapidity and extent of the movement of any part of the membrane would be in direct proportion to its distance from A, A and that is substantially the position in the cochlea.

entails thrust or traction, all movements of the apex of the arch, the upper ends of the hair cells and of the cells of Hensen (Fig. 5*h*). The movements of the lamina are themselves co-related with those of the outer rods and the middle zone of the basilar membrane (the zone beneath the cells of Deiter and Hensen) by means of the intervening cells and their filaments (Fig. 9, arrows 4).

The hair cells are situated between the upper ends of the cells of Deiter. Their upper ends pass up to reach the upper surface of the lamina reticularis through apertures in it formed at the junction of four phalanges, by the conjunction of circular

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recesses in their adjacent sides (Fig. 6). As the filaments approach the hair cells from below a wisp of fibrils leaves each filament to form a nest for one of the cells and complete its protection from distortion. The remaining fibrils deviate towards the apex to form an attenuated terminal to reach its appropriate phalanx some cells further forward.

According to this concept the organ of Corti constitutes a resilient framework, the outer wall of which is reinforced by the cells of Hensen and a cuticular tissue, and the inner wall is formed by the arch of Corti, which gives it support and controls its movements. As the framework rotates upwards and inwards the basilar membrane on which it rests, and which forms its base, undergoes extension, while the lamina rectcularis which forms its uppermost part remains unchanged in length. Consequently the framework is subject to stress, but the hair cells, which lie free in recesses in its upper surface, are carried bodily to their new positions without being submitted to any distortion except that due to deflection of the hairs. The exclusion of extraneous sources of distortion is an important factor in so delicate a process as securing a specific degree of distortion in so critical a period of time.

Even without taking these structural details into consideration it is evident that the zona arcuata and central zone cannot participate in a general curve of the basilar membrane. The fluid in the tunnel of Corti communicates with the fluid, or semi-fluid, on the outer side of the outer rods; but the fluid as a whole and the cellular tissue is practically enclosed in a capsule formed by the zona arcuata and the central zone below, by the cells of Hensen on the outer side, by the lamina reticularis above and the internal rods on the inner side. The greater part of the capsule is inelastic and it is contrary to reason that the zona arcuata and central zone, which form part of the capsule, should move as if they were free. The entire capsule must move in great measure, if not entirely, together. The zona arcuata and central zone, even though they undergo curvature cannot do so to an extent comparable to that of the outer free part. They must move, substantially, as if they covered the lower surface of an extensile lever, which was being simultaneously extended outwards and rotated upwards. Fig. 5 gives a general idea of the movement described. The pressure in the cochlea is primarily outwards and the upward curve of the membrane is almost exclusively due to the upward

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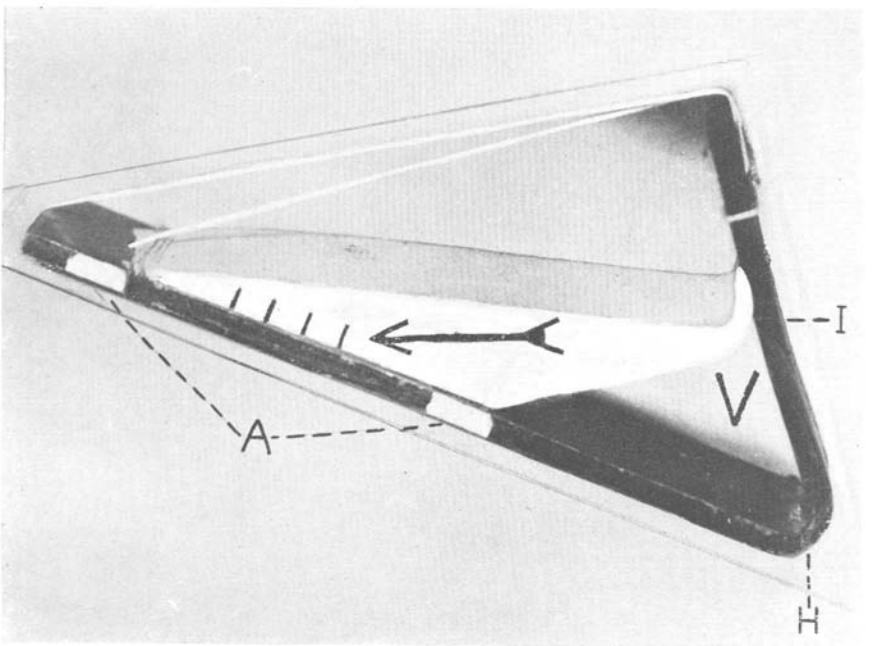


FIG. 7.

A rubber pencil eraser was cut into the shape shown and fixed in position as described in the text. A, represents the lamina reticularis. I, the limbus. V, the sulcus spiralis. The arrow represents the force which retains the rubber in contact with the surface of A.

[face page 210

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curve of the outer wall, which produces a curve such as that depicted.

The inner zones of the membrane, and the organ of Corti, rotate round the inner side of the feet of the inner rods (Fig. 5). The rotation of the upper surface of the cells of Hensen is represented by the continuous line A1, and the rotary movement of the hair cells by the similar lines A2, A3, A4, A5 and A6. Corresponding arcs are drawn in interrupted outline with the limbus as centre and the different hair cells at the circumference, and are marked with corresponding B lettering; the distances between the A and B lines indicate the extent of the movements towards the limbus.

Membrana Tectoria. This membrane consists of a jelly-like matrix containing numerous fine radial fibres interlacing in its upper part and in its deeper layers lying more or less parallel to each other with a curve towards the apex of the cochlea.*

Fig. 7 supports the natural geometrical conclusion that the shape of the membrane is responsible for retaining its lower surface in contact with the lamina reticularis. The arrow in continuous outline indicates the direction of pressure due to the shape of the membrane and the relative positions of the limbus and lamina. When the rubber lay on the metal slip subject only to the influence of gravity, the right and left ends of the lower surface were opposite the left ends of the white bands. The rubber was then forced to the right to the extent shown, and the extreme left end was fixed. The force used is indicated by the distortion of the right end. Nothing beyond the recoil of the rubber, and the angle of the metal was utilized to retain it in position, and it will be seen that the entire lower surface is firmly in contact with the metal. If the upper surface were convex and the lower surface were adhesive the effect would be very much more certain; and both of these characteristics are possessed in marked degree by the membrana tectoria. The force with which the membrane is held in contact with the lamina, and which increases as the surface of the latter is rotated towards the limbus, together with the adhesive nature of the surface of the membrane, cause the two surfaces to move as if they were firmly united. Yet the flexibility, extensibility and compressibility of the matrix allow free movement of the membrane at any level across the membrane beneath it, between it and the lower surface,

* *Histology*, Maximow and Bloom, 1938.

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producing a gradually increasing movement of the matrix from below upwards, in which the hairs, embedded in it, participate. The construction has the advantage of effecting firm union between the under surface of the membrane and both the lamina reticularis and the upper surfaces of the hair cells, holding the latter in position and yet permitting the traction associated with deflection of the hairs to rotate the upper surface of the cells towards the limbus.

The lamina reticularis is attached at its central end to the apex of the arch, and at its outer end to the outer margin of the membrana tectoria. As the arch moves inwards the margin of the lamina draws the outer margin of the membrane inwards with it towards the limbus, leading to compression of the intervening membrane. Compression is, in fact, the approximation of any two points in the line of compression. If any two points are moving in the same direction and the distance between them decreases, it is because the object behind is moving more rapidly, or has moved to greater extent, than that in front. Compression of the membrane is, therefore, a movement inwards of every part of it more rapidly, or to a greater extent, than any other part on its inner side, the maximum movement being at the margin. On the contrary, every part of the lamina moves inwards at the same rate, that is, with the rapidity of the margin of the membrane. The more slowly any part of the membrane is moving, the more rapidly and the greater extent to which the corresponding part of the lamina will move inwards beneath it. In other words, the nearer to the limbus, the greater is the disparity of movement between corresponding parts of the membrane and the lamina reticularis.

Fig. 8 gives a graphic representation of the effect on the hairs. A length of compressible resilient material (T), represents the segment of the membrana tectoria over the hair cells ; an incompressible slide (L), represents the lamina reticularis ; this is provided with a vertical arm (U), to secure compression along the length of the segment. The segment is divided into equal parts by the line 3, passing through dD, and the right half is subdivided into four equal parts by the upright lines (aA), (bB), and (cC) ; and the outer subdivision is again subdivided into two by the line (yY). See legend, Fig. 8.

In the lower diagram, Fig. 8, the slide is represented as having been moved to the left until the segment occupies

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75 per cent. of its original length. The right end of the segment has moved from the line 1 to the line 2; but the centre of the segment has moved half of that distance, from the line 3 to 4. The points A, B, C, D, retain their positions relative to the upright (U); but (d) is at the centre of the compressed surface, and a, b, and c divide it into four. In the figures corresponding positions on the upper and lower surfaces are joined by lines.

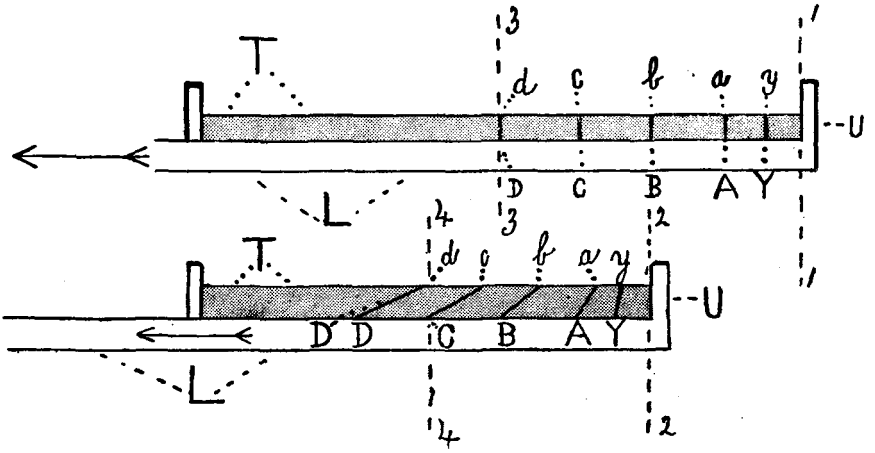


FIG. 8.

T resiliant, compressible material, representing a vertical transverse section of the membrana tectoria in the region of the outer rods. If an incision were made through the membrane at right angles to the long axis of such a section in the position indicated by the line 1, and the surfaces of the incision were juxtaposed and forced inwards by compression of the membrane from without in, the effect of the inward movement of the incision on the membrane on its inner side would be similar to an inward movement of the arm U on the material T.

If the lines were replaced by short detached rods, they would remain vertical as they moved to the left. This is obviated in the case of the hairs by the attachment of their lower ends and the adhesion of the surface of the membrane to that of the lamina. The disparity of movement is between the lower surface of the membrane and its upper parts and the disparity, therefore, increases with the distance from the lower surface and a shearing movement is replaced by deflection of the hairs.

The hair cells undergo two forms of rotation; firstly round the feet of the inner rods, in the manner which has already been described and, secondly, round their own axes; the lower ends being carried outwards by the outward movement of the outer

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rods consequent on any extension of the zona arcuata. This movement of the outer rods, which has not been mentioned, nor introduced into Fig. 5, fulfils another very necessary function. The centre of rotation is situated on the outer side of the head—see legend, Fig. 9. The centre (C) is also indicated in Fig. 5. In Fig. 9 the circles in continuous outline (C2, C3, etc.) indicate the movements of the upper surfaces of the hair cells, and the arcs in interrupted outline (B2, B3, etc.) are arcs of circles of which the limbus (B) is the centre. A comparison of the two series of arcs indicate both the nature and extent of movement. But there is another feature of the movement. The lamina and outer rods are at tangents to the circumference, and consequently the lamina moves downwards and inwards towards, and the outer rods move downwards and outwards away from, the articular surface of the inner head and *vice versa*. These movements carry the lamina towards the limbus and the feet of the outer rods downwards and outwards and provide perfect accommodation for the extension of the zona arcuata.

Any movement of the basilar membrane necessitates extension of the zona arcuata, and this, in turn, necessitates either the rotation of the outer head which has just been described or, alternatively, distortion of one or both rods of Corti. There is an average of about twelve transverse fibres to three inner or to two outer rods. The heads of the outer rods, therefore, articulate with more than one of those of the inner, and a great number of the inner rods with more than one of the outer. If there were no movement at the inter-rod joint a number of rods would necessarily move to approximately the same extent, and distortion of every inner or outer rod, or of all the rods, in the movement, would be necessary to permit extension of the zona arcuata. Lengthwise curvature, which is essential to resonance, would meet with such resistance that response to delicate impulses would be impossible. Independent movement of the outer heads permits a limited movement of both rods with a minimum of resistance.

The articular surface of the head of the inner rod is obviously designed to prevent dislocation of the head of the outer rod either upwards and inwards in the line of the outer rods, or downwards and inwards in that of the lamina reticularis. It is also designed to permit a very limited movement. It is a perfect construction for providing for a very limited movement with a minimum of resistance, and compelling it to assume a

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curve such as that shown in the diagrams, but which provides for the introduction of stress, due to distortion, when the movement reaches a certain point or tends to change in character. It is inherently unlikely that so beautifully appropriate an arrangement would have been brought into being as the result of evolution were that not its function.

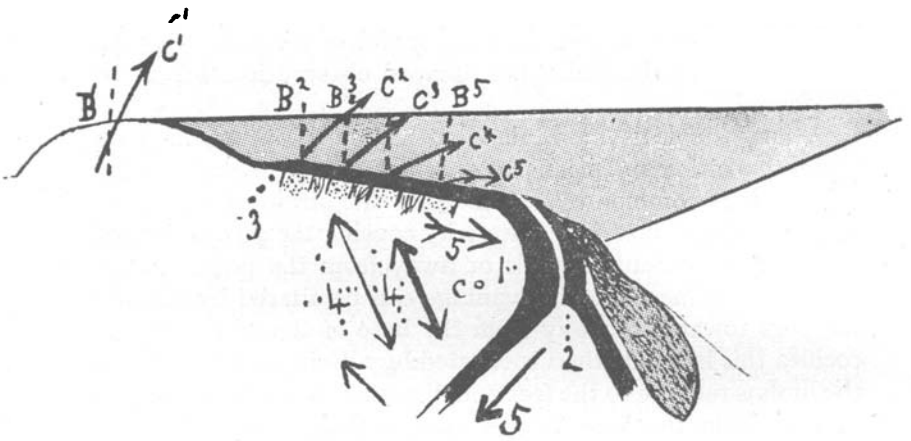
The Control of Frequency. In addition to the effect of the variation in length of the fibres of the basilar membrane, which has always been recognized, the control of frequency by the membrana tectoria, which has escaped observation, has to be considered.

When a pole is maintained in anything approaching an upright position by means of stays attached to pegs in the ground, it is common experience that the strain on the stays can be varied almost indefinitely by causing the pole to incline to a varying extent towards or away from the pegs. Alternatively, the mechanical advantage can be altered by moving the pegs towards or away from the base of the pole. In the cochlea this latter method is effected by altering the position of the limbus relative to the feet and direction of the internal rods, so that from the base to the apex the angle at which the membrane meets the rod is altered from a right angle to one becoming progressively more acute. This progressive reduction in mechanical advantage has a corresponding effect on the time in which a movement of the membrane upwards or downwards is brought to rest; that is, on the frequency. The membrane, it will be remembered, consists of matrix and fibres, and the fibres are tough though elastic and, as far as can be judged by prepared specimens, offer considerable resistance to extension. They offer no resistance to an upward movement, nor to a downward movement until the neutral plane has been passed and they have reached their greatest length without extension, but the movement will then be arrested as rapidly as is consistent with safety. Sudden drag, or even deflection, of the hairs, is avoided by an upward and inward movement of the lamina reticularis towards the limbus. The downward movement of the basilar membrane carries the feet of the outer rods downwards, but simultaneously the extension of the zona arcuata carried them outwards with rotation at the apical point and movements as indicated by the arrows marked 5, Fig. 9.

In this instance the rotation neutralizes, instead of increasing the effect of rotation round the feet of the internal rods. The

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quantity of fluid in the sulcus internus is determined by the position of the membrane above it, when at rest; but the fluid controls the position of the membrane during its movements, since its lower surface must remain in contact with the fluid in order to avoid the formation of a vacuum. Any movement of the internal rod alters the capacity of the sulcus spiralis and necessitates a corresponding displacement



Vertical section through the membrana tectoria and heads of the rods of Corti. 1, the outer rod; 2, the inner rod; 3, the lamina reticularis; 4, arrows indicating the position and action of the cells correlating the movements of the lamina reticularis and the outer rods. The outer head can be seen to rotate like the rim of a wheel in a reciprocally shaped socket; C, the centre round which it rotates; the lamina and outer rod are at tangents to the circumference and, consequently, while they rotate, move towards and away from the articulation. B, the limbus; the lamina moves inwards as well as rotating towards the limbus, and the outer rod while it rotates outwards undergoes the equivalent of an increase in length. B and C followed by numbers, arcs of circles of which B and C are the centres respectively, and of which the cells of Hensen, and the rows of hair cells, from without in, are at the circumference.

of the inner (free) part of the membrane; and any curvature, or increased tension, of the membrane, however produced, and whether upwards or downwards, causes an approximation of the lamina reticularis and apex of the arch to the limbus, which is of advantage in movements of the basilar membrane in both directions.

In an upward movement the frequency is determined by compression of the matrix. Fig. 7 illustrates an essential difference between compression and extension of a resilient body such as the matrix of the membrana tectoria. Deflection,

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such as at I, is the movement encountering least resistance and is liable, where possible, to replace direct compression. In extension the membrane is automatically retained between its attachments. In the basal regions of the cochlea the matrix is so situated between the lamina reticularis and the limbus, that the upward and inward movement of the former results in pure compression. Owing to the change in the relative positions of the limbus and the lamina from the base forwards and the consequent acuter angle at which the membrane meets the lamina, a curvature upwards of the outer part of the membrane in great measure replaces direct compression. The alteration in the direction of the movement of the lamina relative to the limbus also progressively reduces the extent of their approximation by a given movement of the basilar membrane.

Other features have been mentioned which play an important part in controlling the upward movements, and thus contributing to the control of frequency; but had it been necessary, or expedient, it appears to me that the movements upwards might have been regulated by the membrana tectoria alone.

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