XXVIII.

THE PROBLEM OF MIDDLE EAR MECHANICS.

CHAPTER II.

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The first chapter of this paper introduced some of the facts of comparative anatomy and physiology of the middle ear complex and their relation to the inner ear. The mechanics of the mass displacement theories was discussed by taking the recent theory of Wrightson as a type. Seven leading questions were asked and answered in some little detail. It may be well to summarize the conclusions reached in Chapter I by repeating these questions and giving a brief answer to each.

I. Do the members of the ossicular chain act as an intensifying press which decreases the amount of excursion at the stapedial footplate in response to the drum membrane displacements occasioned by sound vibrations?

Reactions in the drum membrane and ossicular chain to actual plus and minus pressures in the air of the external canal and middle ear have been demonstrated. The drum membrane displacements arising from pressure fluctuations and from contraction and relaxation of the M. tensor tympani and the chain of events which appears to follow these displacements in the dead animal have been applied directly to the conditions as they obtain in the living animal and to the problem of sound transmission. This has been done without reference to the power, the frequency and the distance through which sound pulses of minimum or optimum amplitudes operate against an aperiodic apparatus. The experiments of Koehler will be considered in detail in Chapter III. The work to be done lies beyond the force applied under the conditions imposed and with the type of apparatus which must respond. The sound transmission apparatus gears down the drum mem-

brane movement, but this function is not related to sound transmission. The double lever system of the mammal makes an altered mass response in relation to sound transmission physically inconceivable.

II. Is the antagonistic action of the *M. tensor tympani* and the *M. stapedius* responsible for a balance in the ossicular chain?

Wrightson has followed the conception of the muscle function as proposed by Politzer without considering the recent work of Mangold and of Kato. If we are to assume that the ossicular chain is balanced by the antagonism of the two muscles, then these muscles must be reciprocally innervated. The contraction phase of one muscle must be accompanied by a relaxation phase in the other. It has, however, been demonstrated that the *M. stapedius* may contract independent of either contraction or relaxation of the *M. tensor tympani*. It has also been shown that the *M. stapedius* will hold its contracted condition on a stimulation of the *M. tensor tympani*. Further, in birds, the single *M. tensor tympani* represents a physiologic peculiarity in that we find a striped skeletal muscle without an opponent.

The writer has described the function of the passive traction system of elastic ligaments associated with the incus as positive return agents against which the contraction of the *M. tensor tympani* operates. The statement that the *M. tensor tympani* and *M. stapedius* are opponents cannot be accepted. These two muscles do not balance the ossicular chain in the mammals any more than does the single *M. tensor tympani* in birds balance the columellar apparatus.

III. Is the intratympanic pressure equal to that of the atmospheric?

Wrightson assumes that intratympanic pressure is normally equal to that of the atmosphere, and yet he furnishes a reflex mechanism which is supposed to maintain this relation. He does not consider the possibility of tubal closure increasing the pressure within the middle ear, nor does he consider the possibility of air absorption creating a negative pressure in this cavity.

IV. Is the otic capsule filled with liquid and membranes to be regarded as an inelastic container apart from the fenestra

vestibuli and fenestra cochleæ, and what relation have these two windows in preserving the balance of perilymphatic pressure which Wrightson assumes is that of the atmosphere?

The otic capsule may not be regarded as an inelastic container; the liquid and membranes may not be considered incompressible; and the two windows do not have the function of regulating the perilymphatic pressure in the manner described. The relation of atmospheric pressure to that of the perilymph is an essential feature in the Wrightson theory but it is not a fact.

V. May the membrana basilaris be considered a transformer of vertical into transverse vibrational displacements at the hair cells because of the relation of stapedial footplate and the membrana tympani secundaria, and because the route through the basilar membrane offers less resistance than the liquid displacement through the helicotrema?

This inferred functional relation rests upon two premises, neither of which can be demonstrated. First, if the membrana tympani secundaria shows no response to the contractions of the M. tensor tympani, it is logical to assume no response will occur to any mass displacements in the drum membrane brought about by sound vibrations. Second, the amount of resistance at the helicotrema is computed with the idea that there are no other pressure regulating factors save a compensation movement at the membrana tympani secundaria. Other regulating factors have been noted. The Wrightson basilar membrane response is therefore a hypothetical solution for the hypothetical mechanic assumption which in itself is not in accord with the facts.

VI. In what manner does the Wrightson piston action of the basilar membrane occur when the sound vibrations are transmitted through the temporal bone to the inner ear?

Wrightson considers the otic capsule inelastic to the forces which drive the stapedial footplate into the oval window. In spite of this he contends that the condensations and rarefactions in the petrosum as a result of bone transmitted sound vibrations may give rise to a pressure response in the perilymph which results in a thrusting of both window areas into the tympanic cavity. We are therefore confronted throughout the Wrightson theory with an involved series of elastic

and inelastic containers and a compressible and incompressible liquid membrane filler in all possible combinations. This appears essential to make the theory conform with the observed data.

VII. Wherein does the comparative anatomy show a confirmation of the Wrightson theory?

The weakness of the confirmatory evidence proposed by Keith consists in the strength which his evidence gives to the contention that the structure of any organ is dependent on its ancestral pattern. The similarity of inner ear structure in various animals in no way confirms the Wrightson theory any more than it does a dozen others. It has been mentioned that the theory does not meet the requirements in birds as well as it does in mammals. This is particularly true in those forms which have a *membrana tympani secundaria* which is practically extratympanic in position. The appeal to the comparative anatomy by Keith practically avoids every consideration of the mechanics of the Wrightson theory save the possibility of the basilar membrane response. Keith offers no detailed account of wherein the comparative anatomy of the middle ear region may help us to understand the obscure relations in the higher forms.

The displacement theories of hearing are based on the premise of an indirect activation of the end organ. They assume that the ear mechanism operates something like the phonograph which, as Wrightson has stated, engraves a molar displacement. The drum membrane accordingly swings in and out and transfers this movement through the ossicles to the perilymph. The shiftings in the perilymph are transferred to the end organ through displacement of the *membrana basilaris* or the *membrana tectoria*, or both, and are compensated at the round window. We have presented objections to this conception and have stated there is no evidence that the restorative forces in this aperiodic apparatus are sufficient to produce the end result. We therefore present the mechanics of the second possibility which assumes that part of the energy striking the drum membrane is transmitted as a sound pulse into the ossicular chain and is discharged as a sound pulse into the perilymph. The theory supposes that all mass movements which arise in the drum membrane, due either to excessive

sounds or to other causes, are damped out before they reach the perilymph.

The presentation of another method of sound transmission may perhaps appeal to the reader as new. As a matter of fact, however, it is so old that it has been practically forgotten. Carlisle⁹ in 1805 makes the following statement: "It does not appear that any degree of motion ever subsists between the ossiculæ auditus as wholes which bears any relation to the peculiar vibrations of sound; but rather that the different motions of these bones only affect the membrana tympani and alter the degrees of contact in their articulation so as to influence the intensities of violent impulses; sounds of less impetus, not requiring such modulation, are transmitted through the conducting series by vibrations of the integrant parts of these bones, unaccompanied by muscular action. This reasoning is suggested by the columella in aves and amphibia."

Johannes Mueller,²⁸ in his *Handbuch der Physiologie* in 1840, devotes some space to careful experiments on the behavior of sound vibrations in reference to the problem of molecular transmission. Several interesting statements are made concerning the transmission of sound in terrestrial vertebrates. "Sound vibrations in air undergo a pronounced damping in being transmitted into water but pass readily into water through a tense membrane applied to its surface." "Sound vibrations in air pass readily into water if the tense membrane is applied to a short solid body which alone touches the water." "A small solid body which is applied to the water through a window in the container and is attached movably through a membranous border transmits sound vibrations into the water more readily than other solid parts. The transmission is, however, rendered more effective if the small movable solid is attached to the central area of a tense membrane which is flanked on both sides by air." "Sound vibrations pass more readily from a membrane to a freely movable solid to water than from membrane to air to membrane into the water. Comparing the conditions with those of the tympanum, greater intensity in transmission will occur through drum membrane, ossicular chain, oval window to the liquid of

the inner ear than through the air of the tympanum through the membrane of the round window."

The fountain of knowledge in so far as it pertains specifically to the middle and inner ear behavior in relation to sound is none too limpid. It took the writer six years to precipitate any very tangible information out of a voluminous and detailed bibliography. Accordingly it may be reasonably safe to assume that any other individual of average intelligence might experience similar difficulties. The effort made in this paper is to present the facts and the viewpoint clearly. The suggestion of the simple telephone as a solution for the drum membrane and ossicular chain complex in the transmission of sound must therefore be considered somewhat in detail. The object is to describe the reactions to sound vibrations—not merely to name them. We may agree with Zimmermann when he says that the drum membrane and ossicular chain are not directly related to sound transmission. It is therefore necessary to analyze the behavior of the energy coming through the air to the drum membrane and the route by which it travels to the inner ear.

VIII. May some of the energy of the sound pulse impinging upon the drum membrane be transmitted to the liquid of the inner ear as a sound pulse and without mass displacement in the apparatus?

Let us consider our sound transmitting system in the form of the primitive wooden stethoscope—with a wide flared end applied to the patient and the smaller flared end applied to the external auditory canal of the observer. The sound vibrations arising within the patient are readily transferred to the wood and pass to the opposite end because wood is an excellent medium for sound transmission. The vibration in the wood will tend to remain within it rather than to pass into the surrounding air. It will appear at first sight that the efficiency of this form of stethoscope might be increased if the interval between the aural end and the drum membrane were filled with water. This, however, is not the case, as may be readily illustrated by the insulation which a drop of water affords to the discharge of the vibrations of a tuning fork when it intervenes between the stem and the resonator. It may also be demonstrated by filling the external auditory canal with

water and applying the stem of the vibrating fork directly to the liquid. The experiments performed by Mueller, who filled the external canal with macerated paper, may be duplicated by placing the tip of the finger in the external canal. We may apply the base of the vibrating fork to the metacarpophalangeal joint. The sound intensity through this source is considerably greater than if the fork is applied to the mastoid or the cartilage of the ear with the finger in place. That the finger furnishes an excellent medium for the transmission of sound vibrations may be observed in placing the tip of the finger on the resonator and by applying the fork to the knuckle. The response in the resonator is directly affected by the amount of pressure on the finger tip. In other words, the bone and cartilage transmission is excellent, but the connective tissue acts in the same manner as soft rubber. Sound transmission is rendered more efficient through compression of both connective tissue and rubber.

The tip of the obturating finger discharges the sound vibration into the air of the external canal. It also confines the pressure to this area by not allowing an escape through the external meatus. It will appear from this alone that the drum membrane affords an excellent catchment area for sound vibrations in air. It must also be noted that a large amount of the energy of the sound vibrations entering the external canal is normally damped out through reflexion and through escape of energy toward the outside. This point will be considered in detail later.

We must therefore consider the string telephone. We will indicate the behavior of energy schematically, in a diaphragm (drum membrane) supported by a bony ring (annulus), connected through a bone-cartilage rod (sound transmission system) to a hole in the bony container (otic capsule) which includes a liquid (perilymph). It must also be remembered that the rod is insulated from its window by the interposition of elastic connective tissue. The scheme presented in the accompanying figure 2 indicates the behavior of the energy, and the entire surface of the drum membrane will necessarily be affected by the wave front striking upon it.

The sound wave (SW1) strikes upon the surface of the diaphragm (D), which is supported by a ring of bone. The

diaphragm separates the air-containing middle ear from the external auditory canal (E.A.C.). The sound wave impinging upon the drum membrane will be reflected back and may therefore be represented in two quantities: (a) showing the back reflection and (b) indicating the quantity entering the substance of the membrane. The quantity (b) will tend to remain within the diaphragm or will pass through it as (d). The (d) quantity has a reflection back at the inner surface of the membrane owing to a decided change in medium (d1). The remainder of (d) will pass on through the air of the tympanic cavity to strike against the otic capsule (O.C.). Its course will be interrupted at every change of medium: mucous membrane (d2), connective tissue, periosteum, bone (d3), and finally periosteum (d4) before it enters the perilymph (d5). The sound vibrations entering the bone may perhaps also follow the lamellar grain because the transmission is more rapid in this direction. The amount of energy transmitted to the perilymph will be materially reduced. It is unlikely that any appreciable amount of the energy enters the perilymph through this route under normal conditions with drum membrane intact.

The quantity (c) will travel out toward the periphery, where a certain amount would be reflected back (c1), and a certain amount will enter the annulus (c2).

The quantity (e), made up not only of a part of (b) but also added to by c1 and d1, will pass to the sound transmission element. Part will reflect back at the area of the change in medium (e1), and part will follow the bone-cartilage rod to the oval window. Here it will be more or less insulated from a discharge into the petrosus, not only in the reflection back at (e2), but because the elastic tissue is a relatively poor transmitter unless it is under tension (see later). The quantity (e3) will therefore arrive at the perilymph (P1).

The quantity (SW2) indicates the behavior of the energy striking the drum membrane from the cavity of the middle ear. Apart from a difference in the behavior of the quantity d and a which have changed places, the results will be about the same. The small insert figure merely emphasizes the mechanical relation of the second opening in the otic capsule (round window) to a large mass displacement in the dia-

phragm. The round window is not necessarily associated with the transmission of sound vibrations.

It must be remembered in considering this scheme that we are regarding the transmission of the energy. It may be likened to the transmission of sound vibrations from a diaphragm along a tense iron wire to another diaphragm. Compare this figure (2) with that reproduced from Wrightson's book (Fig. 1), in Chapter I.

Disregarding the quantity (c), it will be seen that the bone-cartilage system affords a more efficient means for discharge of the energy within the diaphragm than air on either side. The force passing through as (d) not only undergoes more numerous reflections but must pass through a more efficient transmitter, bone (O.C.), into a less efficient one of the perilymph. This is naturally disregarding the various surfaces in the (d) route which may be multiplied in the mucous membrane on the diaphragm and the mucous membrane and the submucous tissues of the otic capsule in bringing the relations over the animal condition. It must also be noted that the physical character of the membrane in comparing periphery and center will be altered by the relative tension exerted. All other conditions being the same, the energy will travel in the direction of greatest tension, whether the diaphragm be pushed out by the rod or pulled in. Let us again liken the condition to the string telephone. The diaphragm tension must be greatest at its application to the transmission system. This tension is indicated in the diaphragm (D) by stippling. It will also be observed that the efficiency of the apparatus is not dependent to a great extent on the original direction of the sound wave. The same amplitude (S.W2) applied to the inner surface of the diaphragm, disregarding the dead area of the attachment of the transmission system, will give the same result as (S.W1).

This diagrammatic representation of transmitting the sound vibration answers the argument of Zimmermann⁴³. Zimmermann contends that we disregard the drum membrane and ossicular chain as transmitters of sound. He does not explain the decreased hearing capacity in individuals with lacinated drum membranes.

IX. On the basis of the string telephone transmission system, in what manner are sound vibrations influenced in their passage from the air through the middle ear complex?

The suggestion of the molecular nature of sound transmission was first noted in detail by Johannes Mueller. It has recently been specifically championed by Boenninghaus⁶ in his interpretation of the relations in the water-adapted mammal, the whale. This mammal keeps the regions of the external auditory canal submerged and presents a form in which the effects of mass movements in the water upon the perilymphatic space may be eliminated. The range of acuity of hearing in the whale is, after all, a doubtful quantity in spite of the well developed end organ, the large auditory nerve and the extensive crossing of the axones from the cochlear nucleus (corpus trapezoideum). The whale displays a notable departure from the usual middle ear picture in mammals in that the external auditory canal is obliterated. The small rudiment of the lumen near the drum membrane is filled with desquamated epithelium; the ossicles are heavy and united; the stapedial footplate is joined to the massive petrosium through synchondrosis; and the fenestra cochleæ is rudimentary. It may also be mentioned that the petrosium is markedly separated from the remaining head bones through spongy bone containing air cells which are continuous with the *cavum tympani*.

Boenninghaus contends that the entire system is directly opposed to mass movements in so far as sound transmission is concerned. He also believes that hearing may only result in terms of molecular vibration, to which the writer agrees. However, our conception of what the whale actually does hear and a conception of what sounds might arise within the water are necessarily somewhat limited. At any rate, the development of the internal auditory system may not be considered a safe criterion. However, the proposal that the condition represents one of adapted efficiency to transmit vibrations from the water to the perilymph is open to contention on the basis of the diaphragm-rod theory. In particular this is true when the inferred functional relations in the whale are carried over, as Boenninghaus has done, to the remainder of the mammals. Boenninghaus believes that the stapedial footplate is

directed through contraction of the M. stapedius, so that vibrations are discharged toward different points of impingement on the vestibular wall. This accommodation proposition is entirely beyond a physical and physiologic possibility.

The writer is in absolute agreement with Boenninghaus' interpretation that the end organ is affected only by molecular vibrations and not by mass movements. The functional adaptation placed by Boenninghaus on the whale's apparatus is, however, not in keeping with the physical requirements. Whatever a whale does hear, it probably hears through bone transmission other than the ossicles. It lacks an efficient drum membrane, and the synchondrosis of the stapes will tend to diffuse the energy transmitted into the petrosum rather than concentrate it on the perilymph. The adaptation is therefore not one which makes use of the old ossicle chain. It is rather one which eliminates the ossicle chain from the function of sound transmission. The massive development and persistence of ossicles are therefore no better criteria of a functional requirement than the development of the internal mechanism. Let us remember the preliminary paragraph in this article and the statement that "a persistence of phylogenetic structure and phylogenetic function must therefore be carefully borne in mind. Both structure and function may persist in a system without reference to its apparent office at the present time and may be entirely overlooked because the 'adaptations' appear to be complete and the present relation of structure to function too plainly obvious."

The physical requirements for sound transmission may be fulfilled with a proper catchment membrane and a stethoscope-like cartilage-bone transmitter which is insulated from the petrosum by an annular ligament so that it may transmit its energy to the perilymph. There is still another point to be explained. This is in reference to Zimmermann's work in which he deduces that the drum membrane and sound transmission system do not function for sound propagation but merely act as dampers. Zimmermann,⁴³ while he agrees with Boenninghaus on the molecular nature of the sound transmission, disagrees violently with the latter in practically every other detail. The interesting statement of Zimmermann that sound vibrations pass directly through the middle ear and through the

otic capsule to the perilymph is in keeping with the writer's diagrammatic representation of energy behavior (see Fig. 2d quantity). So far we are in agreement. In so far as a consideration of this as an efficient route, let alone *the* efficient route, is concerned, we are absolutely in opposition. Let us therefore look into a matter which practically all of the exponents of mass movement have completely disregarded and which Zimmermann has not considered. The general physics of both propositions is the same and must be clearly understood.

The efficiency of catchment of energy in the diaphragm will depend not only on its physical character, its shape, its tension and its thickness, but also on its position in reference to the wave front striking upon it. It should therefore be placed parallel to the wave front so that its thickness is in line with the displacing force applied to it. Let us consider this disregarded point in some little detail, because no drum membrane in nature is placed in this position. The position of the binaural hearing with the attention directed toward the source of the sound, as determined by eyes and nose, places the external auditory canals roughly at right angles to the line from the source of the sound. Further, no animal possessing an external auditory canal has a drum membrane placed at right angles to the axis of the canal. It is always found in a very oblique position. Let us assume a drum membrane placed at 45° to the axis of the canal. The efficiency of this membrane toward stopping the energy in wave front entering and traveling parallel to the long axis of the canal would be markedly reduced to what it would be if the membrane was at 90° . However, not only is this canal markedly curved and crooked but the orifice of the canal lies almost parallel to the direction of the sound wave from its source. The result of this condition is that not only a mass movement force be tremendously interfered with but necessarily a molecular one as well. This may be stated in another way: the amplitude of the original sound pulse at the external canal must very considerably exceed the amplitude of drum membrane reactions.

The laboratory of nature, particularly on the basis of natural and sexual selection in reference to sound, has been subject to great experiments. Yet we find no animal in which

the drum membrane is placed at right angles to the direction of the sound. Can one imagine a phonographic registration resulting through a horn the diameter of the diaphragm? Suppose the horn were turned about on itself like a reproducing phonograph with a small external opening, and with the singer singing across this opening and not into it. Clearly, as Boenninghaus has well stated, the phonograph and the ear mechanism are different in their reactions.

Immediately two mechanical factors suggest themselves: First, if the most efficient position of the catchment membrane is at right angles to the line of thrust, then if the membrane is placed obliquely the amount of surface offered to the thrust must be markedly increased; second, the reactions in the membrane will not only be influenced by its size and position but also by its relative size to that of the external opening in the auditory canal. It is found that in all higher forms the drum membrane is placed obliquely to the axis of the external auditory canal. Its area computed at a right angle position is also considerably greater than that of the available external opening. In other words, the megaphone of a phonograph recorder is reversed. The big end of the horn is at the diaphragm while the small end is roughly at right angles to the line of the sound source.

The phonograph represents a type of instrument in which mass movements resulting from sound vibrations are efficiently recorded. The recording phonograph operates through the mass reactions in a diaphragm which responds to intense sound vibrations. The apparatus of the middle ear, however, operates under conditions where no phonographic registration of sound vibrations will occur. The entire apparatus of the middle ear is not physically constructed for the rapid response essential to efficient mass reactions. Further, when sound vibrations of sufficient intensity are exhibited to give rise to mass responses, such responses are either inhibited or entirely "damped out."

Zimmermann's contention that the drum membrane and ossicles are not the means of transmitting sound vibration might perhaps be thought to be in harmony with the foregoing statement, but this is not the case. Zimmermann is basing his contention on the assumption that sound vibrations pass

through the drum membrane, practically as if it were nonexistent, and that the sound vibrations are transmitted through the otic capsule to the perilymph. He is therefore not concerned with the efficiency or the inefficiency of the drum membrane. He merely disregards it in favor of a better and therefore more efficient route. This conception is somewhat like that proposed by Kleinschmidt.^{22 23}

It appears from Zimmermann's work that although he holds the molecular propagation of sound vibrations, he misconceives the behavior of the sound pulse in reference to the physical character of the media through which it passes. Moreover, he has not considered the working of a string telephone. Inasmuch as this last point has been thoroughly considered, it is essential that we analyze the efficiency of bone transmission in the sense employed by Zimmermann.

It was shown in Fig. 2 that the (d) factor was reduced through a failure of a more rapid transmitter (drum membrane) to yield its energy readily to the less rapid transmitter (air). It was also pointed out that a reflection back occurred at every step in the change of medium dependent on its coefficient of density/elasticity. Let us eliminate the drum membrane and bring the full energy of the sound wave against the medial wall of the otic capsule. The course of the sound pulse through mucous membrane, connective tissue, periosteum, bone, finally periosteum and perilymphatic membrane will involve an innumerable series of reflections and dampings. As soon as the sound vibrations enter a rigid material like bone they may tend to remain within it through reflection back of the insulating connective tissue. They may tend, moreover, to follow the lamellar grain rather than pass across it. A great amount of energy therefore may be translated from a longitudinal to a transverse direction because sound vibrations behave in this manner in solids but not in liquids. The thickness and intrinsic structure of the petrosus may also limit the amount of energy discharge into the perilymph. The reason that individuals with stapedia fixation and normal end organ are deaf is not explained by Zimmermann. We may deduce that they are deaf because amplitudes of sufficient intensity and low pitch may not be introduced into the external canal under normal conditions to affect the perilymph through the

petrosium. This, at least, does not appear possible with the drum membrane intact.

The drum membrane, by reason of its position and structure, interferes with the sound vibrations passing through it from the external auditory canal. It does so because of the change in medium through which the energy must travel and because of the marked reflection back from its surface, and from that of the tortuous canal itself (see later).

The problem of the damping effect upon sound vibrations in their transmission to the perilymph is a complicated one. It is well to indicate that at least four phases must be considered: first, the effect of the shape and position of the external auditory canal; second, the damping effect of the drum membrane to sound vibrations passing through it into the cavity of the middle ear; third, the effect of drum tension on the sound transmission apparatus; and fourth, the damping effect of muscle contraction.

The photographic registration of sound pulses has been markedly improved within the past few years. In particular, the behavior of the sound pulse in reference to its passage through various tubes and membranes, by Foley of Indiana University,¹⁴ are well worth a close study by otologists. The following four photographs, presented through the courtesy of Professor Foley, shows the silhouette of a sound pulse which may be likened to serial photographs of a distending soap bubble. In the later, a limiting membrane is formed by a film of soap and water. In these photographs a limiting zone is created by the refraction of light caused by condensation and rarefaction in the air. The limiting zone of condensation (dark) and rarefaction (light) is therefore a criterion of the enormous amplitude in this short wave length produced by an electric spark. The sound pulse in the first three photographs, taken at about $1/1,000,000$ th sec., shows the behavior of the distending pulse in its passage through four kinds of schematic tubes: A straight cylinder (a); a megaphone with convex walls, small opening in and large opening out (b); a megaphone with the large opening toward the sound source (c); and a crooked tube (d). The reader will remember the dark band is in advance of the light band and indicates the direction of transmission. (Figs. 3, 4 and 5.)

In following the progress of the pulse through the straight tube (a) it will be noted that but little reflection occurs. There is but little decrease in the width of the band and practically no "bowing" in the wave front. Compare this with the megaphone (b). Again we find little evidence of reflection but a marked "bowing" of the wave front and a consequent dilution of amplitude due to the "side-slip" or diffraction. This "bowing" of the wave front may be readily seen when the position of the band at the edge of the megaphone is compared with that of the sound pulse in the straight tube. Compare this with the megaphone (c) and observe the enormous reflection back from the curved sides. Practically all the energy is reversed except that in the small area traveling on through the end of the megaphone. This small area compares favorably both in position and intensity with that of the corresponding point in the straight tube.

It is interesting to note the behavior of the sound pulse traveling through the crooked tube. Here an enormous dilution in the original amplitude takes place through reflection of the energy at the convex sides of the tube. The position of the wave at the opening corresponds to that in the straight tube (i. e., the velocity of the sound is dependent on the medium through which it is traveling) in spite of the irregular course. The energy of the sound pulse as indicated in the width of the band has been materially damped out.

These photographs demonstrate the damping effect of a crooked tube very convincingly. In likening the behavior to the conditions in the external auditory canal, it must be remembered that in the photograph we are dealing with a single pulse of great amplitude and extremely short wave length in which the wave front enters the opening directly. Whereas, in the case of the external ear, we are dealing with much smaller amplitudes, much greater wave lengths and a wave front which enters the canal almost entirely through diffraction. It is not unlikely that a diagrammatic canal may be constructed and placed in the form and position of the human external ear and external auditory canal. If the same amplitudes were applied as in these figures, the amount of energy arriving at the lateral opening indicated in Fig. 5 in the crooked tube would be so greatly reduced it might even fail

to register by this method. And in any event, were a delicate membrane placed across this opening no photographic registration of a sound pulse passing through the membrane might be observed (see Fig. 6). The diffraction of the sound vibrations into the external auditory canal is undoubtedly supplemented through reflection from the external ear, as Kato's experiments seem to indicate (see later).

We may carry over this information to the report of Burnett's⁸ experiments which were undertaken in Helmholtz's laboratory. The sound vibrations in this work are carried over from the source by means of a rubber tube 1 m. long. The aural end of this tube was connected with a glass tube fixed in the external auditory canal. "The position of the glass tube in the external auditory meatus has a great influence on the experiments. When the tube is directed downwards and forwards, the experiments were almost invariably successful, but in any other position they may be partially or entirely unsatisfactory. For in the former position the sound waves strike directly against the membrana tympani and hammer, whereas in any other position they are forced against the sides of the auditory canal and are deflected or destroyed before they reach their destination."

It must be remarked in this type of experiment the external auditory canal was closed to the outside and the escape of back reflected energy through the external meatus was limited. The amplitudes of the sound vibrations conveyed in this manner are probably beyond normal intensities. The writer experienced no difficulty in hearing a low pitch fork attached to the end of a meter long rubber tube under similar conditions, even when the tube itself was twisted. It also appears mass drum membrane reactions arise only when the route to the membrane was rendered straight so that a direct impingement of intense sound vibrations might take place.

Nagel and Samajloff³⁰ made similar observations by means of the clever arrangement of connecting the middle ear region in such a way that it was so interposed in the feed to a sensitive flame. "It was found necessary to maintain an open pathway through which the sound vibrations might pass to the drum membrane, and the tube, tied in the external auditory canal, was placed under tension so that the canal could be

rendered straight." "We applied a vibrating fork upon a cranial area corresponding to the head of the malleus and observed pronounced reactions in the flame. This was more pronounced when the external auditory canal was closed. This may be considered new evidence of the incorrectness of the Harless notion that the interpretation of the Weber and Wheatstone experiments (that a tuning fork is heard more loudly through the teeth when the external auditory canal is closed) might be regarded as a deception or error in judgment. The experiment further demonstrated that vibrations in the bone are carried over to the air of the external auditory canal and from this to the drum membrane."

Nagel and Samajloff also observed that similar reactions took place in the sensitive flame to vocal and bone transmitted sounds. It is not unlikely that the Harless interpretation is not a correct one. The transmission of vibrations through the finger in the external auditory canal with the fork applied to the knuckle illustrates this in a simple manner. It is also probable that bone transmitted sound vibrations normally pass through the ossicular chain. On the other hand, the experiments of Nagel and Samajloff were performed under abnormal conditions. They probably were dealing with abnormal intensities in a dead animal, and the explosion waves which arise in speaking or whispering into a tube were not ruled out. The detailed article of Harless on "Hearing" is worthy of careful consideration by any student of this subject. Harless was a prominent exponent of the theory of molecular transmission and even diagrammed the "centering" of the energy upon the footplate of the stapes.

Dennert¹¹ is also an exponent of the molecular transmission of sound vibrations through the ossicular chain. He makes an interesting series of objections to the experimental evidences on the mass movement reactions. We take the liberty of quoting from his work because his article has not received merited attention:

"An attempt has been made to confirm the theory of mass movements in the sound transmission apparatus by means of ear models and through the findings in normal and pathologic specimens. These experiments are indeed germane because they indicate the interrelation of the entire intratympanic ap-

paratus including the labyrinth contents in toto. A movement of the apparatus, including the contents of the labyrinth, has been established with the manometer as a result of gross mechanical causes, such as the experiment of E. Weber, in which pressure was exerted upon the apparatus through the finger; those of von Helmholtz, in displacements of the manubrium mallei in a model constructed by him; in the registration of plus and minus pressures; and under the influence of very powerful sound vibrations. But these observations do not demonstrate that similar mass movements of the sound transmission apparatus, including the labyrinth contents, actually occur under normal conditions of hearing, because under normal circumstances we are dealing with extremely minute power factors. The observations on the phonograph have been regarded as an important substantiation of the mass movement theory, and it may not be denied that these observations are apparently in accord with the ideas of mass movements in the sound transmission as applied to the ear. But here also, as has already been mentioned in regard to the experimental investigations on models and preparations much greater forces are required, and the demonstration is one which shows a tremendous superiority of the ear over the phonograph in relation to sound vibrations of small intensity. According to Morak, whispered numbers may be correctly understood at a distance of 89 m., but they are not registered by the phonograph even when spoken directly into the megaphone. The vast superiority of the ear over the phonograph may still better be demonstrated in the quantitative method of testing hearing devised by myself in which, with a low pitch fork, a certain number of vibrations are permitted to impinge upon the drum membrane in a certain unit of time. While one of my forks with a vibrational duration of 30 sec. may be picked up as intermittent in passing it by the external canal three or four times a second, practically throughout its entire duration, the phonograph, in spite of its diaphragm and its lever mechanism, fails to record this same fork when vibrated continuously deep in the megaphone. We may therefore regard the observations on the phonograph as analogous to the above mentioned observations on models and specimens and as gross mechanical processes of sound transmission, while the molecular trans-

mission to the ear is a more ideal, and much more delicately refined process connected with minute forces in the sound vibrations." This may also be regarded as an answer to the Wrightson contention that the inner ear must operate under similar conditions to those under which the phonograph registers the molar movements of its diaphragm.

The damping effect of the drum membrane on the sound vibrations impinging upon it and being transmitted through it into the air of the middle ear also deserves mention. According to Zimmermann, the membrane offers little or no resistance. Professor Foley obligingly made a photograph of the reflection back of a sound pulse projected against a delicate collodion membrane probably not one-fifth the thickness of a human ear drum. (Fig. 6.) This membrane was supported by a wire holder which appears as a heavy dark band. The amount of reflection back is enormous, and if the reproduction of the figure is successful only a delicate line will complete the circle on the far side of the wire holder. This may be taken as evidence of two things: First, the actual damping effect of a membrane, and second, the very small amount of energy which is required to stimulate the inner ear through the sound transmission system. If one can overhear the conversation in an adjoining room through a closed door it is probably safe to assume that not 1 per cent of the energy in the first room passes into the second through the door and walls.

The damping effect of the drum membrane will therefore mean on the basis of the diaphragm-rod theory that only a very limited amount of the energy transmitted through the external canal will pass into the drum membrane. This will necessarily limit the amount of transmission of sound vibrations to the perilymph because of the small and inefficient catchment area.

It has been demonstrated that the position and character of the external auditory canal has a decided damping effect on sound vibrations. These vibrations must enter through diffraction or a sideslip in the wave front of practically 90°. It was also shown that a large amount of the original energy entering the external canal is reflected away from the drum membrane area. It has been indicated that only a small

amount of the energy striking upon the drum membrane enters that membrane. A large part is reflected back into the external auditory canal. It was also pointed out that the drum membrane yields but little of the energy it receives to the air of the tympanum. We are now prepared to consider the relation of the tension of the membrane in reference to the problems of sound transmission into the ossicular chain. The relation of drum tension to the amount of back reflection must be considered and the influence of drum tension upon the transmission of energy into the ossicular chain also taken into account.

It has been shown by Mangold and Eckstein²⁸ that "even if a true damping of sound vibrations may not be disputed and has been established during the voluntary contraction of the M. tensor tympani in E. (an individual), we must, however, emphasize that neither of us received the impression that an irritating sound stimulus is damped and rendered less irritating through the tension of the M. tensor tympani as determined by the noise of its own contraction. Even strong tensor contractions, which lead to distinctly recognizable tensor noises as well as to demonstrable pressure variations in the external auditory canal, show themselves powerless to damp the disagreeable sensation. The assumed protective reflex against strong and high pitch sound stimuli is even more problematic in individuals in which the contraction of the tensor in its assumed reflex function is not subjectively recognizable and, until this time, could scarcely be classed as objectively demonstrable."

The increase in drum tension, according to this statement, does not produce a pronounced damping effect. This must be interpreted according to the diaphragm-rod theory. The string telephone operates through a tense membrane and with its most tense area at the attachment of the transmitting element. If the medial displacement of the malleus increases the tension in the connective tissue of its periosteal attachment to the drum membrane, it will also increase the efficiency in transmission of sound vibrations from drum membrane to the malleus. Any damping effect therefore which may come about must be referred to the less efficient catchment through a more tense drum or to the subtraction of energy through the tensor

tendon itself. Connective tissue under tension is a better transmitter than nontense connective tissue.

The point that the efficiency in the sound transmission apparatus depends in part on the positive pull of the malleus against the drum membrane is not merely a speculation. It lends itself well to the interpretation of the deafness caused by a hypertense drum membrane. Hypertension is usually due to the medial displacement of the drum membrane through air absorption or through adhesions. The connective tissue between the drum membrane and malleus is relaxed in these conditions and sound transmission from drum membrane to malleus impaired. It appears that the M. tensor tympani through its contraction will tend to damp out mass movements through the increased "weighting" of the drum membrane itself.

Both the Burnett and the Nagel and Samajloff experiments appeal to the writer as insufficient in the determination of the optimum, and in particular the minimum energies. Both series of experiments appear to show that mass oscillations of the drum membrane may arise under circumstances of unusual intensity in sound vibrations. One would not test the efficiency of a dictaphone by removing the mouthpiece some distance from the lips and whispering softly in its general direction. The two experiments noted in the previous paragraphs demonstrate the "damping out" effect of the external auditory canal and the drum membrane, even when the sound vibration is conveyed directly to the external canal. The damping effect will be more pronounced when the sound pulse undergoes a lateral dilution in its "side slip" at an angle into the external auditory opening. We must also bear in mind the surprisingly small amount of additional damping which even large masses of cerumen occasion. This will be discussed in Chapter III.

Kato has considered the problem of the "damping out" of the sound vibrations in their transmission through the ossicular chain, and the reader is referred to his article for details. "While it has been more or less generally accepted, in spite of the evidence to the contrary presented by Bockendahl, that the intrinsic muscles respond to sound vibrations with lightning-like contractions, comprehensive and repeated experiments have demonstrated that both of the intrinsic muscles respond

with prolonged contractions as long as the sound may operate." "Opposed to this, however, are the findings that actual medial displacement of the ossicular chain does not occur as a result of the reflex contraction of the M. tensor tympani, because the M. stapedius always responds and fixes the stapes. The M. tensor tympani reacts to stronger stimuli while the M. stapedius responds to weaker intensities; the contraction of the former is therefore always accompanied by reaction in the latter. However, no actual medial displacement of the stapes ever occurs, as has already been pointed out. This would only take place if the M. tensor tympani contracts independently, under which circumstances (with the M. stapedius out of commission) a medial displacement of the stapes may be observed in the reactions of the membrana tympani secundaria. Inasmuch as muscle contractions arising from sound vibrations never occasion an increase in the perilymphatic pressure, the 'damping out' effect suggested by Zimmermann (in terms of increase in the tension of the membrana basilaris) may not be considered."

"In conclusion, some mention must be made of the manner in which the intrinsic muscles perform their function of 'damping out' the intensity of sound vibrations. There are two possibilities: either the fixation of the stapes and the more marked drum tension results in a decrease in the amplitude of the vibrating masses, or a diminution of the intensity with which the sound vibrations are transmitted to the labyrinth is brought about through these changes. Naturally it is possible to conceive that both mechanisms may operate."

Kato's experiments on the reflex reactions to sound vibrations in the rabbit and the cat are extremely instructive. They give a possible test for acuity and range in hearing in various forms which is much more satisfactory than any hitherto known. The cat responds reflexly to pitches of 200 to 300 vibrations per sec., while the rabbit reacts to 128 and occasionally to 64. The fact that the M. stapedius contracts to 50,000 vibrations per second, which is entirely beyond the range of hearing in the human being, indicates a molecular transmission rather than a mass response. It is impossible to conceive a mass response in sound transmission apparatus to a frequency of 50,000.

The rabbit reacts to the pitch A3 at a distance of 60 m., but if the external cartilage is removed this distance must be cut down to 29 m. Removal of the drum membrane reduces the distance still farther to 8 m.; while reflex contractions are, however, again provoked with the pitch A4 at a distance of 5 cm., with malleus and incus gone and even with the stapes removed, reaction in the muscle may be observed if the source is applied immediately to the external canal. This evidence is very important in considering the efficiency of the damping effect of the external canal, and also the efficiency of the membrane and ossicular chain route for the transmission of sound vibrations as opposed to the direct route through the medial tympanic wall or round window as suggested by Zimmermann and others.

The normal cat under certain test conditions becomes reflexly deaf in about five hours, while rabbit under similar circumstances is deaf in from five to six minutes. The time is markedly reduced if one of the muscles is out of commission, and still more markedly reduced if both muscles are cut or thrown out of function by means of profound narcosis. It has also been shown in various mammals and birds that cochlear degenerations occur earlier as a result of the exposure to prolonged high pitch vibrations in animals with the intrinsic muscles incapacitated than in those with muscles intact. Objections may be made to these experiments in that the animal is subjected to abnormal conditions of sound intensity. The extent of the lesions in both animals and birds indicates that at least two factors operate in producing the results. First, a fatigue and possible degeneration of a small cochlear area as a result of overstimulation; and, second, the spreading and relatively indefinite area of degeneration shows that mass movements in the perilymph are also probably responsible for the greater part of the resulting lesion. The relation of the problem of experimental cochlear degeneration and its bearing upon occupational deafness may not be taken up at this time.

It is, however, permissible to indicate that further work is demanded on the problem of the damping out of sound vibrations. Attention has already been called to the effect of the position of the external auditory canal and to the "side slip" of the sound wave front entering it. Investigations also ap-

pear to show that a great amount of the original energy entering the canal and registering in the form of drum membrane responses is "damped out" through reflection from the tortuous walls of the canal itself. Foley's sound pulse photographs indicate that a very large amount of the original energy striking upon a thin celloidin membrane is reflected back toward the source. Finally, the writer has emphasized the oblique position and the physical character of the drum membrane as objections to a mass response as a result of normal or optimum amplitudes of sound vibrations. It does not appear likely that the muscle tension or the stretch of the elastic ligaments can subtract any very material amount of the energy passing through the transmission apparatus. This appears to conform with the inability, voluntary or otherwise, to actually damp-down or damp-out sound vibrations. The damping response must be correlated, however, with the experiments of Kato, where he finds a stapedial contraction to extremely high pitches (50,000). He also obtained reactions to sounds of reasonable pitch at a distance of 60 m., which is probably beyond the range of the explosion or concussion waves arising from the sound source.

There can be little doubt that the rabbit hears the sound indicated in Kato's experiment at a considerably greater distance than 60 m. The fact that the response was not elicited beyond this distance with the external ear intact or at more than 29 m. with the external ear removed will show that sufficient energy is being applied to cause mass response of some kind and contraction of the muscle to "damp out" these movements of the stapes as a whole. This is to the writer a very important point because it indicates that the M. stapedius is definitely opposed to mass movements in the sound transmission system. The amount of molecular transmission is already limited through the size of the catchment area itself and by the factors already noted. It appears unlikely under normal conditions that sufficient molecular response through the drum membrane and ossicular chain could be produced to effect an actual degeneration of the cochlear apparatus. However, the excessive amplitudes could, and undoubtedly would, provoke mass responses which the intrinsic muscles might eliminate as long as they are functional. This is equiv-

alent to saying that the cochlear degenerations arise at least for the most part from mass movements in the sound transmission apparatus due to excessive amplitudes. As long as the muscles are physiologically capable of cutting down these mass movements, the reflex deafness does not come about. It is not fair to assume that the rabbit has a keener sense of hearing than the cat and therefore becomes deaf in five minutes under conditions that produce reflex deafness in the cat in five hours. The cat may be able to damp out vibrations more readily. It may also flatten out its external ear and offer a certain amount of additional damping out to the diffraction of sound vibrations into the external canal. This is apparently what takes place, because the cat not only flattens the ears against the head but also presents its tail toward the sound source.

The deafness which comes about through lateral displacement of the drum membrane, either due to a plus pressure in the middle ear or relaxation of the *M. tensor tympani*, or both, is probably not due to a disengagement of the incus from the stapes, which, as Bezold has noted, breaks the contiguity in the ossicular chain. It has been mentioned that the passive traction system of incudal ligaments opposes the contraction of the *M. tensor tympani*. It therefore contributes to a lateral drum membrane displacement on relaxation of that muscle. The lateral displacement of the long process of the incus from the stapes will readily come about because the ligamentum annulare is a very strong stapelial attachment when compared with the delicate elastic capsular ligament at the incudostapelial articulation. This disengagement may be observed in the guinea pig, where the malleus and incus are united by bony ankylosis and where the lateral displacement of the malleus necessarily carries the incus with it.

If Secchi's observations³⁶ are correct, then the middle ear is normally under a slight plus pressure. A tonus contraction of the *M. tensor tympani* might be assumed to maintain a contiguity at the incudostapelial articulation. The problem is not to be regarded as definitely settled. The suggestion may, however, be made that drum membrane tension is, after all, only an incidental result and is not the purpose of the contraction of the *M. tensor tympani*. This will at least con-

form with the relations as they are observed in birds where the M. tensor tympani function does not appear to be definitely related to the drum membrane tension.

Kato's experimental evidence on reflex contraction of the intrinsic muscles and the reactions which may be interpreted in terms of acuity in hearing demonstrate that the drum membrane and sound transmission system are the efficient means of transmitting sound vibrations. This is in direct opposition to the contentions of Zimmermann, Kleinschmidt,²⁷ Secchi,³⁵ Kretschmann,²⁵ and others, that the transmission takes place through the air of the tympanum, either through the medial wall of the tympanum or through the fenestra cochleæ. The reader is referred to the excellent reviews of Treitel,³⁵ of Frütiger¹⁷ and of Lucæ.²⁶

The writer feels justified in presenting the diaphragm-rod theory of sound transmission and declaring that the mass movements ordinarily described lie beyond the physiologic maximum. In other words, the entire apparatus from drum membrane to hair cells is set in for molecular vibration. The moment mass movements of the drum membrane arise they are damped out in so far as this is possible. The sound transmission system therefore represents a most efficient area of bone transmission to the inner ear, and in particular is this true in small amplitudes (intensities) and long wave lengths (low pitch).

The registration of vibrations in the auditory cells may therefore be effected by the sound pulse passing on them or through them. Neither membrana basilaris nor membrana tectoria can effect the mechanical stimulus essential to a reaction. The fact that the auditory cells are hair cells and the fact that they are definitely related to a membrana tectoria may be due to the ancestral type of pressure organ or displacement organ from which they are derived. The membrana tectoria may perhaps offer inhibition to mass movements. It may be a sort of stabilizer. This X quantity, which occasions a reaction in auditory cells to vibrational frequency and intensity, is not particularly different from the behavior of the retinal cells. Is it really essential to our conception of the behavior of the light in the various media of the eye that the workings of the rods and cones be established? Perhaps

then we have arrived at a point where our limitations confront us. We may assure a sensitization of cells to picking up frequencies and their amplitudes. We may harmonize this behavior with the extensive researches in cochlear degenerations as a result of prolonged auditory irritation. But we may also at this time remember the words of the immortal Goethe: "Eben wo Begriffe fehlen da stellt ein Wort zur rechten Zeit sich ein."

It appears therefore that the drum membrane and entire sound transmission system is set in for appreciation of sound vibrations of small amplitudes. When amplitudes of sufficient intensity are produced, the tiny mass vibrations of the drum membrane are absorbed and dissipated in the hinge system of the sound transmission apparatus and further inhibited by the contraction of the intrinsic ear musculature. The very minimum which the displacement theorists grant may therefore represent a maximum of hearing or even beyond the capacity of appreciation in terms of intensity of hearing.

The writer appreciates this last statement is a decided shock to anyone who has followed the mass displacement theories in any one of the various forms. Perhaps the first thought which comes to mind is this: if a balanced drum, a straight rod and an insulated opening in the otic capsule to the perilymph fulfill the requirements for sound transmission from air to end organ, why do we find a more elaborate mechanism with muscle attachments and elastic ligaments? Why is it essentially that a fenestra cochleæ with its limiting elastic membrana tympani secundaria be found in practically all forms of terrestrial vertebrates? These questions, proposed by Beyer, may be quite successfully answered. If the explanation does not hold on the basis of comparative anatomy and physiology, then the diaphragm-rod theory cannot be employed as a working basis. If this be accomplished, the problem stands open for the tests of repeated experiment before the theory may be accepted. The essential differences between all displacement theories and that of molecular transmission consists in this—not only must the inner ear be physiologically guarded against any factors of displacement arising from sound vibrations, but all displacement factors arising in the middle ear must also be ruled out in so far as this is possible.

X. What is the function of the middle ear complex?

Keith remarks in relation to the Wrightson theory that we must seek an explanation in the comparative anatomy and physiology for matters which are not clearly defined in the human being. Objections were made to the confirmatory evidence proposed by Keith because the close agreement in the general structural pattern of the inner ear merely shows that the structure of a given part must bear some definite relation to the ancestry of the organ. This is neither a discovery of Keith's in reference to the inner ear nor does it substantiate the Wrightson hypothesis more than it does any one other of a dozen theories. It was also pointed out that the mechanical relations in the bird are less readily associated with the Wrightson hypothesis than they are in the mammal. This also obtains for any other displacement theory. The very similarity in structure will make any theory of hearing which includes the facts obtain for mammal and bird alike. In other words, if we solve the problem for one form we solve it for all forms within certain limits which are dependent on individual variations.

Curiously enough, the entire Wrightson hypothesis rests on a middle ear behavior; the mass reactions in the drum membrane; the "intensifying press" function of the ossicular chain; the muscle balance; the displacement of the stapedial footplate in relation to the membrana tympani secundaria. Yet Keith furnishes no evidence wherein the comparative anatomy such as that of another acutely sensitive form, the bird, furnishes a confirmation to the correctness of these fundamental conceptions. Perhaps therefore a study of the comparative anatomy and physiology of the frog, the bird and the mammal may furnish a clue to the complex middle ear system. It must be remembered that the middle ear region has a far more interesting phylogeny than that of the inner ear. It was stated in the beginning of this article that a consideration of the reptiles would be eliminated. This family presents an extremely variable picture which must, of course, not be disregarded. The reader is entitled to first hand information in so far as this is possible. We have not investigated the reptilian ear. Three forms have been selected—the frog, the bird and the mammal, because they represent three distinct

possibilities in middle ear mechanics. The information on the frog has been largely derived through courtesy of Terence Ahearn, S. J.,¹ who is at present writing his doctor's thesis on the problem, undertaken in this laboratory. The reader is referred to Ahearn's article when it appears for a detailed description. The work on the bird and the mammal are a result of personal investigation. The report on the elastic ligaments of the cat (dog may also be included) are presented for the first time.

A. The middle ear mechanics in the frog. (Fig. 7.)

The drum membrane in the frog is relatively thick (d. m.) and is supported by an annulus (an.) of cartilage. The sound transmission system is roughly in the form of a twisted U, with one extremity of the U markedly thickened and the connection between the two arms is swollen. The cartilage portion (lateral) displays two definitely weakened areas at which bending occurs upon light pressures. Following the apparatus from the otic capsule (o. c.), the small descending process displays a hinge at (a) and then swells to be attached to the medial drum membrane surface. This attachment area runs upward, loses its connection to the drum membrane and forms a small process which bends sharply on itself at hinge (b) to continue medialward in an enlarged club shaped mass—the columella proper—which occupies the upper area of the fenestra vestibuli. It will be noted that the surface of this process is in relation to the perilymph (pl.) and is insulated by elastic ligaments from direct contiguity with the otic capsule at its upper surface. Below it is mortised into another cartilage element the operculum (o). It is joined to the operculum by elastic ligaments. The operculum is confluent with the otic capsule at another cartilage hinge (c) so that all movements of the sound transmission system are accompanied by accompanying movements in the operculum. The outward displacement of the cartilage is resisted by a stout elastic ligament (not indicated), while the inward displacement is resisted by the M. opercularis, the action of which is indicated by the arrow (m).

The inner ear system is represented as a hole in the otic capsule filled with perilymph (pl.) and containing a ductus cochlearis (stippled). The capsule has three chief openings—

the fenestra vestibuli filled by columella, operculum and elastic ligaments. The second opening is the foramen perilymph sup. (F.P.S.), where the perilymph liquid is separated from that of the spatium subdurale (S.S.) by a thin membrane. The third opening or foramen perilymph, inf. (F.P.I.), is closed in by an elastic membrane, the membrana tympani secundaria (M.T.S.), which faces the mouth cavity but is separated from the mucous membrane by a lymph sac (L.S.) and by muscle fibers (not indicated). It will be seen that the tuba auditiva (t.a.) is a short wide open duct leading from the mouth to the cavity of the middle ear.

When the frog swallows the air, the middle ear cavity is placed under a plus pressure with a resulting lateral drum membrane excursion indicated by the arrow $+$. This force, because of hinge "a," is translated at "b" into a reverse motion indicated by the arrow. The motion of the drum membrane outward tends to thrust the sound transmitting system into the perilymphatic space so that increases in pressure would escape along the lines indicated by the fine arrow—through the cochlear duct or around the cochlear duct (helicotrema) toward the foramen superior and foramen inferior. Minimum motions are probably compensated for in the vascular supply. However, larger movements are prevented by the contraction of the M. opercularis. This muscle is therefore opposed to both displacement factors in the columella proper. It is also interesting to see that if a medial displacement factor is applied to the drum membrane (arrow x), the area at hinge 'b' will become applied to the drum membrane and the resulting motion in the columella will be the same as before.

The mechanism in the middle ear in the frog is a response to an adjustability in the sound transmission system which arises because of the lateral drum membrane motion. This motion is dependent on respiration and allows a maximum excursion at the drum membrane area with a minimum response at the perilymphatic end. The active phase opposed is the plus pressure due to air injection. It may also be stated that according to the diaphragm-rod theory an inefficiency in the apparatus may be seen in the direct connection of the sound transmission system to the otic capsule, and in the thickness in the membrana tympani. The articulation of the columella

with the opercular cartilage merely indicates a large adjustment area toward preventing pressure fluctuations in the perilymphatic system. It is also necessary to bear in mind that the helicotrema in the frog is an extremely wide opening offering none of the objections of resistance to displacement mentioned by Wrightson for the mammal and bird.

While the frog does hear certain things, its sound transmission system and drum membrane do not appear particularly well adapted. Nor does the development of the inner ear suggest a refined sense of hearing.

B. The mechanics of the bird's ear. (Fig. 8.)

The schematic diagram of the bird's inner ear shows similarity to that of the frog excepting that the *membrana tympani secundaria* (M.T.S.) (*fenestra cochleæ*) has rotated to face the middle ear. It must be remembered in some birds (the goose, etc.), the *fenestra cochleæ* is separated from the *cavum tympani* by the *vena jugularis*. The *membrana tympani* (D.M) in birds is thin and markedly convexed outward into the external auditory canal; the two middle ear cavities are confluent, and the two *tubæ auditivæ* (t.a.) open through a common tubal duct (t.d.) into the mouth. This small opening is normally closed. The sound transmission system consists of a cartilage tripod which occupies the posterior drum area. The *M. tensor tympani* attaches to one element of this tripod. This muscle is extratympanic and the line of its pull is indicated by the arrow M. The muscle is resisted by elastic ligaments, notably the columellar-squamosal ligament (c.l.) of Platner. The cartilage apparatus joins the bony columella just medial to the attachment of this ligament. The bony columella (C) is attached to the margins of the *fenestra vestibuli* by elastic ligaments, and the *membrana tympani secundaria* is also elastic in structure (M.T.S.). The otic capsule is now well separated from the *cavum subdurale*, and a hole is left in it to represent schematically the *aqueductus cochleæ* and *aqueductus vestibuli* (aq.). It will also be noted that the *membrana vestibularis* (Reissner's membrane) is indicated in a heavy vascular *tegumentum vasculosum* (T.V.).

When the *tubæ auditivæ* open freely to the mouth, the air pressure on each side of the drum membrane is probably equal. Displacement forces arise with closed tuba, either through air

absorption or through positive pressure at the external auditory canal. The latter tends to thrust the columella inward and beget increased pressure in the perilymphatic spaces. This increased pressure will be absorbed by the blood vessels (note the position of the tegmentum vasculosum), or may escape through the aqueductus cochleæ et vestibuli or at the membrana tympani secundaria. The contraction of the M. tensor tympani directly opposes this and tends to hold off the inward drum membrane displacements from increasing the pressure in the perilymph (pl.). Negative pressures in the external canal are also resisted by the elastic ligaments and compensated by the great mobility in the drum membrane. There are also a series of cartilage hinges in the sound transmission system which allow a more pronounced reaction in the tripod cartilage than in the bony columella proper (see writer's article, *American Journal of Morphology*).

The mechanism in the bird's ear is one set in for variations in drum membrane position. The compensation system is found in an adjustability of the sound transmission apparatus and is of direct physiologic importance. The muscle tensor tympani does not figure conspicuously in terms of drum tension, although this necessarily results. Rather the M. tensor tympanum in birds combats active displacement factors which tend to produce excesses of perilymphatic pressure. The cochlear area in birds is poorly placed to be acted upon by sound vibrations direct through the otic capsule. The range of adjustability of blood vessels in the perilymph system is even better developed than in the mammals. It may also be mentioned that the columellar footplate does not lie at the end of the cochlear duct but faces its middle area.

C. The mammal. (Fig. 9.)

The schematic diagram presents the relations in the human being, and some reservations must be made in carrying over this scheme to the cat, the guinea pig and in particular the mouse. The two middle ear complexes are completely separated. A new cartilaginous tuba auditiva is shown as closed with the function of the M. tensor veli palatini (M. dilator tubæ) to open it indicated by the arrow M. d.t. The drum membrane is drawn in and attached to the malleus. The position of the incus and stapes is indicated. The pull of the

M. tensor tympani is represented by the arrow at M. t., while that of the M. stapedius is shown by the arrow M. s. The inner ear is about the same as that pictured for the bird and frog, which will indicate the purely schematic presentation. The heavy vascular tegmentum vasculosum in the bird is replaced by the delicate nonvascular membrana vestibularis.

When the tuba auditiva is opened, the M. tensor tympani appears to relax, allowing lateral displacement of the drum membrane. This lateral displacement of the drum membrane may be due to several factors: first, the intrinsic elastic structure of the drum membrane, which will tend to decrease the umbo-depth slightly; second, the incudal elastic ligaments and character of the incudomalleolar articulation may contribute to a positive push factor outward of the malleus; third, the manner of tubal closure may create a positive pressure within the middle ear region as Secchi has suggested; and lastly, a minus pressure in the external auditory canal (barometric) will tend to draw the drum membrane outward. It appears that the drum membrane at rest is not placed in a position of physiologic efficiency and tendency for a disengagement at the incudostapedial articulation must be counteracted by muscle pull. This mechanical requirement in the mammal does not obtain in any other vertebrate. The diagram presents a possible interrelation between the M. tensor tympani and the M. tensor veli palatini. The arrows indicate the former muscle is set in against any factors which will make for a lateral drum membrane displacement. The medial displacement of the ossicular chain tends under unusual conditions of pressure to force the stapes toward the perilymph and beget increases in perilymphatic pressure. This is opposed through contraction of the M. stapedius. The distribution of the possible excess pressure in the perilymph, apart from that taken care of in the minute veins, is shown in the arrows within the inner ear.

We must grant, on the basis of Kato's experiments, that reflex contractions of the M. tensor tympani do not give rise to fluctuations at the membrana tympani secundaria. It must also be granted that the M. stapedius absolutely opposes minute displacements of the stapedial footplate. The vascular regulator mechanism compensates for what would constitute

mass movements in the sound transmission system in reference to any motion created by responses of the drum membrane to sound vibrations of usual intensities. The compensation area in the membrana tympani secundaria will therefore not be called for in relation to either sound vibrations or to reflex contractions of the *M. tensor tympani*. It will only be effective in the larger drum membrane fluctuations which in the mammal are necessarily limited. It has been mentioned that the relatively larger fenestra cochleæ in birds is suggestive of a compensation area for perilymphatic adjustments to mass movements in the sound transmission system. These movements are not a result of sound vibrations but are due to barometric fluctuations and to air absorption.

The double displacement factor in mammals therefore calls for two muscles. A new muscle, *M. tensor tympani*, is related to factors which tend to produce a lateral displacement of the drum membrane and probably maintains a contiguity in the sound transmission system at the incudostapedial articulation. The second muscle is similar in function to the single *M. tensor tympani* in birds or the *M. opercularis* in frogs. The *M. stapedius* affords protection against increases in pressure through the application of a movable skeletal element to the perilymphatic space. Both of these muscles tend to inhabit mass movements in the sound transmission system.

Throughout the entire comparative anatomy of the middle ear region three prominent features appear: first, a variability in the position of the drum membrane not dependent on hearing but on displacement factors arising within the middle ear; second, an adjustability in the sound transmission system gearing down the mass drum membrane movements in relation to the fenestra vestibuli. These are not related to sound vibrations in their propagation to the perilymph but merely decrease the range of mass motion. Third, protection is afforded to the delicate end organ through muscle contraction against increases in pressure brought about through drum membrane displacements and in inhibition to the mass responses propagated from the drum membrane toward the perilymph. This appears to harmonize more completely with the comparative anatomy and physiology of the middle ear region than any suggestion thus far published. The work on the

intrinsic muscles of the mammal by Kato and the investigations on the human M. tensor tympani by Mangold are certain to stimulate researches along these lines. It is also important that the tubal mechanics and the function of the M. tensor veli palatini be included.

It is only fair to state that the contractions of the M. stapedius to the sound vibrations, as noted in the experiments of Kato, are not readily interpreted. We must assume that the M. stapedius is always in a state of tonus contraction. When a sound is superposed upon the sound picture of the environment to the point that it begins to occasion a mass reaction or a tremble in the stapes, an additional muscle contraction is manifested. This statement means that the stapes, because it is extremely light and because the energy is discharged from the footplate into a medium of shorter wave lengths, may have sufficient restoration forces connected with it to undergo mass reactions. The effect of the M. stapedius in its contraction, as confirmed on experimental animals, would be to act as a damper.

The comparative anatomy and physiology affords certain evidence which distinctly favors the diaphragm-rod conception of the sound transmission. It may be well to reserve judgment on whether this, that or the other theory is the correct one. It is our contention, however, that the older view of a molecular transmission has certain things in its favor. It should at least be included in our discussions of the problem. In particular, the diaphragm-rod theory lends itself well toward the solution of several features in deafness which have been considered as hopeless. Perhaps they have been considered hopeless because the mechanics of sound transmission have been looked upon as quite well established by Helmholtz.

We may take the liberty, in closing this chapter, to refer again to the opening paragraphs in this article, where we call attention to the fact that the "functional adaptation" and "structural adaptation," after all, are merely terms which indicate that we have approached the region where cause and effect may not easily be separated. It may come to pass that what we have been considering as the active stimulating factor in sound analysis—the membrana tectoria, membrana basilaris and the delicately refined histologic structure of the

end organ may, after all, be nothing more than an earmark of the ancestral pressure or displacement organ from which it was developed. The resultant microscopic picture must be followed with this point in view rather than believing it will necessarily explain a selective function in the auditory cells. Let us remember that whatever the method is by which these cells operate, even under the lowest tones, the ear is quicker in its response than the eye. The discrimination of a suppressed vibration up to a frequency in high pitches which exceed that of touch (130 per sec.), implies that marked after-images such as found in the retina do not occur. This is an important point to bear in mind, because a sympathetic vibration does not omit vibrations when the vibrations are eliminated from the activating source. The inner ear therefore appears to operate under no conceivable conditions of inertia, which indicates the activating agent as a sound pulse and not a mass response in the sound transmission system.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.