With the Author's Compliments.

3.

A NEW THEORY OF HEARING.

—BY—

C. HERBERT HURST, Ph.D.

WITH PLATE XX.

From Trans. L'pool Biol. Soc., Vol. IX., 1895, pp. 321 to 353.

3

A NEW THEORY OF HEARING.

By C. Herbert Hurst, Ph.D.

With Plate XX.

[Read December 14th, 1894.]

Introduction.

Kohlrausch's experiments described in Wiedemann's Annalen (Vol. X.), amongst others, show that two air-waves separated by a suitable interval of time suffice for the production of a distinct tone-sensation, the pitch being determinable by the ear within the limits of error expressed by the ratio 24:25. Increase of the absolute number of vibrations with the same time-intervals narrows the limits of error in determining the pitch by the ear, till the absolute number reaches 16, beyond which point a further increase does not appreciably facilitate the determination.

These results, and especially the first one, disprove, not only all existing theories of hearing based on assumptions as to "resonance" or response of sense-hairs, fibres of basilar membrane, or any parts of the organ "tuned" to the same pitch as the sound, but equally disproves all new resonance-theories of hearing which may ever be propounded in the future.

Limits of space forbid me here to repeat a description of the ear and especially of the cochlea. The description given by Professor Schäfer in Quain's Anatomy (10th edition) is accessible to all, and I have taken that description as correct except in that I have considered *both* edges of the tectorial membrane to be attached, the outer edge being, not free, but attached to the upper surface of the cells of Hensen. The measurements given (op. cit., vol.

III., pt. iii, p. 127) are in millimetres and not in micro-millimetres as there stated.

The aim of my investigation has been, not to find an explanation of the sensation of sound, at least not in the first instance, but merely to lay a solid foundation for future explanations by considering the physical changes produced in the ear by the impact of sound waves upon the tympanic membrane.

From this point of view it is equally important to follow out to the end the whole chain of effects in the case of every part, however little may seem the probability of finding in them a solution of the physiological problem of hearing: the problem to be attacked is indeed in the first instance not a physiological one at all, but one in pure physics, and as such it must be treated; leaving altogether out of account any and every physiological consequence which may follow, and carefully avoiding all those suggestive analogies with musical instruments which have led previous investigators into erroneous assumptions as to "functions" of one part or another. Each part must be considered, in the first instance, as an inert body whose properties are to be determined only by observation and not assumed beforehand on the strength of any preconceived notion as to the way in which they "must" act in order to produce certain effects.

For this reason the first portion of the theory is addressed to physicists rather than to physiologists and to the latter only is so far as they are physicists as well as physiologists.

The Physical Effects or Changes produced in the Middle Ear by the Impact of Sound Waves on the Tympanic Membrane.

The movement of the membrane, due to changes of pressure on its outer surface while the pressure on its inner surface remains nearly constant, produces effects upon the ossicles of the middle ear. To determine whether the ossicles move as a whole or as some have maintained they "transmit the sound molecularly" it is necessary to make a rough estimate of the velocity of sound in them and to consider what is the *length* of a sound wave when transversing the series of ossicles.

To determine this accurately is not easy but it is quite unnecessary: an error of even 10000 per cent. is of no consequence. The lowest audible tone is not the same for all hearers, but few if any can hear as a tone any sound due to less than 10 vibrations a second. A pure tone of 40000 vibrations is audible to some and the production of beats and beat-tones by simultaneous action of two sets of waves some of which in one series follow others in the other series at smaller intervals of time than this has been demonstrated by Koenig and others. It is only necessary therefore to consider whether the time required for transmission of a sound wave through these ossicles lies between $\frac{1}{50000}$th second and $\frac{1}{10}$th second, or above or below those limits. The mere consideration of the question even without answering it, suffices to show that the distinction drawn between the two modes of transmission is a distinction in words rather than in phenomena. If the wave length in the ossicles is much smaller than the length of the chain it would be said that the transmission is "molecular;" if it is much longer than the chain it would be said that it is "molar." The nature of the transmission is, however, identical in the two cases and the distinction is purely verbal and useless. The transmission of energy along a pulled bell-wire is of the same nature as the transmission of a sound wave: the energy is indeed transmitted as a true sound wave of enormously long period and enormously great amplitude: the wave length being enormously great as compared with the length of the wire. It is only necessary therefore to point out here that the movements of the base of the stapes follow those of the tympanic membrane but lag slightly behind them: how much they lag probably depends on the wave-length and on the intensity of the sound: the lag is probably less with intense sounds than with fainter ones. It probably amounts to less than a wave-period with low tones and to more than a wave-period with high tones. With very violent waves of long period the elasticity of the displaced membrane, the inertia of the ossicles, and the tension of the muscles and ligaments attached to the ossicles as well as the nature of the joint (saddle-shaped) between the malleus and incus will come into play and reduce the amplitude of displacement to a very small fraction of what it would otherwise be. The *scale* of relative amplitudes of displacements of the fenestra ovalis will therefore be very much smaller than that of the displacements of the tympanic membrane. Very faint sounds, in other words, will produce a *relatively* far greater effect on the ovalis than very loud ones: nearly the whole energy of high tones and of faint sounds will be transmitted to the ovalis, but only a very small fraction of the energy of more violent waves and especially of waves of great amplitude in the absolute sense (*e.g.* explosion-waves). This is a highly important protective arrangement and is analogous to the protective action of the iris in the eye.

The Changes in the Inner Ear.

The whole inner ear may be rightly regarded as a rigid box with only two yielding areas in its walls and filled with an incompressible fluid. The two yielding areas are the *fenestrae rotunda et ovalis.*

The errors involved in so regarding it have been roughly estimated and their effect on the conclusions which follow is *nil*. The chief of them is involved in the assumption as to the incompressibility of the fluids (perilymph and endolymph). These fluids are almost identical in physical properties with water and if we consider the modifications of the following account which would have to be made in the case of water we shall see that the error is one which does not affect the theory as a whole.

Water is compressed to the extent of rather less than $\frac{1}{20000}$th part of its volume by an increase of pressure equal to one atmosphere. No such pressure as this is ever brought to bear on the fluids in the ear; if it were the transmission of the effects, *i.e.*, of the movements, would be accelerated. As I shall give a justification for the assumption that this transmission is *infinitely* rapid nothing tending to increase that velocity can possibly affect our conclusions except in the direction of increased accuracy.

The velocity of sound in water is almost one mile per second. The distance between the fenestræ ovalis and rotunda is about $\frac{1}{8}$ inch. The time required for transmission of a pressure wave ("sound wave") from one fenestra to the other is less than $\frac{1}{400000}$th of a second, *i.e.*, less than $\frac{1}{10}$th part of the time-interval between two successive waves of the highest audible note. I shall regard this interval as *nil*, and shall regard the movements of the two fenestræ as *simultaneous*, which is equivalent to regarding the velocity of sound in the fluids as infinite and the fluids themselves as incompressible. It will be seen later on that the error involved in this assumption does not, even in the most minute degree, affect the soundness of the conclusions.

The assumptions being justified I will take a series of problems in the following order :—

1. The changes produced within the cochlea by one inward movement of the stapes followed by its immediate return to its position of rest.
2. The changes produced by two such double movements.
3. The changes produced by a long series of such movements at equal intervals of time—as by the impact of the sound-waves due to the sounding of a constant pure tone.
4. The changes produced by the simultaneous action of two such series of waves due to sounding two notes in harmony.
5. The corresponding problem in the case of discordant tones.

Problem I. *Changes produced within the cochlea by one double movement of the stapes* (*in, then out*).

The stapes, and of course the fenestra ovalis in which it is embedded, moving inwards, the rotunda must on the foregoing assumptions move outwards *simultaneously*. This involves movement of the fluids between. This movement is interfered with by the membranes lying between the two scalæ, upper and lower (*i.e.*, scalæ vestibuli et tympani), of the walls of which they form parts, and the displacement of these membranes together with the subsequent effects of those displacements presents the fundamental and most important problem we shall have to consider.

For convenience the cochlea will be regarded as a spiral with its axis *vertical* and the apex at the top: the basal region is then the region where the fenestræ are placed: the three scalæ, *tympani*, *media* and *vestibuli* become the lower, middle and upper canals and the basilar and Reissnerian membranes become the lower and upper membranes respectively. Movement *along* a canal will be spoken of as forwards or backwards according as it is towards the apical or towards the basal region.

First as to the upper membrane. The fenestra ovalis is placed at the junction of vestibule and cochlea. Pressure applied to it affects the fluids within and around the membranous vestibule equally, as also around and within the *canalis reuniens*. Any movement of the upper membrane near the junction of the walls of the *canalis reuniens* with it will therefore be due to friction only and not to difference of pressure on its two surfaces. This portion of the upper membrane is moreover loose and flabby and the movements which can only be slight will involve no stretching. The membrane is moreover light, broad, thin, soft and relatively inelastic (on account of its looseness at this point) and it will move therefore freely as part and parcel of the fluids in which it is immersed, such elasticity as it possesses not being brought into play. The effects of a wave of this membrane if one should be produced would be identical with, but enormously smaller than, the basilar wave to be considered directly. For the present therefore we may without error ignore the existence of the upper or Reissnerian membrane, and look upon the basal portion of the cochlea as consisting of only two chambers or canals separated from each other by the basilar or lower membrane.

The lower membrane is very different. It is exceedingly narrow, its basal end may be said to end almost in a point: it is not only exceedingly stiff by virtue of its transverse fibres, but its elasticity is enhanced by the *transverse* tension under which it is stretched between the two bony ridges supporting it. A very slight displacement will therefore instantly call its elasticity into play, and the movement towards the lower canal affecting first its most basal portion will rapidly extend along the membrane during the whole period of positive acceleration of the inward movement of the stapes, tension being greatest at the basal end. During the second portion of the advance of the stapes (with a negative acceleration) this first portion of the lower membrane will commence to return to its position of rest, a longitudinal movement of fluid in its neighbourhood being involved therein. This movement of fluids will be forwards in the upper canal and backwards in the lower canal but will extend through only a small distance, and will affect chiefly the portion of fluid very near to the surfaces of the membrane, but not quite in contact with them. The reverse or the return movement of the stapes will produce a similar effect in the opposite direction, the first portion of the return movement of the stapes augmenting the fluid movements of the second part of the advance. If we now consider the condition of the parts near the base at the moment when the return movement of the stapes is just completed we shall find that they are such as are necessarily transmitted in the form of a wave, though a wave very different from either a sound wave or a wave in water or any wave which has hitherto, so far as I know, been considered by physicists or mathematicians.

Let ABCDE, in fig. 1 (Pl. XX.), represent the middle line of the displaced membrane, A being the basal end of it. The portion AB is moving downwards to its position of rest, the fluid displaced by it below being driven forwards (*i.e.*, away from the basal end of the canal and towards the apex); the fluid above moving downwards with the membrane and somewhat backwards, its place being filled by fluid from beyond B.

The portion BC is moving upwards, being carried by the moving fluid below which is driven forwards by the downward movement of AB. The portion CD is returning by virtue of its own elasticity towards its position of rest, to be immediately carried beyond that position by the movement of the fluid, below it; while it is itself forcing the upper fluid forwards thus depressing the portion DE. The small arrows in fig. 1 show the directions in which each portion of the membrane is moving at the moment, viz:—AB and DE are moving downwards the points A, B, D, and E being momentarily at rest, A and E in equilibrium B and D at maximum tension. BC is moving upwards with increasing tension and diminishing velocity; CD upwards with diminishing tension and increasing velocity. At C is the point of no tension and maximum velocity. The large arrow shows the direction in which the wave will travel forwards.

Fig. 2 shows in a generalised and simplified way the movements of the fluids. In the upper canal the fluid is moving from the central wave-region outwards in both directions, *i.e.*, forwards from N to M and backwards from N to O. In the lower canal the movements are the opposite of these, *i.e.*, *into* the central region N^1 from M^1 in front and from O^1 behind.

The movements of the fluids in each region are first arrested by the elasticity of the membrane and then reversed: that is, the kinetic energy of the moving fluid is transformed (so to speak) into potential energy of stretched membrane, and then again into kinetic energy of moving fluid to be similarly transformed in a portion of the membrane further along the canal.

It may be asked why the disturbance is transmitted *along* instead of *across* the canals; incompressible fluids in rigid vessels can obviously however only move in such directions as the yielding areas of the walls allow: if fluid is forced forwards in the upper chamber a corresponding and equal movement of the fluid in the lower canal must occur in the opposite direction. The upper and lower canals communicate freely at the apex of the spiral and if the displacement of the stapes were infinitely slow the flow would be a steady one alike in all parts of each canal, *i.e.*, during advance of the stapes it would flow forwards (*i.e.*, towards the apex) in the upper and backwards in the lower canal. Or if the basilar membrane were perfectly rigid the same result would follow.

With a rapid movement of the stapes and with a yielding though highly elastic basilar membrane the case is very different: the inertia of the whole column of fluids in both canals prevents their sudden movement and only the basal portion is moved first, the rest being only subsequently set in movement by the elasticity of the membrane called into action by its displacement.

The figures 1 and 2 and the constant reference to the elasticity of the displaced membrane are liable to suggest a *longitudinal* tension comparable with that of a vibrating string. There is, however, practically *no* such longitudinal tension. The stretched fibres lie transversely in the membrane, and each stretched portion of the membrane acts on adjoining parts of the membrane only through the intermediation of the incompressible fluids in which the whole membrane is immersed, fluids which are prevented from moving transversely by the rigid walls of the canals.

We have here the conditions necessary for transmission of a wave-like disturbance: we have indeed conditions which render such a transmission inevitable. The conditions at C for instance are precisely those which at an earlier moment obtained at B and will in a moment later hold at D. The whole of the conditions are such as must give rise to like conditions in an adjoining portion of the membrane further forwards. That is the disturbance will of necessity give rise to a like disturbance in every successive region of the membrane and adjoining fluids throughout the whole length of the spiral.

This disturbance I will call a *wave*, in spite of its difference from any other known kind of wave in the following respect, *viz.*, the potential energy is that of fibres stretched at right angles to the direction of transmission, and the kinetic energy is that of moving fluids; while in other waves the kinetic and potential energy consist in movement and stress of one and the same medium. The inertia of the fibres in the basilar is here insignificant while in the vibrating string of a fiddle or of a cord thrown into waves, or of a solid, liquid or gas transmitting a sound wave or of the water in an oceanic wave the inertia is all-important. Expressed in another way the whole of the kinetic energy of this wave is in the fluids; the whole of its potential energy is in the membrane. The kinetic and the potential are equal, and the whole energy of the wave *remains constant throughout its transmission*, save for a portion, which must be very small, and which is converted by internal friction into heat or other disturbances.

Two important questions now arise which are intimately connected with each other; they are:—

(*a*) What is the extent or amplitude of displacement of each part of the membrane? and (*b*) what is the velocity of transmission of the wave? Neither question admits of a very definite answer but it is important to give a partial answer to both.

The spiral canals of the cochlea are not of uniform width throughout, but are much narrower in the apical than in the basal region. Suppose for a moment, what is not true, that the basilar membrane is of uniform width; then the wave in passing from the wider to the narrower part of the canal would gain in amplitude: for at each successive level the volume of fluid to be moved would diminish and its inertia decreasing the expenditure of like energy upon it would give it a greater velocity and therefore a greater displacement—an effect comparable with the "bore" in the Severn and similar rivers.

The basilar, however, is not uniform in breadth: it is about twelve times as broad in the apical region as in the basal: that is the wave in passing forwards towards the apex comes into successively narrower and narrower portions of the canal and acts upon successively broader and broader areas of the basilar membrane. The effect of this is to exaggerate the effect of the narrowing canal already described. In order that the same amount of energy may be stored in potential form—to speak figuratively—in two fibres which are otherwise alike but of different lengths the transverse displacement of the longer one must be much greater than that of the shorter one. The wave in passing forwards towards the apex will thus rapidly gain in amplitude—and the importance of this fact from a physiological point of view will be seen later.

What changes in *velocity* result from this change in width of the channels and in breadth of the membrane as the wave passes on it is less easy to say. The two influences—narrowing of canal and consequent decrease of mass per unit length to be moved, and broadening of membrane and consequent diminution of elastic pressure per unit displacement—appear to counteract each other, but whether the two effects balance each other or one over-balances the other is a question which I have as yet only guessed at on physiological and not on physical grounds. The guess which will be justified later is that the velocity of the wave and consequently its length (in space, not in time) will be augmented.

As to the absolute velocity at any part of its course—as distinct from its relative velocities in different parts of its course—we are again driven by the difficulties of the physical problem to base an estimate on physiological considerations: what that estimate is will appear later.

The cochlear canals, however, are not only tapered but but also spirally coiled; and the basilar membrane is at the apex continued into the Reissnerian which runs from this point to the base of the spiral narrowing very gradually. When the wave reaches the apex of the cochlea it will pass on to the upper (Reissnerian) membrane, for at this point the lower canal is continuous through the helicotrema with the upper (scala vestibuli); and the middle canal ends blindly in the slightly dilated "lagena," the wall of which is formed by the two membranes (upper and lower) which are here continuous with each other.

The wave of the basilar will thus, starting from the base of the cochlea close to the fenestra rotunda, run forwards to the apex, round the wall of the lagena and down by the Reissnerian membrane to the base of the cochlea.

The elasticity of the Reissnerian membrane being much less than that of the basilar, it appears certain that the displacement at each point will be greater than that of the corresponding portion of the basilar, and further the loss of energy of the wave will be greater for the movements involved being more extensive will involve more internal friction. The smaller waves will hence probably be almost lost before reaching the base, and the larger ones will, apparently, die out at the base in the form of small vortices or eddies of the perilymph gradually coming to rest by internal friction of the somewhat viscid perilymph. This is not the place to discuss the far greater effect of viscidity of a fluid in restraining vortical movements than in restraining wave-like movements which involve only a temporary and relatively small internal deformation (or relative displacement of parts) of the fluid. It is sufficient to state that such is the effect of viscidity, and that it will rapidly arrest such vortices as would be formed when the Reissnerian wave reaches the base of the cochlea.

The effect of the spiral coiling of the cochlear canals will be to concentrate the disturbance in the outer part of each turn of the spiral. The large, longer waves will thus involve a disturbance of a larger mass of fluid at each level, while the smaller ones will involve movements more narrowly restricted to the outer region of the canals that is, to the region where the membranes are placed.

The effects of these waves on the organ of Corti have now to be considered, and the effect of the passage of a single such wave as has been described will be seen to be *nil*, or rather that it will consist only in a bodily movement of the whole organ in each region first down then up and then down again, with little or no relative movement of the parts of the organ among themselves.

The upper surface of the hair-cells is covered by the comparatively stiff and tough reticular membrane connected with the phalangar processes of the rods of Corti, and the whole covering so formed is rigidly connected with the basilar membrane by the stout rods of Corti and the less stout, but still stiff "cuticular rods" of the cells of Deiters. This skeleton, as it may properly be called, insures the movement of the basilar membrane and the whole mass of hair-cells and cells of Deiters as one piece without deformation or relative movement of its parts. The whole organ in fact in each transverse area may be regarded as part of the basilar membrane, moving up and down but retaining its form.

The tectorial membrane, however, lies upon this and is connected with it only at its edges. It is often described as being free at its outer edge, but this edge always presents the appearance of being torn and jagged and portions of it may sometimes be seen attached to the upper surface of the cells of Hensen: a portion so attached was figured by Retzius and is shown in the figure reproduced from his work in such text-books as Foster's Physiology (fifth edition, p. 1351). It is highly probable therefore that this membrane is attached at both edges throughout the entire length, and that its frequent separation is due to shrinkage under the action of reagents. A similar shrinkage of the upper surface of their hair-cells is prevented by the stiff unyielding reticular membrane, and the tearing of the tectoria at its thinnest part when exposed to reagents which cause shrinkage is precisely what might be expected—it might even be said to be the inevitable consequence.

The tectoria when stretched in its natural condition between the cells of Hensen and the lip of the spiral lamina would rest just over the tips of the hairs of the hair-cells. Between the tectoria and the reticular membrane is then a thin layer of fluid which is somewhat viscid and in which the stiff hairs project. The thickness of this layer is about ·004 mm. and in consequence of its viscidity the friction involved in its movement would be relatively great. The fluid in the wide scala media above the tectoria is, however, much more free to move and the tectoria would therefore move with the organ of Corti almost as if it were rigidly bound to it. The passage of the basilar wave would thus simply move the whole organ of Corti, together with the tectorial membrane up and down without disturbing the relative position of one to the other.

This purely physical conclusion accords well with the physiological observation that a single aerial wave impinging upon the ear does not suffice to produce a sensation of sound.

Problem II. *Changes produced within the cochlea by two double movements of the stapes (in then out.)*

If the first wave has already traversed the whole length of the basilar first and then of the Reissnerian, and finally died out before the second wave is started, the second will obviously pursue the same course as the first and produce only the same effects. This consideration enables us to roughly estimate the average velocity of the waves along the membranes; for if the time-interval between the two waves be progressively diminished in successive experiments, a minimum period of no physiological effect will ultimately be reached, and as soon as this is passed a sensation of sound is produced. That minimum time-interval of no physiological effect thus corresponds to the time occupied by a single wave in completing its whole course up the basilar and down the Reissnerian membranes. This time-interval differs with different persons, normally ranging between $\frac{1}{8}$th and $\frac{1}{16}$th of a second.

When the time-interval is less than this the second wave will be started on its journey up the basilar membrane while the first wave is still somewhere on one or other of the membranes; and before the second reaches the helicotrema it must of necessity pass some point on the basilar membrane at the same moment as the first wave passes a point opposite to this on the Reissnerian. Two points have to be considered in connection with this passing of the waves; (1) the point at which the passing will occur, and (2) the effects within the organ of Corti which will be produced thereby.

(1) The velocity of transmission of a wave at any given point of either membrane being constant (as it must be very nearly if the waves are similar to each other), it follows that the distance from the position of the second wave measured along the basilar through the helicotrema

and then down the Reissnerian to the position of the first wave, is the distance which has been travelled by the first wave since it was in the position now occupied by the second; *i.e.* it is the distance travelled by the first wave in the interval of time between the first and the second. This distance thus depends entirely upon the time-interval between the two waves. As the time-interval between the two determines the pitch of the tone-sensation produced by them (as shown by Kohlrausch's experiment referred to above) it is correct to say that if a note be sounded consisting of two vibrations only (in the absolute sense) then the point in the organ of Corti where the two cochlear waves pass each other will depend wholly upon the pitch of the note. In other words, there is in the organ of Corti for each pitch a definite point where this passing will occur. We shall later see that though there is only one such point when only two vibrations are produced, there may be a larger number when more than two are produced.

(2) The effect on the Organ of Corti and associated structures produced by the simultaneous action of these two waves may be most easily grasped by the mind by consideration of a transverse section of the middle canal at this level. First both upper and lower membranes are motionless and the fluids are at rest. Then the two are simultaneously drawn or forced apart, and coming to rest for a moment then move suddenly towards each other driving the fluid out of this region in both directions. A more accurate idea may be obtained from consideration of a longitudinal section through the mid-line of the two membranes in this region.

Figures 3, 4 and 5 represent three phases of the passing of two such waves. They will be more easily understood if compared with figures 1 and 2. The large arrows above and below represent the direction in which the first and second waves are travelling along the upper and lower membranes respectively. The smaller arrows of figures 1 and 2 are omitted. The line XY which is the same in all three figures marks the level at which the two waves pass each other in corresponding (not "like") phases. The first wave, in passing the helicotrema has of course been turned over so that its first phase is one of *upward* displacement, while that of the second wave which has not been reversed is one of downward displacement. Let points in the waves be called ABCD and E as in fig. 1, and phases M, N and O as in fig. 2—it is more convenient to divide the wave into these three phases than in the more usual way. In fig. 3 at the level XY both waves have just reached the end of the first phase (M), *i.e.*, the point D of each wave is just passing the line XY. This means that fluid has just been forced into region of XY from both before and behind, and in the neighbourhoods of both upper and lower membranes. The two points B of upper and lower membranes are now separated to the utmost extent and by virtue of their elasticity have just brought the fluid in contact with them to rest. From this moment onwards the two membranes by virtue of that same elasticity will approach each other, with increasing velocity till at the level XY the stage shown in fig. 4 is reached. The points C (fig. 1) of the two waves are now passing each other at the level XY. At this moment the two membranes are approaching each other with maximum velocity, being forced towards each other by the fluids in the upper and lower canals, and the fluid between the two membranes, that is in the middle canal (scala media, canalis cochleæ) is being forced out from this region, now with maximum velocity, both forwards and backwards. A moment later the stage shown in fig. 5 is reached.

The points B (fig. 1) are now passing each other at the level XY. The two membranes at this level have just come to rest by virtue of their own elasticity, and the fluid will now immediately commence to flow in both directions (forwards and backwards) into the region of XY.

We must now consider how these changes will affect the organ of Corti.

Let fig. 6, represent a transverse section across the middle canal of the cochlea in the plane of the line XY of figures 3, 4 and 5, and let us consider the changes just described from a new point of view.

The condition represented in fig. 3, was brought about by inrush of fluid into the region of XY in both directions *simultaneously*. From this stage onwards the elasticity of the membranes now stretched to their maximum presses on the fluid between them, forcing it out in both directions (forwards and backwards) with increasing velocity till the stage represented in fig. 4 is reached, when the membranes are at their normal position of rest but are now advancing towards each other with maximum velocity. During this first half of phase N (fig. 2) the basilar membrane has been pressing upwards upon the fluid which was simultaneously forced down upon it by the Reissnerian membrane, with the result that not only the fluid above the tectorial membrane but the whole of the fluids between the basilar and the Reissnerian will have been set in movement backwards and forwards away from this region. The whole phase only lasts a moment, but during that moment the fluid between the tectorial membrane (T in fig. 6) and the organ of Corti (C in fig. 6) will have been to some extent forced out, and by way of the spiral sulcus to adjoining regions of the cochlea. In other words the tectoria will have been suddenly banged down upon the hairs which extend vertically between it and the top of the organ of Corti. These hairs are stiff and the ultimate fibrils of the auditory nerve terminate at their bases. This means that at the particular point in the length of the organ of Corti where the two waves pass in corresponding phases the ends of the stiff hairs of the hair-cells of the organ of Corti are suddenly thrust down upon the nerve-ends of the auditory nerve-fibres. Physiologists will understand what result will follow.

Taking a general review of this second problem, the result may be stated thus: *When two sound waves impinge upon the tympanic membrane at a suitable interval of time, one definite region of the organ of Corti will be stimulated by the thrusting of the hairs of its hair-cells upon the nerve-ends; and the region to be so stimulated will be determined wholly by the interval of time between the two sound waves, that is, upon the pitch of the note sounded.*

Problem III. *The changes produced within the cochlea by a long series of in and outward movements of the stapes, such as would be brought about by the impact upon the tympanic membrane of the sound waves produced by the sounding of a constant pure tone.*

If the interval between successive vibrations be of such length that two and only two cochlear waves were passing along the membranes of the cochlea at any one moment, the problem is identical with the previous one. When the intervals are much shorter the problem becomes more complex; and certain details have to be considered which were for the sake of simplicity omitted from consideration in the previous problem. In the first place there will no longer be one place and only one where the cochlear waves on the two membranes will pass each other in corresponding phases. They will pass at many such places and we have to consider whether the results of such passing as set forth in the previous problem will be brought about at all these points or only at some of them; and if only at some, at how many, and at which.

It has already been shown that the effect of the mechanism of the middle ear is to "level down" the amplitudes of the displacements brought about by notes of very different intensities, very intense (*i.e.* loud) sounds being prevented by this mechanism from producing a very much larger displacement of the fenestra ovalis than is produced by a much less intense sound. Pure tones of the same pitch but of enormously different intensity. are by this mechanism caused to give rise to displacements of the ovalis which though greater for intense sounds than for weak ones, are far more nearly equal than are the displacements of the tympanic membrane. We will first suppose that sounds are under consideration ranging between the very faintest audible tone on one hand, and a tone of such intensity as will cause double the amplitude of displacement of the basilar produced by that faintest audible tone of the same pitch. It must not be supposed that this means that the second (upper) limit of intensity represents an intensity of sound twice as great as the lower limit. To suppose this would be to ignore what has been said about the mechanism of the middle ear. A two-fold increase of amplitude of displacement of the basilar will correspond to an increase of intensity of the exciting sound greater than two-fold.

The effect upon the amplitude of displacement of the basilar arising from the narrowing of the canals towards the apex of the spiral and the cooperating and intensifying effect of the widening out of the basilar itself towards the apex have already been referred to. The net result of these two conditions is that the amplitude of displacement becomes rapidly greater as the wave passes forwards along the basilar while it diminishes as the wave returns along the Reissnerian. For any given series of waves therefore due to the continuous sounding of a note of constant pitch, and constant intensity, the maximum effect upon the organ of Corti will be produced at the uppermost only of the many levels at which waves pass each other on the two membranes in corresponding phases. If, therefore, the damping effect of the mechanism of the middle ear be of proper extent then the effect upon the organ of Corti already described will occur at this one uppermost only. That is, though waves pass at many points it is only at the uppermost of them that the disturbance will be sufficiently great to bring the tectorial membrane down upon the hairs of the hair-cells with sufficient force to stimulate the nerve-ends.

Equal intensity of sound in the case of two notes of different pitch, does not correspond with equal amplitudes of displacement of the air or of the tympanic membrane. Nor does it correspond with equal displacements of the basilar membrane. When two sounds—both pure tones—of different pitch are said to be of equal intensity, that means that the energy traversing unit area of a plane at right angles to the direction of transmission in unit time is equal in the two cases. This being the case two tones of equal intensity but different pitch involve displacements proportional to the wave-lengths. A very low note will therefore involve a far larger displacement than a much higher note of equal intensity. Still supposing the limits of intensity above laid down, suppose two notes are sounded *in succession*, a high one and a low one: and suppose the intensity of the two to be at first equal: then the higher note will produce a stimulation at one point of the organ of Corti and the lower at another point. The cochlear waves due to the higher note besides passing higher up may pass at the exact point where those of the lower note do, but the displacement is too small to bring the tectoria down upon the sensory hairs at that point although the amplification of displacement as the wave passes forwards suffices to produce this effect further on in the cochlea. The lower note on the other hand produces in the upper part of the cochlea a larger displacement of the membranes than does the higher tone, but it produces no stimulus because there is no passing of waves in corresponding phases in these upper regions the waves being too long to so pass here; that is one wave goes up to the helicotrema and travels backwards along the upper (Reissnerian) membrane out of the upper regions of the cochlea altogether before it meets the next following wave on its way up the basilar.

Within these or some such limits, therefore, each pure tone will produce a stimulation of the nerve-ends in one region of the organ of Corti and in one region only: and the region stimulated will depend solely upon the pitch of that tone.

Now suppose the intensity to increase beyond the supposed limit.

We shall now have to give names to every point in the length of the organ of Corti. The number of points is infinite and there is no difficulty in providing them with an infinite number of easily understood names or numbers. Let 100 be the name or symbol of that point in the length of the organ where one wave in its backward or return journey along the Reissnerian membrane passes a wave on the basilar separated from the first by an interval of time equal to $\frac{1}{100}$th part of a second. Then within previous limits of intensity, 100 indicates the point in the length of the organ of Corti where a stimulation is produced by a tone due to 100 vibrations per second. Similarly let *a* stand for the uppermost point of passing of waves produced by a tone of *a* vibrations per second.

A tone *a* will thus produce cochlear waves passing at points a, $\frac{1}{2}a$, $\frac{1}{3}a$, $\frac{1}{4}a$, etc. Within prescribed limits stimulation occurs at the point *a* only: at $\frac{1}{2}a$ the amplitude of displacement is too small to produce stimulation.

A tone $\frac{1}{2}a$ of equal intensity is, however, sufficient to produce a stimulation at the point $\frac{1}{2}a$: therefore if the intensity of the tone *a* be so far increased as to produce a cochlear wave of more than double its previous amplitude (which means manifold more than double intensity), it also will be able to stimulate the organ of Corti at the point $\frac{1}{2}a$, but in the first instance the sensation due to the stimulation at *a* will have been so enormously intensified as to overpower this stimulation at $\frac{1}{2}a$, and the weak second tone $\frac{1}{2}a$ will be heard either very faintly or not at all.

I have found by experiment, however, that if a tone *a* be sounded *loudly* for five or ten minutes and then increased gradually in intensity, the note $\frac{1}{2}a$, an octave lower gradually becomes audible. It is therefore possible, by gradually deafening oneself to a tone and then increasing its intensity, to produce a sensation of a tone an octave lower.

The result arrived at in considering this third problem is thus as follows:—

A continuous constant tone within moderate limits of intensity will produce stimulation of one region of the organ of Corti and of one only: and increase of intensity beyond these limits produces a stimulation of a region corresponding to a tone an octave lower; but this second stimulation is so feeble as to be difficult or impossible of recognition, being overpowered by the primary stimulation, until the first region is deprived of its sensitiveness by fatigue. It is theoretically possible to fatigue even the second point and then hear a spurious tone whose wave-length is three-times that of the actual note sounded. Experimentally I have failed to produce this effect and this is probably due to the enormous damping effect of the mechanism of the middle ear upon sounds of such deafening intensity.

Problem IV. *Effects within the cochlea due to simultaneous sounding of two continuous mutually harmonious pure tones.*

The effects arising in various parts of the cochlea when *two* series of periodic movements of the tympanic membrane occur simultaneously will differ widely in the cases when the "period" of one series bears different relations to the period of the other. We will consider first the case of two series the periods of which bear a simple relation one to the other.

We have already seen that a tone due to a vibrations per second may produce a stimulation in the organ of Corti at points a, $\frac{1}{2}$ a, $\frac{1}{3}$ a, etc., but that the primary stimulus at a will be by far the most intense. If while this tone is being sounded, the tone $\frac{a}{2}$ or $\frac{a}{3}$ be also sounded, even though so faintly as to be in itself inaudible, its cochlear waves may, so far as they happen to coincide with certain waves of the series a so increase the disturbance at $\frac{a}{2}$ or $\frac{a}{3}$ (as the case may be) as to render this tone distinctly audible. Similarly if the tone a (*i.e.*, a vibrations per second) be sounded too faintly to be audible, and the tone $2a$ simultaneously sounded so faintly that it would be inaudible if sounded alone, each tone may so cooperate with the other as to render *both* audible, but not quite in the same way in the case of the two.

That one wave may intensify the disturbance in the relative positions of tectorial membrane and sensory hairs produced by another wave, the two must coincide with each other in phase in some part of the wave. Of course if they be of unequal length they cannot coincide in all parts. It would take us too far to consider the question as to whether two series of sound-waves of simply-related periods do tend to arrange themselves in a definite way with relation to each other or not, and if so what that relative position is. Fortunately we need not consider it, for a study of the effects of combination of the waves due to two tones in harmony with each other by simple graphic methods shows that, however, they be combined the combination will lead either to prolongation of the period of advance of the two membranes towards each other at the level of passing of the waves of either series or to acceleration of the advance. Either of these effects will lead alike to the augmentation of the relative movement of tectoria and sense-hairs, at that point. Sounding of two tones in perfect harmony with each other will thus produce a slightly greater effect at each of the two passing-points in the cochlea than the sounding of either of the two alone.

An effect differing from this, so far as the sensation is concerned, may be produced at one or more other points. Let the two notes be c' and g' (*i.e.*, the middle c of the pianoforte and its fifth) and let the musical interval between them be a *true* fifth, *i.e.*, let the ratio of the numbers of their vibrations be as 2 : 3.

Then the points of the organ of Corti stimulated in the way described will be the points called (in accordance with the simple nomenclature I have suggested) c' and g' or c' and $\frac{3c'}{2}$. The series of waves c' pass in corresponding phase at c', $\frac{c'}{2}$, $\frac{c'}{3}$, $\frac{c'}{4}$, etc. The second series pass in the same way at g', $\frac{g'}{2}$, $\frac{g'}{3}$, $\frac{g'}{4}$, etc. These points expressed in the simplified form are c', c, F, C and g', g, c, G, (notation of Helmholtz, Lord Rayleigh and others) and it will be seen that the point c, is common to both series. This means that the simultaneous sounding of a tone and its fifth will produce a disturbance at a point corresponding to an octave below the lower tone and corresponding also to a twelfth below the upper tone. Each of these tones alone produces a small disturbance at this point and we have already seen that whether that disturbance is or is not sufficient to produce stimulation at this point depends upon the intensity of the sound. It will also depend upon the intensity in this case, but if the intensity of each be alone insufficient to produce this effect when sounded alone, the two combined may still be sufficient to produce this effect—an effect well-known to musicians.

Similarly, any other two tones of sufficient intensity may by their combined effects produce stimulation in the organ of Corti at a point corresponding to a tone below these two which is due to vibrations whose number is the the greatest common measure of the vibration-numbers of the two tones sounded. This is also true even when the two tones are not in harmony with each other, that is when this resultant tone is more than an interval of a seventeenth lower than the lower of the two tones. (The ratio of numbers of vibrations of two tones separated by an interval of a seventeenth is 1 : 5, *e.g.*, A flat : c'.) And this leads to the next problem.

Problem V. *Intra-cochlear effects of discords, consisting of two tones.*

It is hardly necessary to define a discord here; I will use the term for any combination of two tones whose beat-number is less than one fifth the vibration-number of the lower tone, that is tones whose resultant tone is removed from both of them by more than a major seventeenth (*i.e.*, more than two octaves and a major third).

If the interval be a major second (ratio of vibration-numbers 8 : 9), the interval between c' and d' for instance, then the highest resultant tone of the two is three octaves below the lower of the two: *i.e.*, it is $C_{,}$.

The basilar waves produced by combination of these two are of complex form, eight waves of one series corresponding to nine of the other. At the points c' and d' and *also at points between them* the tectoria will be brought down upon the sense-hairs, and with rhythmically-varying force. The violence of the disturbance being at its maximum at intervals of time corresponding to eight periods of the lower tone (or nine of the upper): the disturbance being at these moments about twice as violent as that produced by either tone separately, while at the moment intermediate between two of these the disturbance will be practically *nil.*

At the point $C_{,}$, every eighth wave of the series c' and every ninth wave of the series d' will pass simultaneously and there produce a stimulation leading to a sensation of the tone $C_{,}$.

An interesting example of this effect is Koenig's, now classic, experiment of sounding the notes c'''' and d'''' simultaneously (*i.e.*, 2048 and 2304) the resultant ("differential") tone 256 (c') being distinctly heard. (See *Nature*, XLII., p. 190.)

Besides these resultant-tone stimuli there will be produced disturbances of the relative positions of tectoria and sense-hairs at each point in the cochlea where a wave of either series on the basilar passes a wave of the same or the other series on the Reissnerian. Still considering the same two tones *c'* and *d'* (which for convenience we will suppose tuned to 256 and 288 vibrations per second respectively) the secondary points of passings will correspond to the following tones:—

1st Series. *f'* flat*, *g'*, *b'* flat, *d''*, *g''*, *d'''*, *d''''*.

2nd Series. *d*, *c*, G, F, D, C, $B_{,}$ flat, $A_{,}$ flat, $G_{,,}$, $F_{,,}$ $F_{,}$ flat*, $E_{,}$ flat*, $D_{,,}$ $C_{,,}$.

3rd Series. $\frac{1}{10}c'$ (= *b* flat), $\frac{9}{11}c'$ $\frac{9}{12}c'$ (= *g*), $\frac{9}{13}c'$, $\frac{9}{14}c'$, $\frac{9}{15}c'$ (= *e* flat), $\frac{9}{16}c'$ (= *d*), $\frac{9}{17}c'$, $\frac{9}{18}c'$ (= *c*), etc.

In each series except perhaps the first, the intensity of the disturbance would be greater at higher than at lower points. In proportion to their height the effect would be greatest at the points in the second series. At points in the first series the disturbance would occur twice in each beat-period ($\frac{1}{32}$ second) and in the following order:—1, 7, 2, 6, 3, 5, 4, 4, 5, 3, 6, 2, 7, 1.

The rhythm is more complex at the second series of points and in the upper part of the series there is a rhythmic variation of intensity at each. At the points in the third series the intensity of disturbance is not so great as in the other two and the rhythm is very complex.

At *c'* and *d'* there is a rhythmic variation in the intensity of disturbance which in itself would produce an effect like beats, 32 to the second.

How many of these points in the organ of Corti will actually be stimulated will depend largely upon the intensity of the primary tones employed.

It must be remembered that the signs now given, which ordinarily stand for musical tones, here stand for the

(* An asterisk indicates that the point is indicated only approximately.)

points in the organ of Corti corresponding to those tones, and not for the tones themselves: the question of interference between them does not therefore arise.

To which of these results the disagreeable and "restless" effect of a discord is due cannot be said with certainty, but it is probable the following all contribute to the restlessness:

(1) The rhythmic variation of intensity of primary stimuli beyond ordinary limits:

(2) The rapid succession of faint but unequal stimuli in very widely separated regions of the organ, each stimulus being due, in most cases, to two waves only and, hence, giving rise to a comparatively ill-defined sensation:

(3) The probable stimulation of the whole area between c' and d'.

With intervals less simple than this 8 : 9 discord the beat-period becomes longer and the beats more distinct. The "beat" itself is the rhythmically recurring augmentation of the primary stimuli: and their disagreeable effect is avoided in rapid music where the successive chords are not sustained long enough to produce this effect.

It would seem to be inadvisable now to enter into questions of more complex combinations of tones either harmonious or discordant—apart even from limits of space. The examples already given are sufficient to exemplify the principles I have laid down.

An objection has been raised, first by myself and then by almost everybody who has been led to discuss the theory with me.

According to the theory now set forth, the region of the cochlea where the stimulation by high tones occurs is near the apex; low ones producing a stimulation near the base.

Older theories based on assumptions of "resonance" of of one part or another all locate the seat of stimulation by high tones in the basal region and by low tones in the apical. Pathological evidence, with the details of which I am not acquainted, shows that injury—or at any rate some injuries—to the apex of the cochlea lead to a deafness to *low* tones, while the ear may still remain sensitive to high ones.

The objection seems at first sight to be fatal but, if I have rightly understood what is the nature of the pathological evidence, it is not so.

A lesion of such kind as to destroy the elasticity of the basilar membrane and thus prevent the passage of the basilar wave to the apex of the spiral, would itself provide a new passage for the wave direct from basilar to Reissnerian at the injured spot, and the whole course of the cochlear wave would thus be shortened, the injured portion of the basilar serving as the turning-point of the wave, serving in fact as a secondary helicotrema. Under these circumstances waves of short period would still "pass" within the cochlea though not at the normal point, and the whole course being shortened, waves of long period would now fail to pass in the cochlea and deafness to low tones would be the consequence.

In the earlier part of what has gone before, the attempt to discover, by argument from physical considerations, what changes of velocity of transmission the cochlear wave undergoes in various parts of its length was abandoned because the difficulties appeared insuperable. Having now, however, seen the result of the physical consideration, and being, as it seems, justified in concluding that the stimulation of the nerve-ends is actually brought about by the passing of waves on the two membranes, and the resultant thrust of the tectorial membrane down upon the sense-hairs we may use this physiological result as a means of answering the question which I was unable to answer on purely physical grounds.

If the velocity remained constant in all parts it would follow that the length of the region of the organ of Corti set apart for stimulation by the various tones in the lowest octave of audible sounds would be just half of the whole length of the organ. Above this region half the remainder would serve for the next octave; and so on, each octave having thus only one half as long an area as the preceding one. The number of separate nerve-ends in each unit-length of the organ is, however, very much the same in all parts of the organ and the possibility of distinguishing a difference of pitch between two tones depending presumably on their power of stimulating two different nerve-ends, it follows that the accuracy with which we can distinguish between two tones separated by only a small musical interval would be *enormously* greater in the case of low tones than in the case of high ones. And this is not the case. Very minute intervals, such as two or three "cents," can be distinguished more easily in some parts of the tone-scale than in others, but this difference is exceedingly slight. It follows therefore that approximately equal lengths of the organ of Corti correspond to approximately equal differences of pitch—equal that is in the musical sense: or in other words the waves of the basilar membrane must undergo an enormous acceleration in their course along the membrane, the distance (in space, not time) between two successive waves being thus multiplied about 100-fold.

Near the upper limit of audibility there is a very marked falling off in the power of discriminating between tones differing but little in pitch, and this means that this acceleration of the wave is checked before the wave has reached the very end of the organ of Corti.

It will be noted that the physical limit of this acceleration is not closely approached. That limit would be approximately the velocity of sound in the liquid, *i.e.*, nearly a mile per second, 1435 metres.

Explanation of Plate XX.

Figs. 1 to 5. Diagrams, see pp. 328, 329, 337.

Fig. 6. Transverse section across middle canal of cochlea, see p. 339.

Fig. 6a. Part of Fig. 6 enlarged.

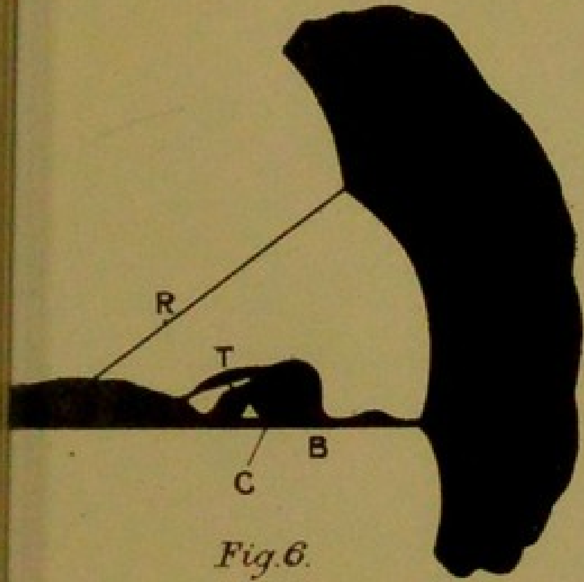

Fig.6.

Fig.6a.

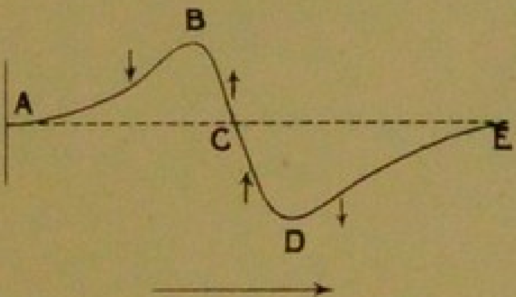

Fig.1.

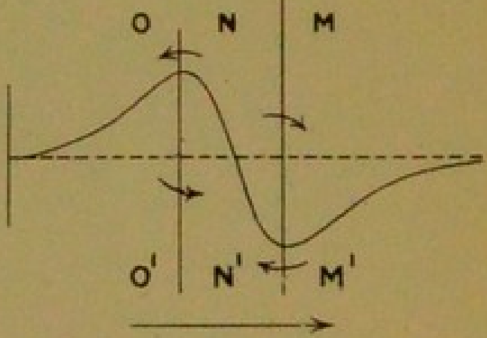

Fig.2.

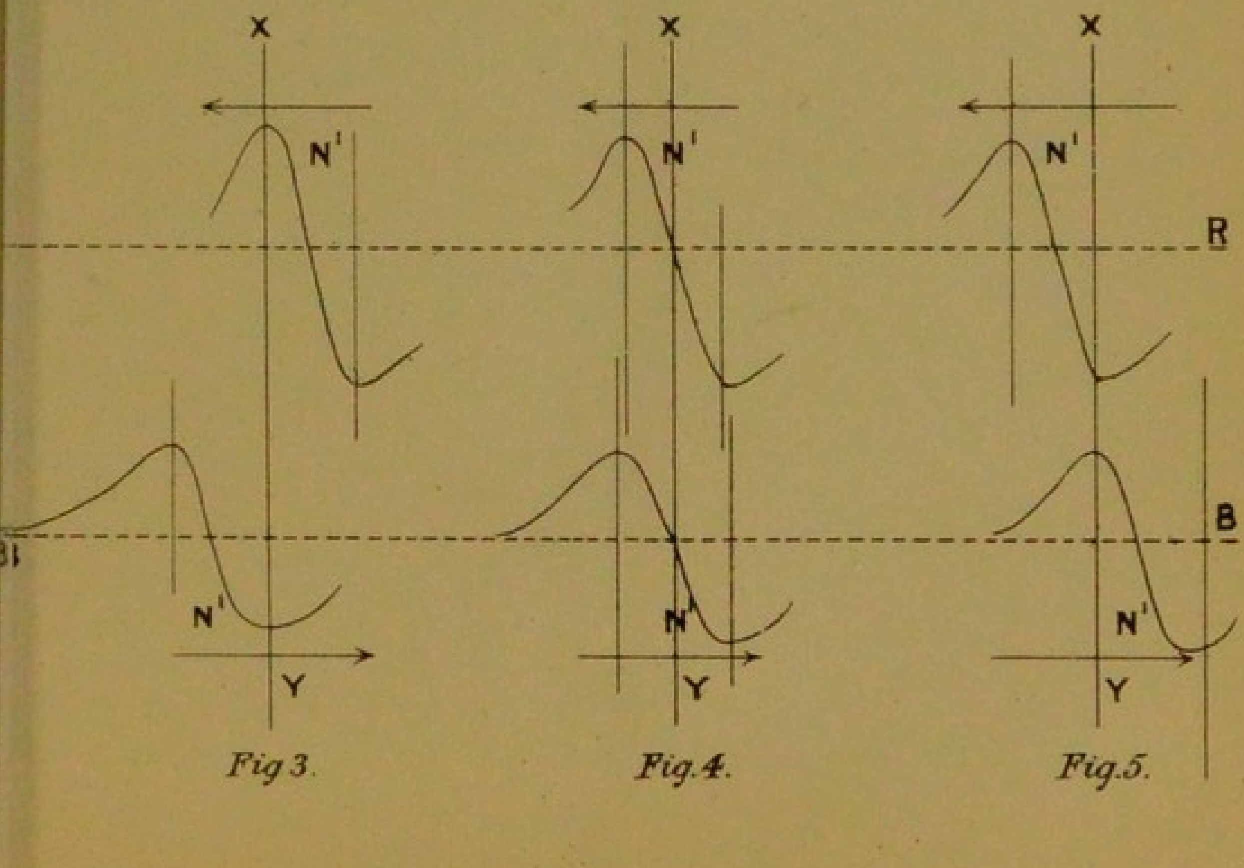

Fig 3.

Fig.4.

Fig.5.