Citation:

H. Zwaardemaker, On the pressure of sound in Corti's organ, in:
KNAW, Proceedings, 8 I, 1905, Amsterdam, 1905, pp. 60-65

Physiology. — *"On the pressure of sound in Corti's organ".* By Prof. H. ZWAARDEMAKER.

(Communicated in the meeting of May 27, 1905).

According to the hypothesis of HELMHOLTZ-HENSEN the vibrations of sound, penetrating into the inner ear by way of the stapes, evoke a resonance in the transversely stretched fibres of the membrana basilaris. Strong vibrations are imparted to different fibres according to the pitch; these vibrations being communicated to the sensory epithelia of Corti's organ and then becoming the stimulus for definite nerve-fibres. We recognise the tone by the nerve-fibres which are affected in this way.

That such short fibres as the transverse fibres of the membrana basilaris can resound to the relatively deep tones of the human scale is explained by HELMHOLTZ 1st by the resistance in the fluid and in the soft cell-masses (CLAUSIUS' cells); 2nd, by their being loaded with Corti's arches on which again a whole system of cells rests.

At first it was imagined that the fibre vibrates in its entire length as a freely stretched string. Later attention has been drawn to the fact that the pars arcuata (the part over which the Corti's arches vault themselves) remains largely at rest while the pars pectinata (the remaining part of the string, not covered by the arches) makes the greatest excursions. But then the difference in length of the fibres is no longer sufficient to explain the difference in the pitch for which they are tuned, so that also a difference in tension and in load must be assumed. [1]) Examining the proportions of microscopical preparations and bearing in mind that the arches are more or less rigid formations, one is soon convinced that the pars arcuata cannot possibly resound to the deep tones of the audible scale. It is not the bottom cells on their upper face that are an impediment to this, but the large vein on their lower surface. Moreover the transverse fibrous structure, which is so distinct in the pars pectinata is entirely absent in the pars arcuata. The property of resounding may on sufficient grounds be attributed to the stretched and loaded fibres of the pars pectinata only.

I have tried, as far as this is possible, to reproduce in a model the conditions prevailing in Corti's organ. A horizontal steel string, $^1/_2$ millimetre thick and somewhat longer than a metre, represents a transversely stretched fibre of the membrana basilaris. On this rests, at one of the ends, a wooden imitation of Corti's arches. The

1) A. A. GRAY, Journal of anat. and physiol. 1900, Vol. 34. p. 324.

other end is fastened, transversely to the direction of vibration, to the vibrating prong of an electrically driven tuning fork. Now, when the Corti's arches are sufficiently loaded (with sponges, or, for demonstrations, with a hollowed little board on which a drawing has been stuck), the tension of the string being at the same time regulated by means of a micrometer screw, it is possible to cause the system to resound to the tuning fork so that with small deflections of the fork the deflections of the pars pectinata become very large.

In the experiments for study proper, it deserves recommendation to attach pins to the wooden Corti's arches, on which smaller and larger sponges can be stuck in various positions. As long as the sponges are dry the whole system partakes in the vibrations. But when water is dropped on them, which is sucked in by the sponges and makes them heavier, the damping system is brought to rest and a node is formed at the base of the outer pillar. The string can be prevented from sinking down too much, by attaching the fixed extremity of the Corti's arch to a spring, which keeps it up. The free extremity of the arch is placed loose on the string. Sometimes it is a little difficult to obtain only vertical movements of the string, but by moving the fixed point of support of the string forward or backward, one always succeeds in this.

We find then :

1. broad deflections of the pars pectinata.
2. immovability of the pars arcuata.
3. immovability of the Corti's arches.
4. immovability of the loading mass.

This immovability is not absolute, of course; on the contrary, the floor, the table, everything in the room vibrates under the influence of the tuning fork, but the movements are infinitely small compared with the excursions of the pars pectinata and are so insignificant, moreover, that a photograph of the parts, called immovable, shows absolutely sharp definition. On the same photograph the pars pectinata is seen in the extreme positions, which it reaches with broad amplitude.

The conditions of the model have purposely been so chosen that they correspond in general outlines to the conditions actually found in Corti's organ. A complete imitation is impossible, but within the limits of technical practicability we have reached here, without any preconceived opinion, what can be achieved with the ordinary means of the laboratory. Now if we may see in the described model a more or less happy imitation of reality and to this assumption we are especially entitled by the manner of loading, then it follows that also in the organ itself as well the Corti's arches as the loading cells remain at rest. But then we must drop all the ideas, which have been broadly developed during a long time,-about the impact of the ciliae of the hair-cells on the membrana tectoria, on the bending of the ciliae, etc. Rest prevails in the system of arches and a covibration of them is necessarily excluded.

Yet the imparting of stimuli, which was supposed to be explained by the co-vibration of the hairs, need not remain a mystery, if attention be paid to the effect of sound-pressure.

In a paper, entitled "the pressure of vibrations", Lord RAYLEIGH [1]) has treated a simple case, which is nearly identical with ours. It is the case of a string, itself infinite, but vibrating between two rings, one fixed, the other sliding. When the string vibrates the sliding ring is pressed outward, towards the extremity, with an average force $F = \frac{E}{l}$; E being the energy of the vibration, l the length of the string.

The base of the outer pillar is in the case of the sliding ring. According to RETZIUS the pillar is one with the semi-solid cell-mass of the bottom-cell; from this cell it would originate and form a whole with it. In this way at the same time an attachment and a small movability in the cell-mass have been obtained.

But the pillar is not only in juxtaposition with the fibre, but also presses on it by the inertia of the large cell-masses with which it is connected, as soon as the fibre begins to execute movements. Hence the vibrating fibre will in this place present a node and the load itself will necessarily have a great influence on the conditions of tension during the vibration.

So the pillar has a double function: 1. that of the movable ring of RAYLEIGH, 2. that of carrier of the inertia of a damping and loading mass. In its first quality it receives a pressure in the direction of the modiolus, a pressure which can be perfectly measured by RAYLEIGH's formula.

In the model this pressure can even be demonstrated. For this purpose the pillars were removed and the base of the outer pillar, which imparts a node to the string, was replaced by a brass lamella, provided with a slit. The split lamella grips the string like a miniature fork. In this way the node is preserved. As the lamella is 19,5 cm. long and 0,1 cm. thick, it possesses a certain mass, which does not press on the string since the lamella is placed normally to it, but gives a distinct damping as soon as the string vibrates.

[1]) Lord RAYLEIGH, Philosoph. Magazine (6) III. 1902, p. 339.

Besides, at its place of attachment the lamella has been made considerably thinner (thickness 0,02 cm.) and consequently flexible over a length of 6 centimetres. The result is that the lamella, although accurately placed in the node of the vibrating string, will slightly deviate outward as soon as the excursions have become large enough. The force by which the little fork is driven outward is undoubtedly extremely small. Accordingly the deviation did not exceed 3 mm. with a semi-amplitude of the string of 0,4 cm. The new position can easily be fixed photographically and be compared with the position of rest which is assumed as soon as the string stops vibrating. This renders it possible to measure the force. But from a physiological point of view it has no meaning to perform the actual measurement on the model although it would be important if it could be performed under the actual conditions, *for this pressure must be the immediate cause of hearing*. This will be easily perceived with respect to the sensory elements at the modiolus side of the pillars.

The pressure of sound acting at the base of these outer pillars is in the direction of the string and hence of the modiolus. It has a component in the direction of the pillar itself. Through this the outer pillar, the upper end of which presses loosely against the capitulum of the inner pillar, is displaced parallel to itself and the cells at the modiolus side of the system must necessarily be compressed, although slightly. The pressure which they experience is either entirely continuous or periodically feebly variable. Beginning at the foot of the pillar the pressure varies from a maximum at the extreme deflection of the string to zero in the position of equilibrium. Higher up in the system these differences will probably for the greater part have disappeared, though they may remain to some extent. The pressure, however, is at all times positive; it never becomes negative, as would be the case if the Corti's arches and the loading cells followed the vibrations of the string. Since they are at rest, the pressure met with in the sensory cells at the modiolus side of the inner pillar must always act in the same sense, which is in the direction of the modiolus. It is quite possible that also the hairs of the hair-cells experience its influence, the effect of which will also be in one direction.

The matter is somewhat less simple for the sensory elements situated at the inner side of the outer pillar. These appear to me to experience no pressure at all from the outer pillar, which is retained in the soft cell-mass of the bottom cell. On the other hand such a pressure is present from the side of HENSEN's cells and also to some extent from the side of the supporting cells.

We are at liberty to consider this cell-group, situated at the exterior of the directly sensory elements, also as a RAYLEIGH ring. We shall have to try this the sooner, since in birds the pillars are absent and so we cannot regard these formations as essential. If we try again to find in Corti's organ an analogon of RAYLEIGH's movable ring, and in abstracto it is always admissible to seek such an analogy, we may never restrict ourselves to the arches alone. For by doing this we should deny the essential meaning of analogy for the physiology of hearing.

So HENSEN's cells may also be regarded as a movable RAYLEIGH ring. They also rest with a relatively narrow foot on the fibres of the membrana basilaris, near the foot of the pillar, when the human organ of hearing is studied. They will also exert a damping and loading influence on the vibrating fibres by their inertia. They will also cause a relative node and be shifted laterally, in the direction of the modiolus, by the vibration. But if this is the case they also squeeze the sensory elements situated between them and the pillar [1]).

Beside this lateral pressure, experienced by the cells themselves, it is not entirely impossible that also the hairs experience a pressure which they now receive through the agency of the lamina reticularis, which forms a whole with the capitula of the pillars. This pressure will then press them against the membrana tectoria with a somewhat varying force, but which is always in the positive direction.

All these reasonings can be simpler for the ear of birds than for that of man. The pillars are there absent and only the sensory elements and the supporting cells are found. Also this whole lies laterally on the fibres of the membrana basilaris and must experience a lateral pressure of sound.

The here developed conception, which deviates from the current one, has the important advantage that it reduces hearing to the perception of a pressure. The mechanical action of the vibration, which in the old form of the theory of HELMHOLTZ-HENSEN is vibratory, intermittently positive and negative, now becomes a permanent pressure of somewhat varying strength, to be sure, but at all times in the same direction, always positive. Hearing becomes the exact ănalogon of touching and all experience gathered for this latter sense we may try to find again mutatis mutandis, in the physiology of hearing.

Also small secondary advantages are gained by the new conception. In the first place the simple juxtaposition of the heads of the

1) For points inward of the node it can be shown in an elementary way that the masses there present and situated unilaterally, continually experience impulses having a permanent component in the direction of the node.

pillars (showing no joint like the auditory bones) finds an explanation. For a pressure which is always positive this is sufficient, not for a vibration. In the second place it explains the varying shapes and aspects presented by the *membrana* basilaris in the preparations. These are very obscure when they concern an *integrating* part of the organ, but are explained very easily if what we see in the preparations, is only a coagulated colloid or elastic mass.

Finally our conception is by no means bound to the theory of HELMHOLTZ-HENSEN. It is also acceptable to those who would exchange this theory for that of EWALD. For Lord RAYLEIGH treats in his paper also the case of a vibrating membrane: "but a membrane with a flexible and extensible boundary capable of slipping along the surface, provides for two dimensions. If the vibrations be equally distributed in the plane, the force outward per unit length of contour will be measured by one-half of the superficial density of the total energy".

So the theory of the pressure of sound might also be applied to a membrane such as is imagined by J. R. EWALD. But his membrane does not answer the conditions mentioned by RAYLEIGH, so that the quantitative relations are not so easily perceived as in the above developed case.

Finally, concerning the modern theories of hearing which I would call the pulsatory ones, since they only take into account the bulgings of the membrana basilaris, caused by the piston movement of the stapes, the hypothesis of the pressure of sound cannot be applied. For these theories purposely neglect the vibratory movements of the smallest parts and only take into account the mass-result. If however we lose sight of what is the essential thing in a vibration, we also lose the right of applying the properties of a vibration. In my opinion there can then be no question of pressure of sound.

The reader will have perceived that the *starting*-point of our reasoning was the probability of the fact that the arcuate zone and the arches vaulting over it remain perfectly at rest. On anatomical grounds this is very probable. Should it appear later that this rest is not absolute but only relative, the preceding reasoning is none the less valid.

Only one objection could then be raised, namely the small amount of the pressure of sound. This would then have to be placed against another small value, that of the possible movement of the hair-cells. Hence the question would be a quantitative one. But also in this case the two forces, the pressing force and the thrusting force, would by no means preclude each other. They would both have to be present. For the present we prefer, by assuming immovability, to neglect the thrusting force and only to retain the pressing force.