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HYPOTHESIS OF COINCIDENCE OF SHEAR STRESSES IN THE EXCITATION OF HAIR CELLS

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A new hypothesis of neuromechanical "sharpening" in the cochlea inferred from the available morphological data and from the geometry of the distribution of stereocilia in OHC in relation to the distribution of shear stresses as determined by Tonndorf and by the author on cochlear models is presented.

Introduction

An idea of lateral suppression or "sharpening" in the perception of pitch was created in its simple form as a result of discrepancy between Helmholtz's theory [15] and the experimental observations. Helmholtz, investigating the perception of transients in musical sounds, reasoned that the mechanical frequency analyzing system in the form of basilar membrane must be damped in quite a significant degree. There was hence obvious contradiction arising from the necessity to assume high selectivity of the analyser to tally with its high pitch discrimination and from the observations which indicated its considerable damping.

A concept, well known as Gray's theory [12], introduced important modification of the Helmholtz theory and by the assumption that only these hair cells which receive the strongest excitation determine the pitch perception, was undoubtedly the first approach to what is presently termed as "sharpening" or lateral suppression. Almost 50 years later Hartline [13] discovered the phenomenon of inhibition of activity in visual receptors in the Limulus eye. This discovery was successfully used by Békésy [3] to refine earlier hypotheses pertinent to the nature of sharpening in the perception of pitch and based on the well-known observations by Mach.

Over the last decade or so the operation of lateral suppression or neural sharpening was considered as a logical consequence of data disparity resulting from the comparison of travelling wave envelopes in the BM with values of DL for frequency (Nordmark [31], Rakowski [32], Verschuure [42]) or with selectivity of tuning curves representing the bioelectrical activity in single fibers of the eighth nerve (Kiang [25]), though in the latter case the differences are smaller.

It can be observed that travelling wave envelopes obtained by Békésy [1], which are frequently referred to, represent nothing but a first approximation of the true pattern because of the limits imposed by the method he used, i.e. direct visual examination with the use of an optical microscope with relatively low resolving power. For that reason he had had to use sound pressure levels reaching 140 dB, delivered to the tympanic membrane, to obtain sufficiently large amplitudes in the basilar membrane. At such pressure levels nonlinear processes are likely to occur at least in the region of the top of the travelling

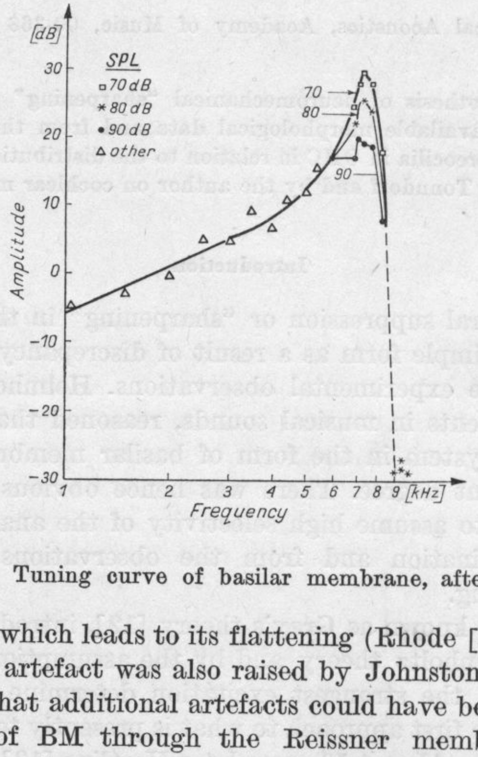

Fig. 1. Tuning curve of basilar membrane, after [33]

wave pattern (Fig. 1) which leads to its flattening (Rhode [33]). The possibility of occurrence of this artefact was also raised by Johnstone and Taylor [21]). They also point out that additional artefacts could have been involved as a result of observation of BM through the Reissner membrane practiced by Békésy and also from the use of post-mortem or proximatus post-mortem samples. However, similar comparisons with the newer results of the investigations of hydrodynamical tuning curves by Kohllöffel [26], which were obtained at excitation levels of approx. 70 dB SPL and using laser light, or of investigations by Rhode [33], Johnstone and Boyle [20] and Johnstone and Taylor [21], in which Mössbauer method (absorption of gamma irradiation) was used at abt. 70 to 90 dB SPL, also show considerable discrepancies with neurophysiological tuning curves and hence call for retaining of the assumption of locus of sharpening to some degree at cochlear level.

Aside of these considerations it can be observed that direct comparison between the envelopes of travelling wave in BM and neurophysiological tuning curves or else a search for direct correspondence between the selectivity of the travelling wave envelopes and the DL for frequency or the selectivity of psychoacoustical tuning curves can be regarded only as exaggerated simplification or misrepresentation. This understanding, however, was fairly widely accepted, e.g. after Davis [7] "each fibre has its "best" frequency but optimum is not sharp. The region of activity, as can be expected, corresponds with the travelling wave envelope". This simplification is likely to result from the uncertainty with regard to the mechanism of excitation or stimulation of hair cells, which leads to their depolarization. For this very reason the comparison of the travelling wave envelope normal to the BM surface and along its long axis with the tuning curves (neural) can be acceptable only as a first approximation.

As it can be learned from the literature a number of various concepts pertaining to the "sharpening" of cochlear selectivity on mechanical or hydromechanical basis or else on the assumption of both neural and hydromechanical processes in "sharpening" have been proposed (Tonndorf [40], [41], Zwicker [46]). There were also attempts to assign the neural "sharpening" to the multiple differentiation at various levels of auditory pathway (Huggins, Licklider [17], Dolatowski [8], Engström [9]). Ideas of different kind, presented by Zwislocki [47, 48], are based on the assumption of phase opposition in the activity of the populations of inner and outer hair cells. This phase opposition in bioelectrical activity of IHC and OHC was found by Zwislocki in the kanamycine-treated samples. This drug has a destructive influence mostly on IHC in the basal turn of the cochlea and mostly on OHC in the apical turn. The neural tuning curve obtained from these experiments at frequency of 5 kHz (a result of subtraction of tuning curves for IHC and OHC populations) is in its top comparable with that determined by Rhode [33] (flat top) and outside this region close to the tuning curves obtained by Kiang [25]. It is like an equivalent of Kiang's tuning curves particularly with respect to the slopes of the upper and lower flank, though delivered from the different experimental method. However, Zwislocki's theory of phase opposition, at least presently, does not seem to be fully and sufficiently documented, especially with regard to the kanamycin influence on both populations of hair cells.

Hydrodynamics of the cochlea

The stapes movement in the oval window results in a travelling wave in cochlea. From Tonndorf [40, 41] experimental works on cochlear models or works by Lesser and Berkley [28] it appears that the travelling wave is trochoidal in its nature, i.e. such a wave in which particles of the liquid medium move along elliptical or circular orbits. Closer examination reveals that particle tracks under certain conditions are even more complicated.

It can be observed that the trochoidal wave field is vectorial and three--dimensional generally, for instance for the case of a surface radial wave. Tonndorf [41], in his considerations pertaining to the hydrodynamics of cochlear models, assumes the two-dimensional field only and concludes that the existence of a trochoidal wave, the similarity of waves in the medium and in BM and also the decrease of the field vector perpendicular to the BM surface with distance, seem to indicate that the movement of liquid medium in the cochlea accompanied byy the BM deformations well resembles Lambs surface waves. It seems likely that this simplification assumed for clarity of dynamical representation of the system behaviour is not pertinent in regard to Tonndorf's observations of the distribution of shear stresses in BM (or between the tectorial and basilar membranes) performed on cochlear models. These observations seem to indicate for the existence of a three-dimensional vectorial field in the cochlear medium.

The latter observations are extremely interesting from the point of view of Tonndorf's [41] and Zwicker's [46] concepts about the mechanical or hydromechanical nature of the "sharpening" process. The envelope of a travelling wave, longitudinal shear stresses and radial shear stresses, as measured by Tonndorf [41] on cochlear models, are presented in Fig. 2. Tonndorfs tates that "these mechanical transformations may be dominant if not the only factors determining the "sharpening" observed in neurophysiological activity", though he does not disregard the possibility of neural processing.

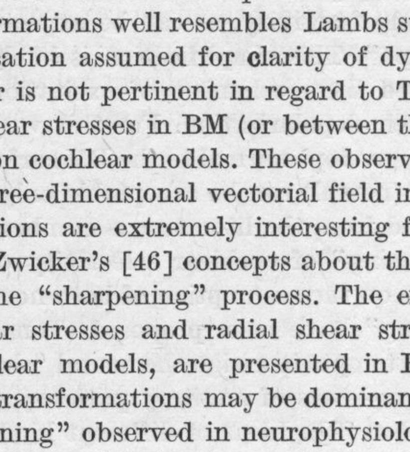

Fig. 2. Shear stresses in the cochlear model, after [41]

It must be, however, stressed in that context that the envelopes of both longitudinal and radial shear stresses, though characterized by better selectivity with respect to the normal deflection travelling wave, are far from the selectivity of neurophysiological tuning curves, particularly their portions close to CF's. Nevertheless, Tonndorf's data [41] on shear stresses in the cochlear models and their redetermination by the autor are, as it seems, the only data available.

Neurophysiological data

The available data practically rule out the possibility of excitation of hair cells through axial stresses, i.e. along the axis of stereocilia exerted by the normal pressure as it was necessary in the so-called "heavy beam theory" by Huggins and Licklider [17]. Békésy's data [2] from the early simple experiments using vibrating needle show that evidently hair cells are mostly sensitive for the stimulation tangential to the BM surface. Hence it is postulated [9] that stereocilia rather perform like levers and behave passively transferring the energy of shear stresses from the tectorial membrane to the basal body. Basal body, according to Engström, should be identified as main element which under stimulation leads to the depolarization of the hair cell.

Basic morphological data concerning both hair cells populations are derived from Held [14] and Kolmer [27]. More recent data by Flock et al. [11], Engström et al. [9] and, particularly, these by Spoendlin [36, 37] supply a vast amount of morphological information; with respect to the mechanism of hair cells stimulation, however, the ideas revealed by these authors seem to have comparatively little in common. Thus Flock et al. postulate radial shear stresses as leading to the depolarization of hair cells, whereas Engström et al. maintain that radial shear can be regarded as the main stimulating factor only with respect to the inner hair cells because of the simple isotropic geometrical configuration of stereocilia of these cells. Again Flock et al. pointa out very characteristic configuration of stereocilia in the outer hair cells in all the three rows resembling "W" to some extent (Fig. 3). This very special arrangement according to Flock et al. (1962) indicates that the sensitivity of OHC is increased in some priviliged directions. These directions of increased sensitivity should correspond

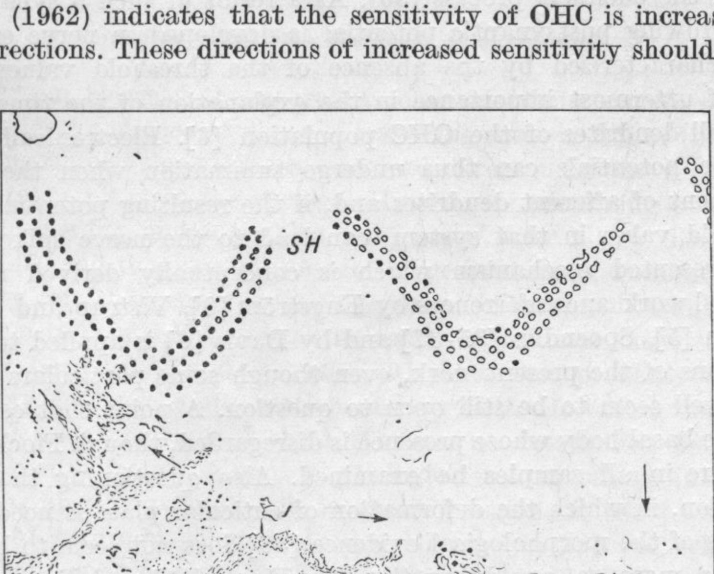

Fig. 3. Arrangement of stereocilia in OHC, after [11]

with oblique radial and longitudinal shear stresses or, in other words, the OHC should demonstrate some degree of directional sensitivity.

Spoendlin [36, 37], by inference from his morphological studies of Cortis' organ using an electron microscope, seems to deny the role of the basal body in the stimulation and eventually depolarization of hair cells since he was unable to find this structure in his samples except in very young animals and guinea pigs [11]. He also argues that the cuticular plate, in which stereocilia are anchored, is so stiff a structure that its deformation under lever action of stereocilia does not seem to be possible. Hence, the deformation of cuticular plate and the resulting stimulation of the basal body seems to be open to question.

A very interesting hypothesis with reference to the initiation of the mechano-electrical transformation process was reported by Vistrup and Jensen [43] and Christiansen [5]. This hypothesis follows the observation of mucopolisaccharides which, under mechanical shear stresses, develop surface electric potentials. Mucopolisaccharides showing even some sort of regular structures were found in between the stereocilia spaces by Spoendlin [35]. The shear stresses which are present between the stereocilia, following stimulation of BM [41], could possibly lead to the initiation of such a reaction [36, 37]. The mechano-electrical transformation of that nature seems also to be in agreement with the observations by Tasaki and Spyropoulos [38] and Butler [4] from which it follows that Cortis' organ space without stimulation is isopotential.

Morphological data are also available which indicate the possibility of synaptic transition from the hair cell to the afferent nerve endings on the principle of the chemical process [36]. As a result of such a synaptic process, gradually growing postsynaptic potential is developed in nerve endings. This potential, characterised by the absence of the threshold values, may very likely be of uttermost importance in the explanation of the time summation process in all dendrites of the OHC population [6]. Electronically conducted postsynaptic potentials can thus undergo summation when they reach the initial segment of afferent dendrites and, if the resulting potential approaches the threshold value in that system, can lead to the nerve spike firing [36].

The presented mechanism which is conceptually derived mainly from experimental work and inferrences by Engström [9], Vistrup and Jensen [43], Christiansen [5], Spoendlin [35-37] and by Davis [6] is applied to the further considerations of the present work, even though some particulars of that concept may well seem to be still open to question. A point that can be argued concerns the basal body whose presence is disregarded, though Flock [11] found this structure in all samples he examined. Also questioning the mechanism of stimulation, in which the deformation of cuticular plate is needed [9], only on the basis of the morphological evidence [36] does not seem to be quite convincing, the more so as observations by Flock [11] and Engström [9] and their conclusions pertaining to the rigidity of stereocilia were not questioned, though it could well have been of advantage for Spoendlin's [36] hypotheses.

It can be learned that mucopolisaccharides were found by Spoendlin between the stereocilia, if not along the whole length, then at least at some definite length. Hence, with the assumption of considerable rigidity of both, the stereocilia and the cuticular plate, it appears to be rather difficult to explain in what a way the shear stresses between the stereocilia can be developed, necessary for the graded potential to appear. Once the complete rigidity of cuticular plate is assumed, the shear stresses between the stereocilia can develop only if the latter undergo bending. However, this concept seems to be contradictory with respect to Spoendlin's finding which indicates that mucopolisaccharides occupy probably some considerable length of the stereocilia space. From classical mechanics it is known that a bending of stereocilia, anchored in the rigid cuticular plate, would take place chiefly if not only in the vicinity of anchored ends. In such a case the presence of mucopolisaccharides outside this small fraction of stereocilia length would appear to be rather a sort of unfounded. Therefore it seems not to be improbable that Spoendlin's inferrences with regard to the rigidity of cuticular plate, which are in contrast with Engström's [9] implications, are wrong. If that was true, and assuming a considerable degree of stiffness in stereocilia, shear stresses would occur at the whole or at the large part of stereocilia length. On the other hand, the assumption of elastic cuticular plate seems to make Spoendlin's argument with regard to Flock [11] and Engström [9] unsound. Summing up it appears that the available empirical data are inconsistent, as are the theories built up thereupon.

Psychoacoustical data and locus of sharpening

A comparison between the neurophysiological tuning curves obtained at the 8-th nerve level and the envelopes of travelling wave in BM or the envelopes of radial or longitudinal shear stresses may lead to reasoning that the sharpening at this level takes place in the cochlea. Hypotheses pertaining to the hydromechanical sharpening in the cochlea were given after all by Tonndorf [40] and Zwicker [46] and they are not new in the general sense. Tonndorf indicates the possibility of sharpening resulting from mechanical transformations of normal deflection of BM to the radial and longitudinal shear stresses and suggests after Lowenstein and Weršall [29] that most probably only radial stresses are engaged in the stimulation of hair cells. However, the envelopes of both radial and longitudinal shear stresses, as determined by Tonndorf, diverge significantly from the neurophysiological tuning curves [25], particularly, as it was already pointed out, in the top region. It can be shown that with respect to neurophysiological tuning curves [22-25] the selectivity of hydrodynamical tuning curves [20, 21, 26, 33], expressed by the slopes of the flanks of TC, is worse by the ratio of 1 : 2 to 1 : 4 and still worse in the top of the curve region.

The results of investigations of psychoacoustical tuning curves [18, 19, 44], which show that the slopes of the upper flank of tuning curves in the top region reach from 10^3 to $2.5 \cdot 10^3$ dB/oct, seem to point out quite soundly that the process of "sharpening" is not completed at the primary neurons level because the slopes of neurophysiological tuning curves at the eighth nerve level are considerably lower [10, 25, 45].

Hypothesis of coincidence of shear in hydrodynamical sharpening

According to Engström et al. [9] the izotropic distribution of stereicilia in IHC suggests that IHC are stimulated only by radial shear stresses. On the contrary, Tonndorf [41] by the analysis of the role of tectorial membrane comes to the conclusion that IHC can be stimulated but only by longitudinal shear stresses. Similar implications were formulated also by Spoendlin [36]. In spite of the lack of sufficient and convincing experimental data it seems likely that IHC at any rate may demonstrate either unidirectional characteristic of sensitivity or, which seems even more probable, have the same sensitivity for shear stresses from any direction (tangential shear). This is not quite in agreement with findings by Spoendlin [36, 37] who was able to show some anizotropic arrangement also in IHC.

The very peculiar distribution of stereocilia in OHC does not seem to permit for the assumption of the analogical hypothesis because in nature rarely structures can be found in which complication would be purposeless. If the structure of OHC and, particularly, the distribution of stereocilia very close in shape to the letter "W" with low tooth in the middle and limbs at approximately 45° to the length of BM is estimated, it seems very likely that the priviledged directions of stimulation may be oblique. In that case OHC would be particularly sensitive or sensitive only for shear stresses oblique with respect to the direction of travelling wave propagation.

Spoendlin [36], discussing the nature of the graded postsynaptic potential development, states that the deformation of the inter-stereocilia mucopolisaccharide molecular structures (and hence the accompanying electrical reaction) is the largest if the rows of stereocilia are parallel to the direction of bending and the smallest if the rows of stereocilia are perpendicular to that direction. Even with the assumption that stereocilia do not undergo bending (as Spoendlin did assume) but only deflection near their place of anchorage, i.e. cuticular plate – which depends, as discussed above, on the relative stiffness of both stereocilia and cuticular plate which can not be determined yet with the sufficient certainty – the principle of directional sensitivity of OHC with their anizotropic stereocilia configuration can well seem true. In case of rather stiff stereocilia and relatively elastic cuticular plate, possibly only over the portion close to the anchorage of hairs, the graded potentials would develop in the whole interstereocilia mucopolisaccharide molecular structures. In spite of the obvious possibility of this reasoning, Spoendlin [35, 36] does not cease from the well accepted and popular assumption that the priviledged directions in sensitivity characteristics of OHC and IHC are radial and longitudinal, respectively.

It is easy to observe that oblique shear stresses appear solely in the region of coincidence of both longitudinal and radial shear stresses, as they were determined by Tonndorf [41] and by the author (this report). There is only a relatively limited region, in terms of BM length in which these two kinds of shear occur together. This region that has been termed the "region of coincidence" is, contrary to the envelopes of travelling wave, longitudinal shear stresses and radial shear stresses, comparatively narrow in the frequency domain. So, if the presented hypotheses and reasoning would gain more experimental evidence and support, particularly by the determination of directional characteristics of OHC sensitivity, then they could be significant in the understanding of the sharpening phenomena at cochlear level and of the pitch perception as well. Thus, assuming that the depolarization of the basal body or the growth of graded potential at the initial dendrites of afferent fibers takes place only for the oblique shear stresses, then this activity would result from the shear determined by the difference of vectors $\boldsymbol{R}(x)$ and $\boldsymbol{L}(x)$. Functions $\boldsymbol{R}(x)-\boldsymbol{L}(x)$, derived from Tonndorf's [41] data and from the own data obtained on 10 : 1 scale cochlear model, are presented in Figs. 4 and 5. The quantitative differences between the two sets of data do not seem to be alarming as obtained from the seemingly different models and most probably also procedures. An important

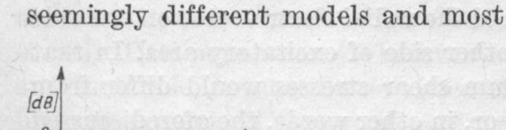

Fig. 4. Region of coincidence of shear stresses in cochlear model calculated from the data by Tonndorf [41]

Fig. 5. The distribution of shear stresses in the cochlear model. Two membranes with different elasticity and thickness $W(x)$ — the coincidence functions of $R(x)$ and $L(x)$

detail in the concept of coincidence of shear stresses in the stimulation of hair cell is that within one full period of stimulation, in the top region of the $R(x)-L(x)$ curve, i.e. where scalar values of both vectors are equal, the phase of $R(x)$ vector changes by 180°. Hence, the stereocilia in the limbs of "W-like" configuration are subjected to the shear forces $F(x)$ of equal amplitude but inclined 45° and −45° with respect to the BM length.

Now then the next or second degree of coincidence occurs which can be considered as the proper coincidence and which results from the action of equal amplitude but directed along the rows of stereocilia in OHC vectors of shear stresses (i.e. 90° aside one from the other). It can be that only and solely that coincidence, which can be found nowhere but at the top of $R(x)-L(x)$ function, is associated with the depolarization of the basal body or assuming different mechanism, the growth of the graded potential in the initial dendrites of afferent network, eventually resulting in firing of the nerve spike if the characteristic threshold value was reached.

Approval of the mechanical transformations after Tonndorf [41] and assumption of the operation of sharpening according to the principle of the hypothesis of coincidence may include, in their nature, explanation for the existence of excitatory and inhibitory areas. Namely, if the envelopes of shear stresses overlap each other, some kind of blocking of at least a fraction of OHC population is likely to occur on both sides of $R(x)-L(x)$ maximum. Such blocking could be expected as a result of prevalence of the radial shear vector on one side and the longitudinal shear vector on the other side of excitatory area. In that way on both sides of $R(x)-L(x)$ maximum shear stresses would differ from those most effective for excitation exertion or, in other words, the aforediscussed second degree of coincidence would not come to effect.

Innervation of the cochlea and neurophysiological tuning curves

It is known that the number of hair cells in man is comparatively small (relative to the number of receptors in other sense organs) and, according to various authors, ranges from about 15000 (Spoendlin [41]) to about 40000 (calculated from data by Teas [39]). Of that number less than 25% refers to the inner hair cells. Each of OHC is equipped with about 100-140 hairs (stereocilia) arranged in the three rows forming together a very characteristic W-like anizotropic structure described above. IHC are equipped with only about 40-50 hairs and the arrangement of them is either izotropic or their anizotropy is unidirectional [9, 11, 36, 37, 39].

Nothing more but the relative number of OHC and their comparatively complicated anizotropy could lead to the suspicion that just this population should demonstrate higher discriminatory ability relative to the IHC population. Contradictory argumentation could be performed using morphological data pertinent to the number of the afferent links; only about 3000-4000 of those innervate the whole population of OHC whereas the most afferents, i.e. about 50000, carry information from the IHC.

Aditionally the IHC have afferent connections almost entirely with the radial fibers whilst the connections of OHC dendrites with afferent network are accomplished by the external spiral fibers, which connects with groups of OHC, covering some considerable space. These reasons seem to have led Spoendlin [36] to the assumption that inner hair cells are dominant in the discrimination of pitch.

It seems that this assumption can be regarded as quite logical from the point of view of morphological evidence but there are also some other aspects which may indicate that it as well can be recognized as doubtful and formulated without sufficient insight into functional evidence.

One of the doubtless facts, which can be used in this argument, follows from the relative number of afferent neurons associated with the OHC and IHC. As it was mentioned, only about 5% of neurons within the eighth nerve are afferents carrying information from OHC. Hence, it well can be that practically all the records of bioelectrical activity, as obtained by Kiang [25] and others, could be pertinent to the radial fibers belonging to IHC population. From that point of view it may seem probable that the neurophysiological tuning curves, obtained by Kiang at the 8-th nerve level and widely accepted as the determinant of the frequency selectivity of the auditory pathway at that level, may turn out not to be actually "true" tuning curves as they may reflect the activity of only IHC population. Whatever we will learn about the activity of OHC and their role, it must be admitted that with regard to facts we know very little at present. However, if nothing more is possible now but speculations, it can be also observed that the hypothesis of coincidence presented implies some possibility to judge that at least equally well the "true" tuning curves at the eight nerve level can be represented by the activity in the considerably less accessible neurons from the spiral fibers innervating OHC population.

Conclusion

The presented and quoted experimental data and the hypothesis concerning the mechanism of neuromechanical sharpening are close to the popular and rather widely accepted, at least up to the beginning of the last decade, assumption that the process of sharpening takes place mainly or even is completed at the cochlear level.

It seems worthy to observe that these concepts were in a way similar to those by Helmholtz [15] who declared that BM and Cortis' organ have basic role in the perception of pitch, though his ideas pertaining to the nature of analysis at that level were quite naturally very simple.

The presented in this report hypothesis of coincidence of longitudinal and radial vectors of the field of shear stresses in the travelling wave demonstrates still further effort to explain the unbelievably high selectivity of the ear analyzer, even as low as at the cochlear level. Assuming that Kiang's [25] tuning curves (in spite of the former criticism) reflect that selectivity to some degree at least, it comes to about 200 dB/oct at 1 kHz as expressed by the upper flank slope [10, 45]. Nevertheless it is by an order of magnitude lower than the selectivity in the psychoacoustical tuning curves reported in the papers cited [18, 19, 44].

The presented data seem to support the place theory. However, it should be stressed that essentially the spatial data do not contradict the temporal data (time theory) and to prove such contradiction was by no means intended by the author. It can also be noticed that the travelling wave theory, though it cannot be questioned in the face of the available experimental data both hydrodynamical and neurophysiological, still offers many problems yet unsolved in detail.

Undoubtedly the data by Hind et al. [16] and also by Rose and al. [34], which show that the regions of activity in terms of frequency at the eighth nerve level evoked by sine signals at from 20 to 100 dB SPL, correspond with considerable regions (dimensionally) in the basilar membrane add to the complexity of pitch perception process. On the other hand, it may seem possible, particularly with morphological data and inferrences by Spoendlin [37] at hand, that the mentioned apparent complications result from the misleading interpretation of the up-to-date available neurophysiological data. In one of his papers Spoendlin expressed his doubts in the statement that "Kiang probably recorded mainly from the neurons associated with IHC and his results reflect the mechanism of IHC coding system".

It is also probable that similar objections may apply equally to the data by Hind [16] and Rose [34]. For that reason, with lack of the sufficiently documented data pertaining to the activity of OHC, any comparison between the slopes of neurophysiological tuning curves obtained heretofore and the slopes of psychoacoustical (or hydrodynamical) tuning curves can evoke quite substantial criticism. Nevertheless such comparisons are evidently popular [10, 30] in spite of that, as it was mentioned, there is actually very little known about the bioelectrical activity and the role which OHC population plays in the perception of pitch.

In this context, the presented hypothetical model of neuromechanical sharpening, working on the principle of common effect of both radial and longitudinal shear on the OHC with the assumption of directional sensitivity characteristics in this population, is an attempt to determine potential possibilities of OHC with respect to the discrimination of pitch. Some aspects of this hypothetical model are in agreement with Evans' [10] inferrences concerning the "second filter hypothesis", who wrote that it is highly probable that "each hair cell is equipped with a separate "private" second filter".

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