

## MECHANICAL FREQUENCY DISCRIMINATION IN THE COCHLEA

W. D. Keidel

This morning, during the previous session of this roundtable discussion, we were presented with a good deal of experimentation concerning the possible role of various tonal stimuli in neural discrimination. The problem of periodicity-analysis, at the very least, must be taken into consideration when discussing the over-all frequency analysis of the ear and the problem of pitch.

There is another point of view, however, which, at least to a certain extent, is still valid. This is what Waetzmann meant in his statement: „If the central nervous system is considered to have the ability of frequency discrimination, then this implicitly means that we are not able to base the frequency discrimination of the ear upon some well-known physical events." This point of view certainly forces those experimenting on the physical background to first search for an explanation of the frequency discrimination based upon the physical function of the inner ear, and to leave not more than all that remains to some neural function of the CNS.

Consequently, when even admitting that some periodicity-analysis at low frequencies of up to a few hundred c.p.s. may occur completely separate from the wave-dispersion within the cochlea, and considering that this phenomenon is comparable to some general ability of all sensory receptors to analyse periodicities (e.g., vibrational sensitivity of the skin and sensitivity of the eye to flickering light), it is indeed well established today that the frequencies of sinusoidal tones, having reached steady state conditions, are distributed along the basilar membrane (Figure 1). This distribution takes place by means of a special hydrodynamic dispersion system, discovered by **v. Békésy** and calculated by **Ranke**, according to the single place theory of **v. Helmholtz**, and of **Gildemeister**. What remains is only one single quantitative problem, first raised by **Wien** and still unresolved.

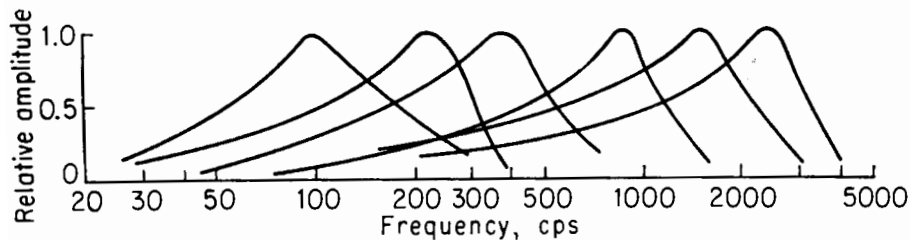


Figure 1: v. Békésy's forms of „resonance" curves for six positions along the cochlear partition. According to **G. v. Békésy** (1960)

**Wien** started with the idea that the ability for the discrimination of two or more different frequencies should be the feature of the same system that is responsible for the dampening of the vibrations of the basilar membrane. The difference-limen for frequency, on the other hand, can easily be reduced to the DL for intensity by the following consideration: Since the DL for intensity shows almost the same value of about 10 per cent for all sensory organs, in the case of the CNS and its decoding system, only that shift of the whole pattern of movements of the cochlear partition can be detected which, for a given group of sensory cells and at a fixed place on the organ of Corti, causes a decay of 10 per cent of the amplitude of the vibrations of the basilar membrane, related to the maximum now shifted to another place. Hence, a small shift,  $dx$ , along the long axis of the basilar membrane, belongs to this drop in amplitude. This  $dx$  becomes smaller, as the decline of the curve on both sides of the maximal amplitude of the cochlear partition becomes steeper. On the other hand, this steepness has a reciprocal relationship to the amount of dampening of the vibrating system. With a knowledge of the dampening factor and the steepness of the envelope of the movements of the cochlear partition, it then becomes clear that this steepness is by far too small to explain the human ear's tremendous acuity in the DL for frequency. With other words, **Wien's** objection not only touches on the Helmholtz resonance hypothesis of hearing, but does so in relation to the modern concept of the travelling-wave theory, which has been so beautifully established by **v. Békésy's** experimentation. **Wien's** objection is still valid, and we should look for some adequate explanation. To be sure, we should at least try to detect **where** our knowledge is still wanting.

In 1957, **Ranke** pointed out, in a speech before the German audiologists assembled in Würzburg, that the human DL for frequency corresponds to a strip on the basilar membrane of not more than 10 micra, or a breadth of only **one** hair cell. He then compared the physiological contrast of the ear with that of another sensory organ — the eye. The pure image on the retina with its flattened light-intensity curve, is compensated by the reciprocal inhibition of nerve cells, i.e. the so-called „spatial contrast” („örtlicher Kontrast”). By this process the resolving power of the eye is considerably improved. In the case of the ear, **Ranke** mentioned that the envelope of the vibrations of the basilar membrane also shows a flattened maximum. Based upon the experimental findings of **Galambos** and **Davis** (1943), he then goes on to compare the slope of this envelope with the steepness of the function describing the dependency of the level of excitation of a single nerve fiber on the stimulus-frequency. The result is a so much steeper gradient that the economic limit — at least at the highest level of the CNS — is reached: the breadth of the local step in excitation approximates the order of the diameter of one cone. For illustration, his original slide will be reproduced (Figure 2).

This figure additionally shows that the main process of adaptation is related to the periphery, since the diagram of the shift of pitch by adaptation to a loud tone is nearly as flat as the envelope of the basilar membrane (according to measurements by **v. Békésy**, 1929). But the curve of the enhancement of the loudness level by the addition of two tones of equal loudness (**v. Békésy**, 1929) is comparable in its steepness to that of the neural excit-

ation behind the process of mutual inhibition. In order to explain the mechanism of the physiological contrast-phenomenon of the ear, **Ranke** (as well as **v. Békésy**) developed his own hypothesis, which was presented at the 1949 meeting of the German Physiological Society, in Göttingen. He cites **Held's** histological finding that several hair cells (at least of the outer cell type) are usually connected with one and the same nerve fiber, in a manner comparable to the hanging of currants on the same branch. The velocity of the travelling-waves depends on the locus of the basilar membrane. For a given frequency of a tone, there is one certain area on the basilar membrane where this velocity has a minimal value. On the other hand, when the velocity of nerve conduction at this area is equal to the velocity of the travelling-wave, then the conditions for the propagation of the spike have been fulfilled. However, when the sub-liminal local excitations in each single cell are electrotonically summated to a spike within the nerve fiber, then this process is highly sensitive to each minimal shift in the travelling-wave velocity, as well as to each small phase shift. **Ranke** goes on to add some possible consequences to this idea: (I) fibers from the basal turn of the cochlea ought to be thicker than those from the apical one, or (II) the distance between each of the hair cell pairs connected to one fiber should be greater on the basal turn than on the apex, due to the higher value of the velocity minimum of the travelling-wave near the apex.

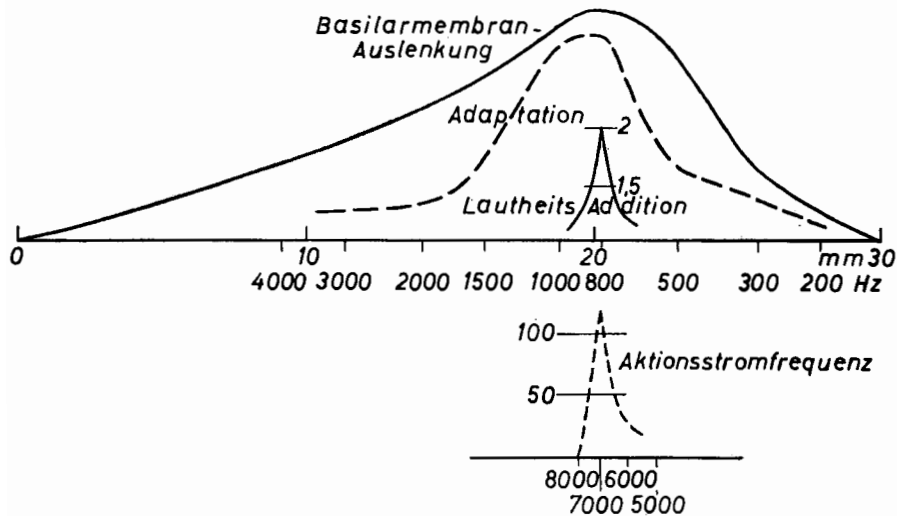


Figure 2: **Ranke's** comparison of one of the „resonance” curves of the cochlear partition both with the loudness curves and with the steepness of the function describing the dependency of the level of excitation of a single nerve fiber on the stimulus frequency (according to **Galambos** and **Davis** 1943). Further explanation in the text.

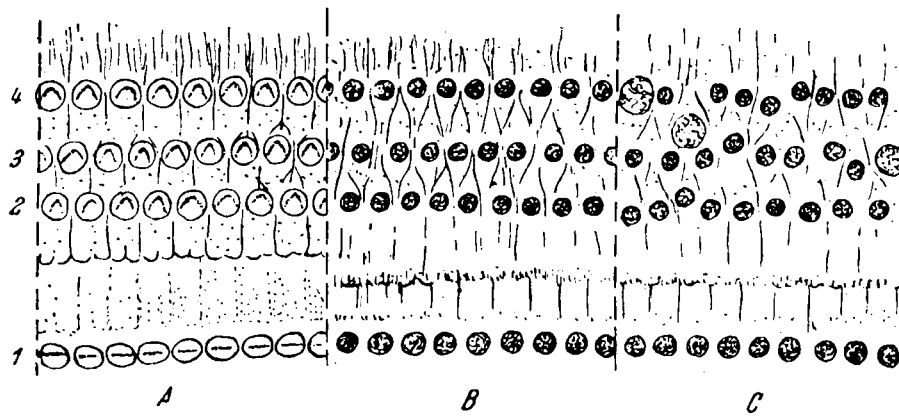


Figure 3a

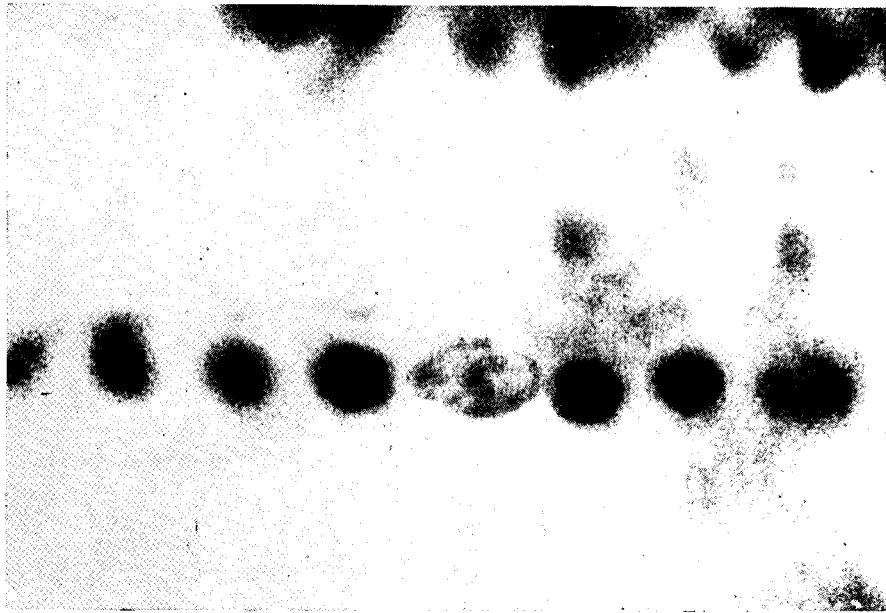


Figure 3b

Figure 3: (a) **Neubert's** schematic drawing of the swelling of the nuclei of only the outer haircells after strong acoustic stimulation (guinea pig). He found that only interruption of the same sound influences also the inner hair cells (figure 3b). According to **Hartzendorf, Wüstenfeld and Neubert** (1961).

In the meantime, **v. Békésy** performed some highly relevant experiments using the somesthetic system for vibrational stimuli as a model of the auditory phenomena. These experiments so strikingly demonstrated the existence of a mutual inhibitory system (although of a very complex nature) within the terminal network of touch receptors, that we have been able to base a new system of **vibratese** language on the fact that the skin is perfectly able to receive both low pitched sinusoidal tones (as the vowels) and the transients of speech (as the consonants), during the steady state and under certain specified conditions (**Keidel**, 1958, **Biber**, 1961). Moreover, **v. Békésy** was able to obtain experimentally quantitative data on the old concept of a duplex set of receptor populations within the ear (**Meyer zum Gottesberge**, 1948; **Ranke**, 1953 \*), **Davis**, 1953, 1957): the outer hair cells are 40 db. more sensitive than the inner ones; the inner hair cells are less sensitive than the outer ones, but with a higher sensitivity for the first derivative in time and, hence, better fitted for mutual inhibition. Indeed, this idea could present an analogy to the duplicity theory of vision with the eye's system of rods and cones.

A fine histologic contribution to this duplicity theory of hearing has been accomplished recently by **Wüstenfeld** and **Neubert** (1960). They showed that only the addition of transients to a steady tone-stimulation histologically affects the **inner** hair cells, while steady tones alone only influence the outer ones. These experiments, of course, carefully excluded the pure intensity effect; the over-all intensity was held constant. Only the time pattern, either constant, or interrupted stimulation, was varied. The results are shown in Figure 3. The histological sign of excitation was a special pycnotic increment in the nuclei of the hair cells.

The duplicity-concept has been given further support as a result of another technique that we recently employed in some experimentation (**Kaufmann**, **Keidel**, **Stange**, **Spreng**, **Theissing**, 1962). It is relatively easy to irritate the two sets of hair cells by means of chemical agents. It is quite conceivable that the various ferment systems, as for example, Coenzyme B, involved in the building and destruction processes of a particular excitory substance, e.g., acetylcholine and cholinesterase, influence the speed of the different metabolic processes within the sensory cells to a different manner and degree. In hearing, then, the speed of the metabolic processes would be slower in the case of the less sensitive population (inner hair cells), and more rapid for the more sensitive one (outer hair cells). It is even experimentally possible to separate the damage on the two processes, there by accounting for the time course of adaptation according to **Ranke's** adaptation theory (see **Keidel**, 1961). While it has long been known (e.g., **Davis**, 1957) that quinine salts seem to have a greater effect on the inner hair cells, with Streptomycin

---

\*) Ranke writes: „Dass die inneren Haarzellen relativ unempfindlich sind, dafür die Tonhöhe sehr genau messen, während die äusseren Haarzellen zwar sehr empfindlich sind, dafür aber nur eine geringe Genauigkeit in der Bestimmung der Tonhöhe zulassen. Es lassen sich jedoch ebensogut Gesichtspunkte dafür anführen, dass auch die multiple Innervation der äusseren Haarzellen zu einer sehr feinen Tonhöhenunterscheidung geschaltet sein kann.“

having, in turn, a greater effect on the outer ones, our own experiments attempted to compare the effects of Kanamycin and Streptomycin sulfate on cats (instead of the dihydrostreptomycin). The following results were obtained (Figure 4). We see here that streptomycin sulfate seems to poison, almost solely, that enzyme involved in the excitation process of the more sensitive population (outer hair cells), while Kanamycin affects both groups of hair cells, as well as indicating a clear and significant difference in the alteration of the adaptation metabolism. Further details are discussed in another paper (Theissing, 1962).

Now, how do these experiments and hypotheses contribute to the problem of frequency discrimination in the inner ear? We obviously do not know **how** the hair cells produce this physiological contrast. What we do know, however,

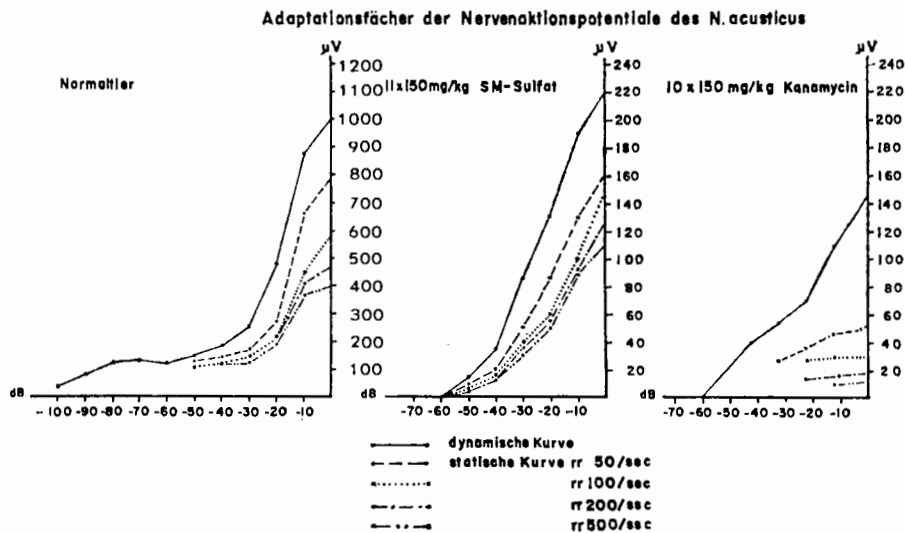


Figure 4: Dynamic (steepest) and static (adapted more flat) intensity functions of the compound action potential delivered by trains of clicks when using different repetition rates thus revealing the status of adaptation (cats). Left row: control; middle row: After 11 injections of 150 mg/kg Streptomycin sulfate. Only the population of the outer hair cells seems to be affected (rise of threshold about 40 dB, but the steepness of both dynamic and steady-state curves is not altered; the inner hair cells seem to be intact; right row: after 10 injection of 150 mg/kg Kanamycin: not only the outer hair-cells seem to be affected but also the metabolism of the inner ones is intoxicated: the steepness of the dynamic curve is less flattened than that of the adapted steady-state curves; this result could be explained in accordance with Ranke's hypothesis of adaptation as a different influence of the Kanamycin upon the two components of the cell metabolism for building and rebuilding of some excitatory substance.

is **how much** they do. To this end, Figure 5 presents a comparison, similar to that made by **Ranke** in Figure 2, but including the new neurophysiological data of **Galambos**, 1952, **Davis**, 1943, **Tasaki**, **Eldredge**, 1954 (Figure 5a). We can compare exactly the excitability-frequency curves of the first and second neurons with the steepness of the envelope of the basilar membrane. Taking into consideration that the ordinate here has a logarithmic value, while the envelope of the basilar membrane excursions is usually plotted linearly, one can easily say that the frequencies **below** the optimal frequency of a given neural unit shows the locus of the origin of the physiological auditory contrast between the first and second neurons. But for the frequencies **above** that

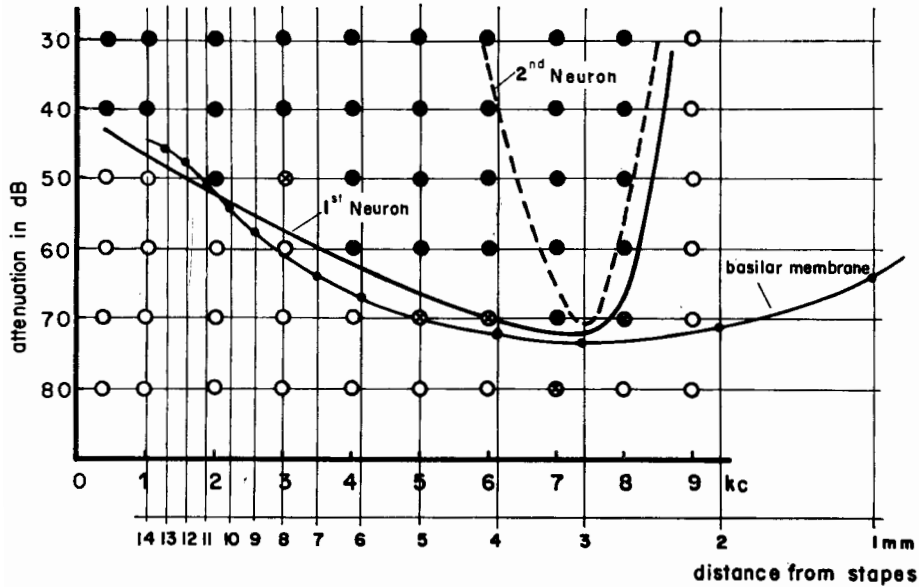


Figure 5a

Figure 5: Neural excitation curves of the first and second neuron (according **Galambos** and **Davis** and **Tasaki** and **Davis**) are compared quantitatively with the „resonance curve” of the cochlear partition (calculated to **Ranke's** formula). The frequency — distance relation is based upon the **Wegel-Lane**-distribution of frequencies along the basilar membrane. The frequencies higher than the optimal frequency of the neural units show the contrast phenomenon between the hydrodynamics of the inner ear and the excitation of the first neuron; however for lower frequencies the excitation curve of the first neuron is as flat as the „resonance” curve of the cochlear partition; the first step in the contrast phenomenon here is clearly a neural one, located between the first and the second neuron (figure 5a); the higher levels of the CNS, e.g. the third and fourth neuron contribute additionally to the over-all-contrast, figure 5b according to **Katsuki**, (1958, 1959).

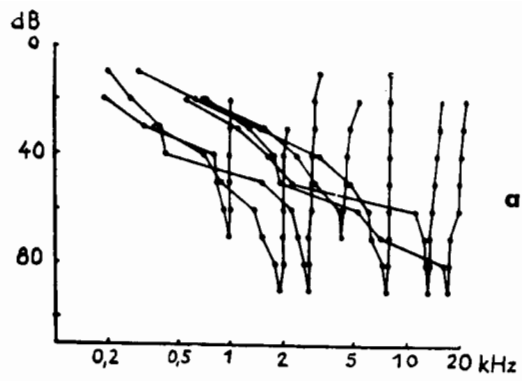
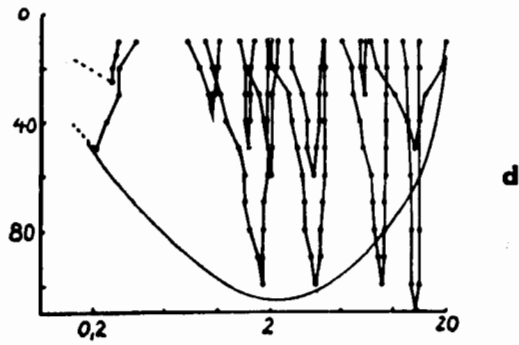
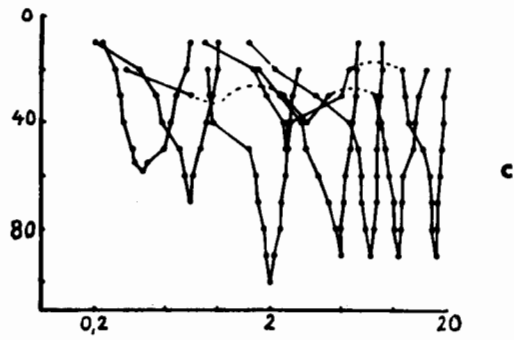
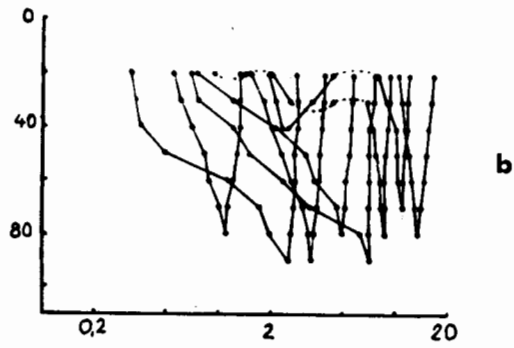


Figure 5b



optimal frequency, the contrast is almost complete in the first neuron. The higher neurons, as **Katsuki's** (1958, 1959) experiments prove so clearly, certainly improve the over-all contrast. But this improvement belongs much more to the lower frequency range (Figure 5b).

What does all this mean? One fact is immediately clear: The „Low-frequency-contrast“ is obviously mainly a neural phenomenon, probably based upon inhibitory neural multiple network circuits, and temporal inhibitory functions of a complex nature, to which **Dr. Katsuki** can perhaps tell us something more. But the „high-frequency-contrast“ seems to occur somewhere between the first neuron and the hydrodynamics of the inner ear. And here is where the largest gap in our experimental knowledge lies, when attempting an adequate and true explanation for **Wien's** objection. Perhaps **Ranke's** hypothesis, mentioned above, can partly resolve this problem. Then again, perhaps this problem is somewhat related to another set of observations by **v. Békésy**, summarized in Figure 6. Since the direction of movement of single cell groups, within the flat envelope of the cochlear partition vibrat-

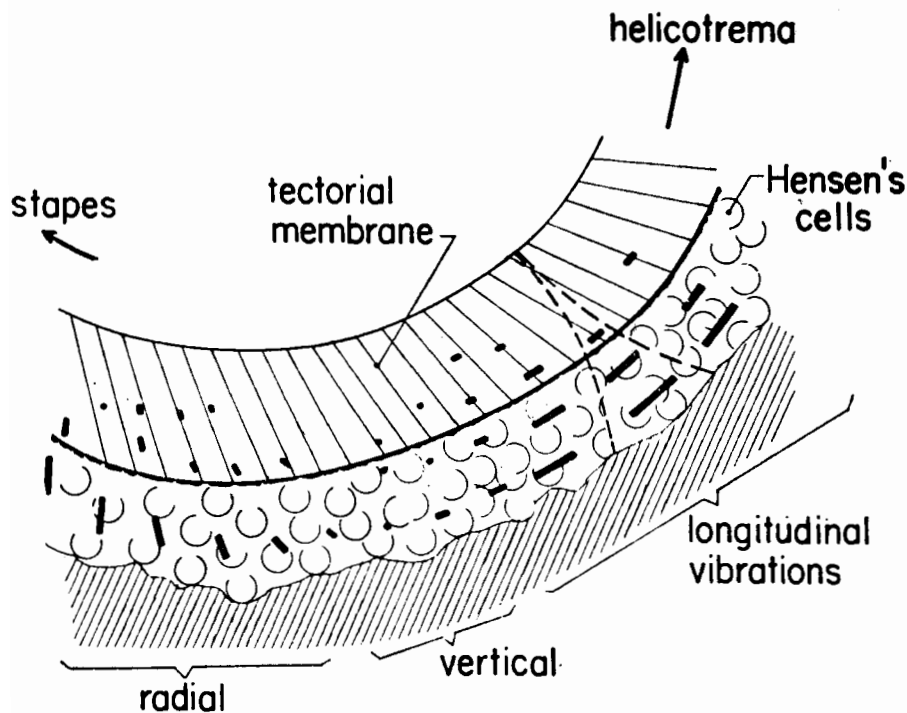


Figure 6: The distribution of the radial and longitudinal vibrations along the organ of Corti for stimulation with a tone, seen through the Reissner's membrane. From **G. v. Békésy** 1953.

ions, varies along a relatively small strip of the basilar membrane, from the radial, to the vertical, and to the longitudinal direction of vibrations, there is certainly enough space available to permit a mechanical explanation for this part of the auditory physiological contrast — in reality then a physical explanation. In other words, what we need here is a completion of our knowledge on the transformation of the hydrodynamics of the perilymph into that of the endolymph, and into the **real** adequate stimulans of a single hair cell, including the inhibitory effect of the multiple network connected to it. Considering the radial movement as the effective one, as far as I can discern, the breadth of the excited band of hair cells would be reduced to the diameter of a few Hensen-cells. But I think that we should reserve this question for our moderator, and refrain, for the present, on any further speculation concerning this part of the frequency discrimination.

Before embarking on this quite interesting discussion, however, I would like to cite another set of experimental data, which, in my opinion, should not be neglected in connection with the problem at hand. Since the original detection of **Rasmussen's** efferent fiber system (1942), this has been repeatedly verified in the experimental work of **Galambos**, 1954, 1955, 1956, **Davis**, 1944, **Desmedt**, and **Mechelse**, 1957, 1958, 1959, 1960. During the past year, one of the assistants in our institute (**R. Pfalz**) succeeded in showing that this efferent feedback slope, descending from higher parts of the CNS, not only influences the degree of efficiency of units of the cochlear nucleus (guinea pig), but also influences single units of the cochlea itself.

By the use of an ultra-fine microelectrode technique, he was able to show that this effect is not only dependant upon the intensity (explored for 50 to 110 db SPL), but is also highly dependant upon the frequency. This result is indicated in the last Figure 7. The left row in Figure 7a is a record of a spontaneously firing unit, the firing rate of which is expressed by intense sound (pure tones and clicks) on the opposite ear, while the ear on the record side is completely deafferentiated. There are different types of such units with respect to the time pattern of inhibition. The last Figure 7b clearly shows the dependency of the sound delivered to the opposite ear upon the frequency. 260 units were explored here, in which the latencies varied between 11 and 500 msec. The frequency-functions for sinusoidal pure tones show an optimal frequency of inhibition at a bandwidth of 1 to 2 octaves, (about half the number of units). The other group inhibited similarly for all frequencies, with the exception of one to two octaves (worst-frequency units). The clicks (0.2 msec) showed distinct, but systematic, effects, so that the transient and non-transient-sensitive receptors of the non-deafferentiated ear could be separated again. Up to the present, the same effect has been established for descending fibers to the cochlea itself. But as this has been found much less often (7 out of 120), no frequency-functions could be obtained (**R. Pfalz**).

Since **Loewenstein** (1955, 1956) proved that the firing rate for single fibers of the skin, in this case the sympathetic fibers, could also be varied by des-



# ELEMENT 203

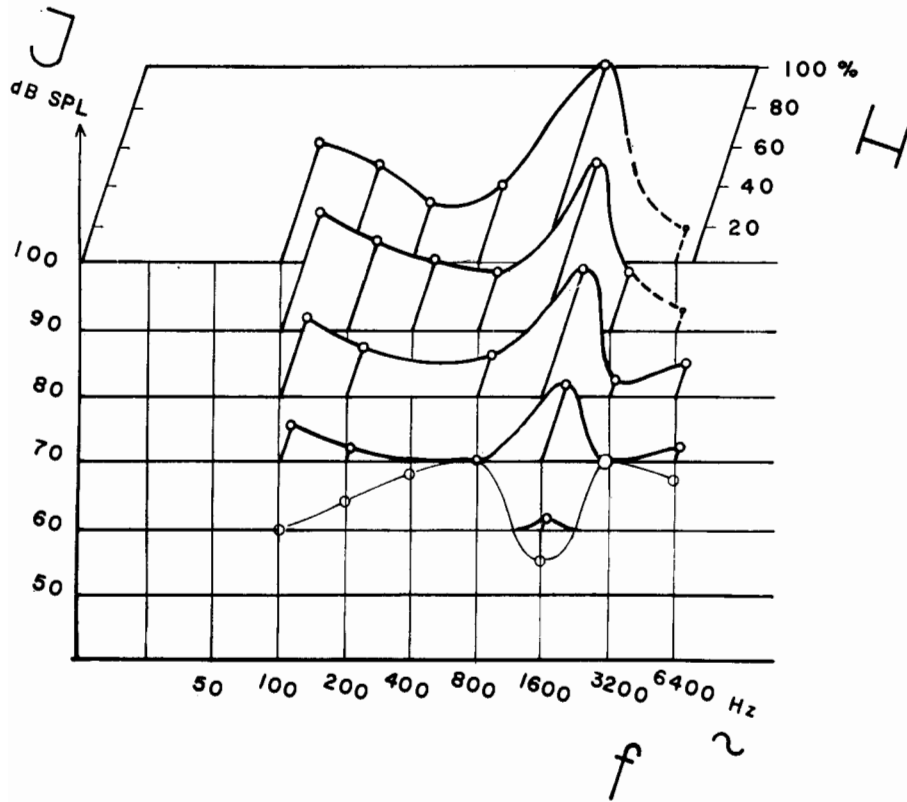


Figure 7b

ending fibers, these experiments seem to be an initial step in the explanation of experiments (v. Békésy), which the dependence of pitch on the firing rate of the nerve fibers, both in the somesthetic and auditory systems, is not always a simple correlation, nor in a simple agreement with the volley-theory.

But the whole set of problems involved converges here on the question of how the inner ear analyses different sound frequencies: the Proportional-differential-sensitivity of the receptors, the Duplicity theory of hearing, the reciprocal spatial and temporal inhibition, and the auditory „Physiological contrast“. Perhaps these should now be discussed together in more detail.

**Summarizing.** The frequency-analysis of the inner ear, according to the single place theory is given emphasis in terms of the exact description by

v. **Békésy** of the travelling-wave theory, and the calculations of **Ranke**. The frequency-dispersion along the basilar membrane, however, is too rough to explain the small human DL for frequency. Recent experiments were then cited to show that only the low-frequency range of the auditory physiological contrast is of a neural (inhibitory) nature, while that for the higher frequencies above a given optimal frequency is still unexplained. This aspect of the auditory contrast might very well be of a mechanical, i.e., physical nature. Possible avenues for discussion are also mentioned.

### DISCRIMINATION MECANIQUE DE LA FREQUENCE DANS LA COCHLEA

Aujourd'hui, pour discuter le problème de la discrimination des fréquences sonores par l'oreille interne, nous nous basons sur une certaine forme des théories du lieu singulier (single place theories), qui fut développé par les expériences de v. **Békésy**, d'accord avec les calculations de **Ranke**, et fut nommé théorie hydrodynamique ou théorie des ondes migratrices (travelling wave theory). Pourtant, il faut considérer, que la dispersion des fréquences le long de la membrane basilaire ne donne qu'une analyse, trop brute qui ne suffit pas pour expliquer la délicatesse énorme de la sensation humaine, c'est à dire le seuil si bas de discrimination de la hauteur des tons.

Dans le domaine des fréquences basses et moyennes, l'enveloppe des amplitudes oscillatoires de la membrane basilaire, en représentation logarithmique de sa distance de la fenêtre ovale, et, par comparaison, la courbe du seuil d'un neurone acoustique premier, en représentation correspondante des fréquences sonores, apparaissent étonnamment similaires (Fig. 5). Ici, tout d'accord, les courbes assez aplaties démontrent un degré de l'analyse des fréquences, sans doute insuffisant. Le contraste tonal de ces fréquences basses a lieu, par conséquent, au-dessus du niveau des neurones premiers, c'est à dire, il y a ici un type de contraste neurophysiologique, bien connu de presque tous les systèmes analyseurs, en premier lieu, de l'appareil optique ou somesthétique: autour d'un élément, excite à un degré plus haut, se fait une zone d'influence inhibitrice.

Mais, au contraire, dans le domaine des fréquences plus élevées, au-dessus de la région du seuil minimum, il y a la différence la plus possible entre l'enveloppe des amplitudes de la membrane basilaire, aussi bien aplatie ici, et, d'autre, la courbe, brusquement élevée, du neurone premier. Ceci nous autorise à la conclusion suivante: en cas des fréquences plus élevées, le contraste tonal, du aux phénomènes tout différents, a lieu au niveau des cellules sensorielles.

Il est impossible, à présent, de résoudre ce problème-là par une certaine réponse, en effet, il y a une poignée des mécanismes possibles, plus ou

moins importants. En premier lieu, **v. Békésy** a observé, en se servant de l'éclairage stroboscopique, de certains changements de la direction des mouvements oscillatoires de la membrane basilaire et de l'organe de Corti, se réalisant en zones assez étroites (Fig. 6).

Deuxièmement, l'innervation spéciale des cellules ciliées externes pourrait représenter, selon **Ranke**, un appareil exceptionnellement sensitive pour mesurer des différences minces du temps, quand les ondes migratrices passent le long de la série des cellules ciliées externes, connexes par une certaine fibre nerveuse. En effet, quand la vélocité de l'onde, en cas de sa correspondance à celle de l'excitation nerveuse, détermine le déclenchement et la propagation des potentiels d'action, ce système peut enregistrer des différences de l'amplitude simultanées par des différences du temps de l'excitation.

Aujourd'hui, par l'applications de certaines drogues comme kanamycine ou streptomycine sulfate, nous pouvons réaliser des lésions et des troubles fonctionnels des cellules ciliées internes ou des cellules externes isolément. Moins sensibles à l'intensité du stimulus, les cellules ciliées internes tiennent à son tour la discrimination de fréquences sonores la plus précise (**Keidel, Kaufmann, Spreng, Stange, Theissing**; fig. 4).

Finalement, nos expériences chez le cobaye, dont la cochlée d'un côté était détruite (**Pfalz**), démontrent d'influence des voies nerveuses centrifuges. Il y a des cellules spontanément actives, situées dans le tronc du nerf acoustique au côté désafférenté, et les variations de leur activité, causées par une stimulation de l'oreille contra-latérale, dépendent non seulement de l'intensité, mais encore de la fréquence du stimulus tonal. La stimulation par clicks donne une influence différente. Ceci indique de nouveau l'existence des deux types de récepteurs. D'autre part, cette influence, le plus souvent inhibitrice, par le système efférent de Rasmussen, représente encore une fois la possibilité d'un contraste acoustique neurophysiologique (fig. 7).

Prof. Dr W. D. Keidel,  
Physiologischer Institut der  
Universität,  
Erlangen,  
W.-Germany.

**Békésy, G. v.:** Zur Theorie des Hörens. Die Schwingungsform der Basilarmembran. Physikal. Z. **29**, 793-810 (1928)

**Békésy, G. v.:** Zur Theorie der Hörens. Über die Bestimmung des einem reinen Tonempfinden entsprechenden Erregungsgebietes der Basilarmembran vermittelt Ermüdungserscheinungen. Physikal. Z. **30**, 115-125 (1929)

**Békésy, G. v.:** Zur Theorie des Hörens. Über die eben merkbare Amplituden und Frequenzänderung eines Tones. Die Theorie der Schwebungen. Physikal. Z. **30**, 721-745 (1929)

- Békésy, G. v.:** Description of Some Mechanical Properties of the Organ of Corti. *J. Acoust. Soc. Americ.* **25**, 770-785 (1953)
- Békésy, G. v.:** Human Skin Perception of Travelling Waves Similar to those on the Cochlea. *J. Acoust. Soc. Americ.* **27**, 830-841 (1955)
- Békésy, G. v.:** Sensations on the Skin Similar to Directional Hearing, Beats, and Harmonics of the Ear. *J. acoustic. Soc. Americ.* **29**, 489-501 (1957)
- Békésy, G. v.:** Similarities between Hearing and Skin Sensations. *The Psychological Review* **66**, 1-22 (1959)
- Békésy, G. v.:** Synchronism of the Neural Discharges and Their Demultiplication in Pitch Perception on the Skin and in Hearing. *J. Acoustic. Soc. Americ.* **31**, 338-349 (1950)
- Békésy, G. v.:** Neural Funneling along the Skin and between the Inner and Outer Hair Cells of the Cochlea. *J. Acoust. Soc. Americ.* **31**, 1236-1249 (1959)
- Békésy, G. v.:** Neural Inhibitory Units of the Eye and Skin. Quantitative Descriptor of Contrast Phenomena. *J. Optic. Soc. Americ.* **50**, 1060-1070 (1960)
- Békésy, G. v.:** Experiments in Hearing. McGraw-Hill Series in Psychology. New York, Toronto, London 1960
- Békésy, G. v.:** Pitch Sensation and its Relation to the Periodicity of the Stimulus. *Hearing and Skin Vibrations. J. Acoust. Soc. Americ.* **33**, 341-348 (1961)
- Biber, K. W.:** Ein neues Verfahren zur Sprachkommunikation über die menschliche Haut. Doktordiss. Erlangen 1961
- Davis, H.:** Mechanism of Hearing. In: *Nerve Impulse* edited by D. Nachmansohn (Tr. of Fourth Conf., Josiah Macy, Jr. Foundation) Caldwell, N. J.: Progress Assocs., 1953
- Davis, H.:** Biophysics and Physiology of the Inner Ear. *Physiological Reviews* **37**, 1-49 (1957)
- Desmedt, J. E. and Mechelse, K.:** Sur un phénomène d'inhibition centrifuge dans la voie acoustic centrale chez le chat. *C. Rend. Soc. Biol.* **151**, 2209-2212 (1957)
- Desmedt, J. E. and Mechelse, K.:** Suppression of acoustic input by thalamic stimulation. *Proc. Soc. Exper. Biol. and Med.* **99**, 772-775 (1958)
- Desmedt, J. E. and Mechelse, K.:** Cortifugal projections from temporal lobe in cat and their possible role in acoustic discrimination. *J. Physiol. (London)* **147**, 17-18 (1959)
- Desmedt, J. E. and Monaco, P.:** Suppression par la strychnine de l'effet inhibiteur centrifuge exercé par le faisceau olivo-cochléaire. *Arch. int. de Pharmacodynamie et de Thérapie* **129**, 244-248 (1960)
- Galambos, R. and Davis, H.:** The response of single auditory-nerve fibers to acoustic stimulation. *J. Neurophysiol.* **6**, 39 (1943)
- Galambos, R. and Davis, H.:** Inhibition of activity in single auditory nerve fibers by acoustic stimulation. *J. Neurophysiol.* **7**, 287-303 (1944)
- Galambos, R.:** Neural Mechanisms of Audition. *Physiol. Rev.* **34**, 497-528 (1954)
- Galambos, R.:** Suppression of auditory nerve activity by stimulation of efferent fibers to the cochlea. *Fed. Proc.* **14**, 53 (1955)
- Galambos, R.:** Suppression of auditory nerve activity by stimulation of efferent fibers to the cochlea. *J. Neurophysiol.* **19**, 424-437 (1956)
- Hartzendorf, G., E. Wüstenfeld und K. Neubert:** Experimentelle Untersuchungen über die Ansprechbarkeit der Kerne innerer Haarzellen im Cortischen Organ von Meerschweinchen. *Z. mikrosk.-anatom. Forschung* **67**, 313-330 (1961)
- Katsuki, Y., T. Sumi, H. Uchiyama and T. Watanabe:** Electric responses of auditory neurons in cat to sound stimulation. *J. Neurophysiol.* **21**, 569-588 (1958)
- Katsuki, Y., T. Watanabe and N. Maruyama:** Activity of auditory neurons in upper levels of brain of cat. *J. Neurophysiol.* **22**, 343-359 (1959)

- Kaufmann, F., Keidel, U. O., Stange, G., Spreng, M., Theissing, J.:** Paper to be presented at the XXII. Intern. Congress of Physiological sciences Leyden 1962. In preparation
- Keidel, W. D.:** Note on a new system for vibratory communication. *Perceptual and Motor Skills* **8**, 250 (1958)
- Keidel, W. D.:** *Rankes* Adaptationstheorie. *Z. Biol.* **112**, 411-425 (1961)
- Keidel, W. D.:** Grundprinzipien der akustischen und taktilen Informationsverarbeitung. *Ergebnisse der Biol.* **24**, 213-246 (1961)
- Loewenstein, W. R.:** Facilitation in a tactile receptor due to sympathetic stimulation. *Fed. Proc.* **14**, 94-95 (1955)
- Loewenstein, W. R.:** Modulation of cutaneous mechanoreceptors by sympathetic stimulation. *J. Physiol. (London)* **132**, 40-60 (1956)
- Meyer zum Gottesberge, A.:** Zur Physiologie der Haarzellen. *Archiv Ohren-Heilkunde.* **155**, 308-314 (1948)
- Neubert, K.:** Zur funktionellen Anatomie des Mittel- und Innenohres. In **Zöllner, F.:** *Audiologie. Vorträge des I. Deutschen Audiologenkurses in Freiburg 1953*, S. 25-36. Thieme Stuttgart, 1954
- Pfalz, R.:** Einfluss schallgereizter efferenter Hörbahnteile auf den de-afferentierten Nucleus cochlearis (Meerschwein). *Pflügers Archiv.* **274**, 533-552 (1962)
- Pfalz, R.:** Erregung efferenter Einzelneurone innerhalb der Cochlea durch kontralaterale Beschallung mit Klickfolgen (Meerschwein). *Z. Biol.* In press.
- Ranke, O. F.:** Die Gleichrichter-Resonanztheorie. Habilitationsschrift. J. F. Lehmann, München 1931
- Ranke, O. F.:** Folgerungen aus der Theorie der Flüssigkeitsschwingungen in der Schnecke. Paper presented at the meeting of the German Physiol. Soc. Göttingen 1949 and *Ronas Berichte* **139**, 183-184 (1950)
- Ranke, O. F.:** Hydrodynamik der Schneckenflüssigkeit. *Z. Biol.* **103**, 409-434 (1950)
- Ranke, O. F.:** Theory of Operation of the Cochlea: A Contribution to the Hydrodynamics of the Cochlea. *J. acoustic. Soc. Americ.* **22**, 772-777 (1950)
- Ranke, O. F.:** Die Fortentwicklung der Hörtheorie und ihre klinische Bedeutung. *Archiv Ohr-usw. Heilk.* **167**, 1-15 (1955)
- Ranke, O. F.:** Reiz und Erregung beim Hören. Invited paper „Audiometrischer Kurs Würzburg“ 1957
- Rasmussen, G. L.:** An efferent cochlear bundle. *Anat. Rec.* **82**, 441 (1942)
- Tasaki, I.:** Nerve impulse in individual auditory nerve fibers of Guinea pig. *J. Neurophysiol.* **17**, 97-122 (1954)
- Tasaki, I., H. Davis and D. H. Eldredge:** Exploration of cochlear potentials in Guinea pig with a microelectrode. *J. Acoust. Soc. Amer.* **26**, 765-773 (1954)
- Theissing, J.:** Doctor-Thesis. Erlangen 1962. In preparation