

CONCLUDING REMARKS OF THE ROUND TABLE DISCUSSION ON THE FREQUENCY ANALYSIS OF THE NORMAL AND PATHOLOGICAL EAR

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First, I would like to express my deepest appreciation to Dr. Gorig, Prof. Schouten, Dr. Licklider, Prof. Keidel and Prof. Katsuki for their willingness to participate in this round table conference. Since everyone is an expert in his field, the problem of frequency analysis in the ear has been illuminated from all possible angles, and now you can form your own point of view. Frequency analysis in the ear is a very old problem, and there were and will be many instances of complete disagreement. These disagreements are of the highest interest since they are connected with the question of how the brain works. I sincerely hope that research in the field of hearing will become the pilot in the field of brain research. The methods in hearing are precise and we are all set for new findings, which will elucidate not only hearing but many other problems.

Looking at the subject of our symposium we should not forget that the ear can be stimulated by at least five different physical stimuli, and that a tone we hear has many different qualities (loudness, pitch, location, roughness, tonal, volume, density etc.). In evaluating the different hearing theories we should therefore take into consideration not only their statements about frequency analysis but also their usefulness in the entire field of auditory sensations.

Hearing theories were known during the last centuries for one thing: They all reasoned backward from sensation to stimulation, seeking to find out from psychological observations how the ear works. Some physicists and physiologists thoroughly dislike this procedure. But I think psychological techniques have improved lately to such a degree that their findings have become reliable (when there is not too much statistics involved), and this procedure now provides a legitimate approach. You have probably realized in this conference also that there is no disagreement on the observed facts but only on the question of their meaning. In earlier times the backward reasoning went as far as the mechanics of the inner ear. Today we are more interested in the electrophysiology. Just as before, we are trying out different physical principles, feedback, filters, etc., to see if they can be used for models. And we are making the same mistakes as before by identifying the working model with the ear, completely forgetting that there are a large number of working models which would do the same thing. The real question is which of these working models is actually comparable to the ear. There is no way from input-output relations for us to make this selection, since in this respect the models are all similar. As I understand, the building of robots improved very

much when any simulation of the human bones and muscles was given up in favor of pure task requirements. Their new structure has nothing to do with a model of the human body but nevertheless, by just looking at them, you would consider them as correct models.

Electrophysiology taught us that the number of nerve discharges sent to the higher levels of the nerve track increases with the frequency of the stimulus, but at the same time also with the increase of the vibration amplitude of the basilar membrane. In hearing we discriminate between loudness and pitch, and therefore we have to expect that a model composed of electric neurons will do the same. There is no question that the interaction between hearing research and communication techniques has been broad and useful to both sides, and that it should by all means be continued. But I do not know who profited more from it, hearing research or communication engineering. I think it was communication engineering since the introduction of resonance by Helmholtz certainly had a large influence in the development of communication. I think the same thing will happen again.

Concerning the specific question of frequency analysis, it is quite clear that Ohm's Law has its range of validity just as every law has. It is valid when the components of the Fourier analysis are far apart, but it is not valid when they are close together. When they are very close they do produce beats, yet nobody claim for this reason that Ohm's Law is not correct. Between the range of complete failure and the range of validity there is the range of uncertainty which is under discussion today. The question is whether that small range of uncertainty is of such an importance that the place theory of hearing should be eliminated. I personally am always surprised that this range of uncertainty is relatively so small (I hear the residue tone only in the frequency range between 50 and 400 cps and mainly with clicks).

I suppose it is difficult to conclude from psychological observations of click series the way the nervous system works for pure tones. There are two reasons: first, a pure sinusoidal tone produces along the basilar membrane quite a restricted area of stimulation, which can be seen stroboscopically and is shown in Fig. 1A. But for a click a travelling wave is produced which goes along the whole length of the basilar membrane until it fades out through the helicotrema.

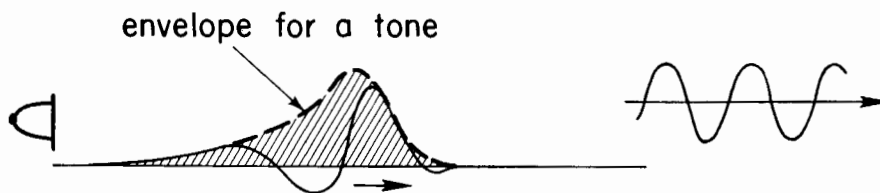


Fig. 1A

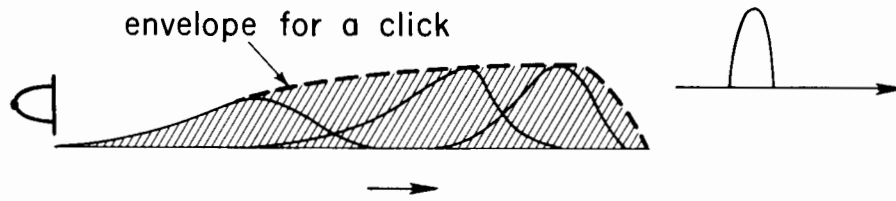


Fig. 1 B

From this we almost expect that a series of clicks will produce sound sensations at the lower frequency range, just as the residue tone does. A model of the cochlea with nerve supply (1) shows the development of this phenomenon step by step. Second, it must be realized that for clicks and for pure tones the electrophysiology in the auditory nerve track is different. It is very probable that in the ear there are, just as in other sense organs, nerve fibers which react to on-and-off effects and other nerve fibers which react to continuous stimulation. Clicks produce mainly on-and-off effects and, as Prof. Katsuki has shown, they are localized in different nervous pathways from those of pure tones. White noise or a frequency band of white noise does not represent a pure tone, but approximates a combination of irregular clicks. (I hope to elaborate this point in a separate paper.)

In general it is said to be difficult to draw conclusions from the periodicity theory, because the whole frequency analysis is performed in the brain, which is a little known area. But there is certainly one conclusion which can be drawn and that is one which speaks against the periodicity theory.

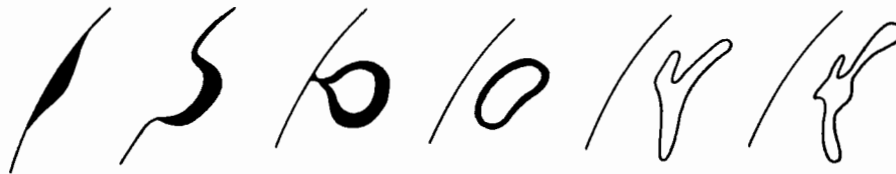


Fig. 2

Figure 2 shows how the inner ear (2) develops in the embryo from a thickening of the surface of the skin. Perhaps I am wrong, but I have a feeling that the nerve endings on the surface of the skin are taken into the cochlea during this displacement. Therefore, there should be in the organ of Corti a certain resemblance to the properties of the skin. When we touch the surface of the skin we have at least two definite sensations — the locus of the stimulus and the sensation magnitude, besides the other attributes. The periodicity theory implies that, in the inner ear, the organ of Corti

does not transmit the locus of sensation — which is one of the most primitive sensations in nature, in spite of the fact that the organ of Corti is stretched out to be ideal for just such a localization determination. I have difficulty in believing this, because in other end organs with large surface areas, like the retina, temperature sense, pain fibers, localization of the stimulus is a distinct feature (3).

In spite of my remarks I hope that the periodicity theory will be developed further, so that more conclusions can be drawn and tested. But I would like to suggest that the periodicity theory be developed first for the skin, since the roughness sensations of mechanical vibrations can be easily observed. The changes with amplitude and frequency of the vibrations will certainly show how periodicity sensations are obtained in nervous tissues, and we can fit these findings to electric neuron models. Only when neuron models can explain the sensations on the skin will they be useful for hearing research.

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DISCUSSION OF THE FIRST ROUND TABLE

Langenbeck:

Macht auf folgendes Phänomen aufmerksam.

Wenn ein reiner Ton lauter und lauter wird, so bekommt er mehr und mehr einen „sandigen“ rauhen Charakter unabhängig von eventuellen Harmonics. Wenn der Ton über einem weissen Geräusch erklingt, ist das nicht der Fall, der Ton klingt bis zu größten Lautstärken „glasklar“, im Vergleich mit dem selben Ton auf dem anderen Ohr, das nicht Geräusch belastet ist neben dem reinen Ton.

Im gleichzeitig gerauschbeschallten Ohr, klingt der Ton immer glasklar ohne Rauigkeit auch noch eine Zeitlang nachdem das Geräusch abgeschaltet wurde. Ich habe keine Erklärung für diese Erscheinungen, möchte es aber als Anregung mitteilen, wenn sich heute keine Erklärung geben läßt.

Bocca:

The problem of binaural fusion, to which a hint was made in Dr Licklider's report, receives some further contribution from clinical investigation, regarding the level at which fusion takes place.

It seems suggestive to think that, among other functions, the auditory cortex may have that of summing complementary parts of a complex sound, possibly through interhemispheric connections. However clinical evidence proves that this is not the fact.

Brain stem lesions provoke the most severe losses of discrimination in summation tests, whereas the same losses are not present, contrary to expectation, in pure lateral cortical lesions. This proves that binaural summation takes place at a lower level, probably in the midbrain and that each of the two opposite auditory areas of the cortex can integrate complementary binaural messages provided that they have been fused at the lower stations of the auditory pathway.

Bocca:

Dr Katsuki, most rightly stressed the point that the task of the auditory cortex is not the mere recognition of pitch and loudness of a sound. This is also gaining evidence in clinical investigation. But what is really the cortical integration? Is it a temporal integration of rapid changes of intensity, as Katsuki pretends, or is it a spatial integration of areas of activity and inhibition, or is it an integration of rhythmic patterns, which are the essence of all significative messages. We are of the opinion, on the base of human clinical investigation, that there may not exist a dynamic integration at one

level, a rhythmic integration at another level etc. Cortical integration seems to avail itself of all possible elements, such as pitch, duration, dynamic changes of intensity, rhythm, etc., which may contribute to shape up the form of a significative message. The lack of any of these elements may induce serious troubles of integration as proved by clinical investigation in cases of isolated pathology of auditory cortex.

Azzi:

I should like to ask Prof. Schouten if the phenomenon described is related in any way to that known as the "missing fundamental". Thank you.

No answer received.

Iurato:

Employing the methods both of the experimental neurology and electron microscopy I succeeded in showing that Rasmussen's efferent fiber system ends in synaptic contact with the sensory cells of Corti's organ and with the afferent nerve endings.

In fact, 16 hours after the transection of the efferent fiber system the "much granulated" nerve endings show degenerative changes, and disappear completely 8 days after. These experimental results confirm Engström's hypothesis that afferent and efferent nerve endings have a different structure.

By comparing the aspects of the receptoneural junctions of the outer and inner hair cells, it is evident that there are some differences. The outer hair cells type A show the richer efferent innervation, whereas the outer hair cells type B and the inner hair cells have less efferent nerve endings. Moreover in the outer hair cells the efferent nerve endings apparently are in synaptic contact with the sensory cell, whereas in the inner hair cells are in synaptic contact with the afferent nerve endings and sometimes also touch the hair cell. These data could be of interest in discussing both the "duplicity-concept" of the hair cells and the problem of the descending inhibition and its contribution to the "overall-contrast-phenomenon".

Keidel:

Besides a possible rôle of the descending fiber system in some sharpening-function, for which however the number of fibers is very small (around 500 according to Dr Davis, personal communication) and latency may be too high. The efferent fiber system seems to be involved also in some process of optimisation (for funneling of total information capacity of the receptors of all sensory shannels from 10^9 bits/sec down to 10^2 in conscious perception and 10^0 in storage), and in the election and extraction processes involved in "listening".

Fex:

Dr Katsuki suggests that the inhibition by sound in auditory neurons in the dorsal cochlear nucleus results from the interaction of afferent fibres. Would the experimental data also agree with the hypothesis that this inhibition is caused

by efferents to the dorsal cochlear nucleus, such efferents being described by Lorente de Nó and by Rasmussen?

Katsuki:

Dr Fex. I must thank you for your kindness sending me a reprint of your paper. I carefully read it and was very much impressed by your results. We attempted many times to show the efferent effect on the cochlear nerve and didn't succeed in it irrespective of repeated experiments. But you showed them so beautifully. How was the latency of the efferent effect? I understand that the efferent effect described by yourself has a long latency. In our experiments, we noticed sometimes very similar phenomena to those you reported and their latencies were quite long, longer than twenty or thirty milliseconds. The inhibition which caused the narrow response areas at the dorsal cochlear nucleus has a very short latency, so I don't think the narrowing of the response area is due to the effect of efferent fibers described by Lorente de Nó and by Rasmussen. The efferent inhibition at the cochlear nerve which you discovered may rather be the servo-mechanism in the auditory system. Thank you.

Dixon Ward:

Let me bring up a matter mentioned by Dr Schouten but not further discussed. We certainly all agree that, ideally, one should explain all the bothersome contradictions known to exist in psychoacoustics. However, I would like to caution against the notion that in setting up a theory of hearing, especially in regard to perception of pitch, one must account for octavity — the cyclicity of musical pitch as described by Revesz in his "pitch cylinder". These are those of us who hold that there is nothing particularly unique about the octave, that the "sameness" of two tones an octave apart is merely a cultural (learned) overlay: an accident, if you will, of nature. It is, of course, difficult if not impossible to settle such a nature-nurture argument. However, the fact that the subjective octave is not quite the same as a physical octave, plus the ease with which one can account for the observed phenomena, make the hypothesis quite tenable that the pitch cylinder is a psychological fact, at least for musicians, but a physiological fiction in a peripheral sense, and therefore need not concern us in the pursuit of a theory of hearing.

No answer received.

Lehnhardt:

Man kann den technischen Aufbau eines korrelators auf das Binaural-system und die zentralen Bahnen übertragen. Wenn dann dem einen Ohr weisses Rauschen mit einem darin „versunkenen“ Ton dargeboten wird, und dem anderen ein frequenzähnlicher Vergleichston, dann kann das Zentralnervensystem den Ton aus dem Rauschen herauskorrelieren und ihn mit dem Ton der Gegenseite zu binauralen Schwebungen überlagern. Wird statt dieser laufenden Pfasen eine konstante Zeitdifferenz benutzt, dann kommt ein Richtungseindruck auch dann noch zustande, wenn beispielsweise die Clickfolge auf dem einen Ohr vom Rauschen verdeckt ist. Schliesslich

scheint mit der Korrelation auch die Beobachtung zu erklären, daß der Informationsgehalt einer weitgehend unverständlichen Tiefbandsprache auf dem einen Ohr durch eine im Rauschen versunkene Breitbandsprache auf dem Gegenohr deutlich gesteigert wird. (vergl. Arch. Ohren-u.s.w. Heilk. 7878, 493 (1961).

Licklider:

Let me express my appreciation to Dr Bocca for his excellent statement bearing on the clinical contribution to solution of the binaural problem. Interpretation of the effects of lesions in terms of mechanism or process is, of course, very difficult, but it is important to have this evidence, and to take it fully into account in determining the focus of the fusion process.

Dr Schouten and **Dr Licklider** put some questions to Prof. Von Békésy. Prof. Von Békésy has asked us to publish the following statement.

Békésy:

After having studied carefully the transcripts of my answers given to Dr Schouten and Dr Licklider at the Sixth International Congress of Audiology, I have come to the conclusion that most of the problems in hearing are much too complicated to be answered in one page. Such a short answer generally leads to misunderstandings and does not contribute anything to further scientific solutions.

I have therefore compiled my opinions in regard to the matters discussed at the round-table discussion in two papers, one with the title "Hearing theories and complex sounds" (with 28 figures) and the other "Three experiments concerned with pitch perception" (with 10 figures). These two papers are scheduled for publication in THE JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA, in the April 1963 issue. Explicitly or implicitly, they answer some of the questions raised during the round-table discussion.