

A Model Describing Nonlinearities in Hearing by Active Processes with Saturation at 40 dB

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Abstract. Data from literature related to nonlinearities of the peripheral part of the hearing system are collected and extended by results from measurements of acoustical responses, masking, cubic difference tones and Zwicker tones. The data indicate 40 dB as a significant value for the dynamic range in neurophysiology as well as for the sensation level in psychoacoustics dividing the total level range into two areas of different characteristics. A preliminary model assuming that the outer hair cells act as an amplifier which contains saturation (corresponding to 40 dB) and feed back to sensitize the inner hair cells is used to describe the measured effects at least qualitatively.

1. Introduction

Many nonlinear processes in hearing have become known within the last two decades. The measured facts comprise not only effects of transmission through nonlinear transfer functions but also other nonproportionalities like level-dependent effects, saturation effects or the disappearance of effects with increasing level. These nonlinear effects can be classified according to different fields of hearing research, namely physiology, cochlear mechanics, neurophysiology and psychoacoustics. Many of the nonlinear dependencies between stimulus and sensation measured in psychoacoustics (e.g., pitch, loudness, roughness) may be strongly influenced by central processing and hence nonlinear behaviour may be expected. In contrast, however, simultaneous masking seems to be created predominantly by peripheral processes and the corresponding nonlinear behaviour should be based on nonlinearities in the periphery.

This paper deals with that ensemble of nonlinearities which may be related to the very peripheral

signal processing in hearing. Although the effects may be collected with some emphasis on psychoacoustics, a common view of all the facts may be helpful in obtaining an explanation for the nonlinear behaviour of the peripheral part of the hearing system.

2. Nonlinearities in Cochlear Mechanics

2.1. Basilar Membrane Vibration

From his early studies, v. Békésy [1] concluded that the traveling wave along the basilar membrane does not show any nonlinearity. During the last 10 years many experiments have been conducted in this field using a variety of new techniques to measure the displacement of the basilar membrane (e.g. Rhode [23]; Kohllöffel [17]; Wilson and Johnstone [34]). The recent results are consistent with respect to the frequency response even for different animals and show sharper frequency selectivity than reported by v. Békésy. As concerns the linearity, however, the results are not homogeneous: The basilar membrane motion seems to behave linearly in the guinea pig (Wilson and Johnstone [34]). In the squirrel monkey, however, the vibrations show saturating nonlinearities for SPL's above about 70 dB at least in the frequency range near 7 kHz, as reported by Rhode [23, 24]. Due to limitations of the technique, these measurements can be established only at medium and high levels of stimulation. The data regarding threshold of hearing have to be extrapolated and linear behaviour for lower levels is assumed. With the use of a capacitive probe, measurements down to the threshold of neural activity are possible. The results (Evans and Wilson [11]) indicate almost complete linearity to well below neural threshold. However, nonlinear behaviour at low levels is measured psychoacoustically very clearly by cubic difference tone compensation (for recent summary see Zwicker [40]). Hence, it may be possible that the

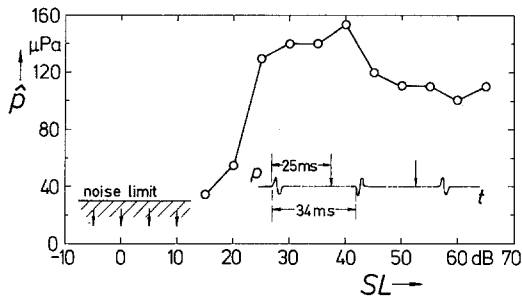


Fig. 1. Peak sound pressure amplitude \hat{p} of the acoustical responses (picked up 25 ms after the stimulus) of a very effective subject "S" as reaction to short sound pressure impulses as indicated in the inset. The sensation level SL (level above threshold for the stimulus) is abscissa. The response is phaselocked in the whole range of possible measurement as could be confirmed by reversing the stimulus (one period of a 2-kHz tone)

motion of the basilar membrane is relatively linear, while systems coupled to the basilar membrane, like the organ of Corti with the rows of hair cells and tectorial membrane, may behave nonlinearly. This way, the search for nonlinearity in the inner ear can fail when measuring only the displacement of the basilar membrane.

2.2. Acoustical Responses

Measurements of the acoustical echo from the inner ear using the method described by Kemp [14] seem to be another interesting tool to search nonlinearities, especially at low levels. In a recent study using a similar technique, Schloth [28] described – besides the results from other subjects – the following remarkable behaviour in one subject: When stimulated by a short impulse, he responded with an almost stationary tonal sound pressure decaying only about 1 dB within 30 ms. This response was extremely nonlinear, i.e., for increasing stimulus level the response level increased very little above a kind of threshold, if at all. As in Kemp's study, this nonlinearity was found at relatively low levels.

A small study on this particular subject was carried out in order to obtain the stimulus-response function in detail. The method used is the same as described by Schloth [28], the result is shown in Fig. 1. The peak sound pressure amplitude \hat{p} of the response, picked up 25 ms after the short stimulation impulses (one period of a 2-kHz tone, alternately presented each 34 ms) is plotted as a function of the sensation level SL for that stimulus. The response \hat{p} confirms an even stronger nonlinearity than expected: it rises very quickly from the limit of measurement for sensation levels of about 15 dB, reaches a maximum at $\hat{p} \approx 140 \mu\text{Pa}$ for SL near 35 dB and seems to decay somewhat for larger sen-

sation levels. This means that low levels of stimulus do not produce measurable acoustical responses, although the stimuli are audible, while the responses decrease although the stimuli increase for $\text{SL} > 40 \text{ dB}$. Two findings should be noted: (a) the phase of the response (although ringing quite a long time) is very stable and reverses for reversal of the stimulus (each 34 ms). Hence, only a small amount of noise remains if the time functions of the reversed responses are subtracted; (b) the subject is the only one so far responding so strongly.

Summarizing the facts reported in this section it can be stated: Results of direct measurements of the motion of the basilar membrane indicate no clear nonlinear effect. Acoustical responses to impulsive stimulation of the inner ear at medium and low levels, however, reveal strong nonlinearities.

3. Nonlinearities in Neurophysiological Recordings

3.1. Single Auditory Fibres

The activity of single fibres in the cochlear nerve has been studied by neurophysiologists in a variety of animals (for a summary see for example Evans [7]). One of the most distinct nonlinear effects is the saturation observed when discharge rates of single fibres are measured as a function of stimulus level. The saturation appears not only for stimulation at the characteristic frequency of the fibre but for lower and higher frequencies as well. The so-called dynamic range (i.e., the difference in stimulation level for activity just above spontaneous discharge and the level at saturation) depends somewhat on the frequency of stimulation. Nevertheless it remains within 25 to 55 dB for most of the frequencies and species. For squirrel monkey, the Wisconsin group has published many data on this effect (e.g. Rose et al. [26]). Other studies were carried out mainly on the cat (Kiang et al. [15]; see also Evans [7]). Interestingly, all authors report this relatively small dynamic range of about 40 dB. This discrepancy between these 40 dB and the total level range of hearing of more than 100 dB still puzzles hearing researchers.

3.2. Haircell

Recently, Russel and Sellick [28] measured the receptor potential of inner hair cells as a function of frequency and stimulus level. Receptor potential versus stimulus level shows saturation characteristics for both AC and DC very similar to those measured in single auditory fibres. The dynamic range varies somewhat, i.e., insensitive cells need 20 to 30 dB, sensitive cells 30 to 50 dB level increment to reach saturation.

The frequency selectivity, measured for receptor potentials, also seems to behave in a level dependent way, i.e. nonlinearly. This effect, however, may just be a reflection of the saturation effect mentioned above. Using the iso-amplitude curves published by Russel and Sellick [28], the effect becomes very clear, when the curves measured for different values of receptor potential are shifted in such a way that they coincide for low frequencies. Two such iso-amplitude curves (stimulus level needed to produce a certain value of receptor potential versus frequency of stimulation) are shown in Fig. 2. The curve for 10 mV is shifted downward by 17 dB to coincide at low frequencies with the 2-mV curve. Around the characteristic frequency of about 15 kHz, the 2-mV curve shows an increment in sensitivity of about 30 dB, a value which may rise to about 40 dB for a parameter of even less than 2 mV.

3.3. Cochlear Nucleus

The saturation of the discharge rate has also been measured in neurons of the anteroventral cochlear nucleus. Generally, the effects are very similar to those reported for single auditory nerve fibres. Recently, Brugge et al. [2] recorded responses from young kittens, which develop hearing during the first two weeks post partum. The results indicate that sensitive but nonlinear responses occur as soon as the peripheral hearing system has completed its development.

All neurophysiological data mentioned indicate saturation effects in discharge rates resulting in a dynamic range of about 40 dB on the average, mostly independent of frequency and animal. The peripheral system of hearing, however, has to be fully developed.

4. Nonlinearities in Psychoacoustical Studies

4.1. Simultaneous Masking

Simultaneous masking in the steady state condition has been explored in many details since the classic study by Wegel and Lane [33]. While masking of a test tone by broad band noise does not show any "relative dependence" on masker level (Hawkins and Stevens [13]; Zwicker and Feldtkeller [42]) masking of tone by tone does. As concerns tonal masking, artifacts, such as the audibility of difference tones, of roughness and of beats, somewhat disturb the results produced under normal conditions. With a suitable stimulus configuration (Schöne [29]) it is possible to overcome most of these difficulties. The results thus produced indicate systematic nonlinearities. For test-tone frequencies above the masker frequency, a steeper rise of test-tone level versus masker level shows up below 40 dB sensation level of the test tone but a normal rise

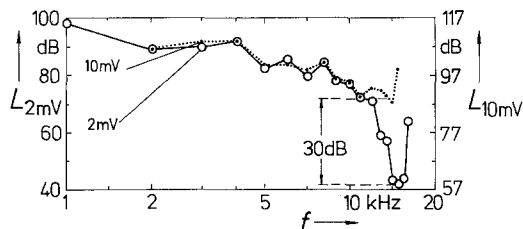


Fig. 2. Iso-amplitude curves of DC component of a hair cell, i.e., stimulus level L needed to produce a certain voltage (2 mV: circles; 10 mV: dots) as a function of frequency f of the stimulus. The data are adopted from Russel and Sellick [27]. Note that the 10 mV curve is shifted 17 dB downward (right ordinate), in order to match the 2 mV curve at low frequencies. This way the frequency responses can be compared directly

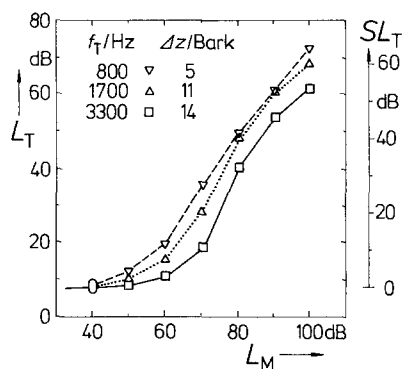


Fig. 3. Masked threshold level L_T of the test tone as a function of the masker level L_M of a 225-Hz tone. The sensation level SL_T of the test tone (given on the right side) indicates a steep rise of the curves for values SL_T below 40 dB. Frequencies f_T of test tones and corresponding differences Δz in critical band rates are indicated. Average of two measurements (tracking method) of the trained subject "B"

corresponding to proportionality above 40 dB SL. Schöne measured this effect for a large variety of masker frequencies and for different subjects. Although there are individual differences which may partly result in distinct deviations of the individual masking pattern, the basic characteristics remain the same. Schöne studied masking for test tone frequencies up to four critical bands above the masker frequency. In order to confirm these findings for even larger distances between the frequency of masker and test tone, results have been obtained using the same technique for a 225-Hz masker and test-tone frequencies up to 3300 Hz. This corresponds to a difference in critical band rate between masker tone and test tone of 14 Bark. The data displayed in Fig. 3 show that the test-tone level versus masker level curves follow the characteristic mentioned above.

This effect seems not to require steady-state conditions since masking-period patterns (Zwicker [38]) i.e., masking of synchronized tone bursts by low

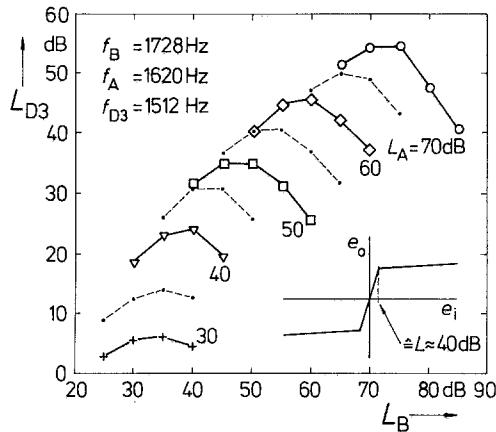


Fig. 4. Level L_{D3} of the test tone necessary to compensate the audible cubic difference tone as a function of the level L_B of the higher primary with level L_A of the lower primary as parameter. Frequencies are indicated. Average of two settings of the subject "B" experienced in compensation measurements. The inset in the lower right shows an input-output characteristic (with a break point corresponding to a level of 40 dB) which produces similar data

frequency maskers, show the same effect. Corresponding data (Zwicker [39]) indicate that the nonlinearity revealed in masking may react instantaneously.

4.2. Cubic Difference Tones

Nonlinear distortions in hearing are mostly characterized by the audibility of quadratic and cubic difference tones. Quadratic or other distortions of even-order seem to be created – at least for man – in a broadly tuned source different from the source for cubic or other odd-order distortions. The latter may be produced in the inner ear because they reflect a strong frequency resolution (Zwicker [37, 40]). In order to obtain at least an idea about the nonlinear characteristic producing the cubic difference tone, measurements with the method of compensation have been undertaken. Since the cubic distortion product is assumed to be the vector sum of many wavelets (Zwicker [41]) the phase difference of which may increase with increasing frequency difference Δf of the primaries, this difference was chosen to be as small as possible. For $\Delta f = 108$ Hz at 1620 Hz, the frequency separation of the primaries and of the difference tone still allows the use of the method of compensation, although the sound produces an audible roughness. The level L_{D3} of the cubic difference tone needed to cancel the audible cubic difference tone is plotted in Fig. 4 as a function of the level L_B of the higher primary at 1728 Hz. The level L_A of the lower primary at 1620 Hz is parameter. The data show consistent features for large values of L_A down to about 45 dB. For lower values of L_A , the level L_{D3}

diminishes more rapidly and the peak of the curves remains above $L_B = 30$ dB, indicating a crucial value of the level of the primaries near 40 dB. Modeling odd-order nonlinearities in electrical networks and imitating the method of compensation, a nonlinear characteristic was found which exhibits the corresponding behaviour. This characteristic is given as an inset in Fig. 4. It shows a symmetrically saturating input-output function with break points which correspond to a SPL of about 40 dB (threshold is assumed at about 0 dB as is the case for the subject producing the data of Fig. 4). The break points are somewhat lower than in the very first model (Zwicker [35]) because the frequency distance of the primaries used was smaller for the data of Fig. 4. The characteristic of the nonlinearity, however, remains the same. Nonsimultaneous (Smoorenburg [20]) as well as simultaneous (Zwicker [41]) measurements on the time- and duration-dependence of the cubic difference tone have indicated that the nonlinear characteristic involved works instantaneously, similar to the behaviour of masking.

4.3. Negative Afterimage

Auditory afterimages (Zwicker [36]; Neelen [21]; Lummis and Guttman [18]) depend on the level of the sound producing the effect. In order to make the description short but the effect distinguishable from other effects of similar nature, Lummis and Guttman proposed to refer to the negative afterimage as the "Zwicker tone". Using this expression, it can be summarized that the Zwicker tone becomes audible for several seconds after a sound with strong spectral edges is switched off. The Zwicker tone is elicited by low-pass, high-pass or band-suppressed sounds, which have to be presented to the listener in bursts with pauses or as continuous sounds for about half a minute. Most interesting in our context is the effect that the Zwicker tone remains inaudible for small as well as large levels of the producing sound. In all three papers mentioned, numbers of 20 to 40 dB for L_{CB} , i.e., the level within the critical band of the producing sound, are mentioned as the optimal condition for producing the Zwicker tone. However, no values of the level L_{eq} of an unmasked pure tone producing the same loudness and the same pitch as the Zwicker tone are given. To fill this gap, data were collected for nonsimultaneous comparisons between a Zwicker tone produced in one ear and a pure tone of controllable level and frequency in the other ear. The stimulations to the two ears have been reversed and the data averaged. The sensation level SL_{eq} of the equally loud pure tone measured this way is plotted in Fig. 5 as a function of the critical-band level L_{CB} of the band

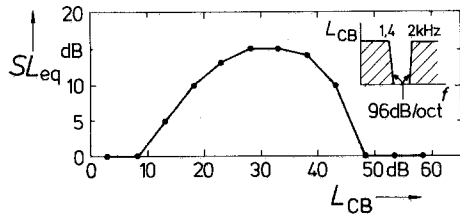


Fig. 5. Sensation level SL_{eq} of a tone equally loud as the Zwicker tone produced by a bandsuppressed noise presented for 30 s as a function of the critical-band level L_{CB} of the noise outside the band suppression. The frequency characteristic of the noise is indicated in the inset. Balanced average of two comparisons (method of adjustment) of the trained subject "B"

suppressed noise (see inset of Fig. 5) producing the Zwicker tone. For the conditions mentioned above (30 s on-time of the noise), the sensation level SL_{eq} starts to rise for critical band levels L_{CB} of about 10 dB. SL_{eq} reaches maximal – although small – values of about 15 dB for critical-band levels between 25 and 40 dB. For levels L_{CB} larger than about 50 dB, however, the Zwicker tone is not produced, at least not audible anymore. This behaviour constitutes a strong nonlinear effect, which – interestingly enough – takes place only in the low-level range.

Summarizing the nonlinear effects measured using psycho-acoustical methods, it seems that the dominant effects are produced for relatively small levels around a value of about 40 dB.

5. Preliminary Model

Although the data known so far are not sufficient to postulate a precise quantitative model, it may be fruitful to stimulate the discussion on peripheral signal processing by conceptions which may at least lead to a kind of preliminary and somewhat speculative but directional model.

The much sharper frequency selectivity of neural tuning curves in relation to the vibration of the basilar membrane as well as the crossed olivo-cochlear bundle

effect has stimulated several authors to produce models assuming interactions at different stages (Geisler [12]; Zwislocki and Sokolich [43]; Evans [8]; Manley [19]; Dallos and Harris [4]; for a summary see Manley [20]). Manley [19, 20] as well as Dallos and Harris [4] propose an interaction between the outer and the inner hair cells such that the frequency response is sharpened. However, they use different approaches in order to create this effect.

The model explained in this paper uses also an interaction between the outer and the inner hair cells. From this point of view it is based on the models of Manley or Dallos and Harris. It is interesting to note that the model ends up with this interaction although it was originally intended to explain psychoacoustical data on cubic difference tones. It uses, however, exclusively AC-values and assumes in addition a strong nonlinearity as well as a feedback.

When expressed in excitation or similar locally-relevant values, the ear shows a high sensitivity for levels below 40 dB but some kind of saturation for higher levels. Additional to the assumption that this high sensitivity is produced by an active process, the model contains the following assumptions: A boost produced through the outer hair cells' activity by mechanical, electromechanical, electrical or biochemical processes enhances the sensitivity of the inner hair cells but contains a saturation at levels corresponding to 40 dB. The saturation may act somewhat smoothly instead of very abruptly but it reduces the sensitivity for higher levels to normal values, i.e., values without enhancement. This active process acts instantaneously i.e., without inertia. The sensitization process is limited laterally by electrical fields, mechanical wavelengths or chemical transfer to an area which corresponds to a relative frequency bandwidth of ± 5 to $\pm 10\%$.

Figure 6 may illustrate the preliminary model using a blockdiagram which, however, contains only few elements instead of an almost continuous differential segmentation. The displacement or the velocity of the basilar membrane or sheering forces relative to the

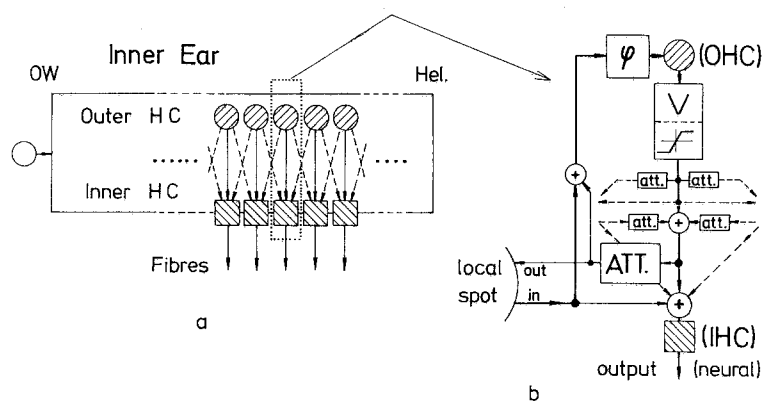


Fig. 6a and b. Explanation of the model. The principal structure is shown in **a** along the basilar membrane. **b** shows in more detail the functional interactions between outer (OHC) and inner hair cells (IHC): The local input influences predominantly through a phase shift φ the OHC, which through amplification and saturation (with breakpoints corresponding to 40 dB) influences the IHC. Feedback is possible through the attenuator (ATT) not only locally but also laterally via the attenuators (att) and the dashed lines. Only IHCs have a neural output

motion of the tectorial membrane stimulate outer and inner hair cells, respectively (Fig. 6). The outer hair cells are more sensitive, but are assumed to produce no information which is carried through action potentials and fibres towards the brain. However, outer hair cells strongly influence the activity of the inner hair cells as indicated in the detail schema of Fig. 6b: The adequate stimulus may be different for inner and outer hair cell as indicated by the phase shift. The outer hair cell's activity (amplifier with nonlinear saturation curve, the breakpoint of which may actually be somewhat rounded) produces mechanical vibrations and strongly influences in a quasi-analog way the inner hair cells. The activity of the latter is transferred in values of discharge rates (mean values and temporal cues) carrying information towards higher levels. The outer hair cells' influence on the inner hair cells has a lateral spread so that the neighboring inner hair cells are influenced as well (indicated by the small attenuators (att) and the connections with dashed lines). In other words: a single inner hair cell is influenced by many outer hair cells as well as from its own adequate stimulus as indicated at the summing point. The inner hair cells' own sensitivity is assumed to be 10 to 100 times less than their maximum sensitivity when activated by the outer hair cells. Finally, the activity of the outer hair cell (amplifier and saturation) has some feedback influence on the stimulation through the attenuator (ATT). Hence, the adequate stimulus may be even enhanced under effective phase conditions, producing thereby a special frequency selectivity (second filter or two tone inhibition) which is much more pronounced than that of the inner hair cell and/or basilar membrane alone. The feedback loop may even contain an additional self-regulating system with a time-constant of several seconds (not indicated in the figure) which protects the system from ringing under normal circumstances.

The described model is only a preliminary arrangement which without question needs clarification, proof and verification. It may be used, however, as an explanatory cue to some effects described in literature.

6. Discussion

In recent anatomical studies (e.g. Spoendlin [32]) the neural pathways have been clearly described: There is evidence that the afferent neurons of the outer hair cells are not effectively connected to the central nervous system. This means that the outer hair cells may act only at a very peripheral stage (as already mentioned by Manley [19]) as they do in the model. This implies that hearing is not possible without inner hair cells, as suggested by Deol and Gluecksohn-Waelsch [15].

Nonlinearities in the motion of the basilar membrane produced by the nonlinear activity of the outer

hair cells may hardly be measurable, since the coupling (for example by mechano-electrical and electro-mechanical transformation) represented by the attenuation is small and cannot be effective for higher levels because of saturation.

For low levels, however, the model contains a feedback which may act in a two fold way: (a) The frequency selectivity is predicted to be strong (like a second filter) for intact outer hair cells, because for certain gain and phase conditions the feedback system enhances. This takes place near the characteristic frequency. Outside of that, feedback may even act in the opposite way causing inhibition. Whether two-tone inhibition can be described by such assumptions has to be clarified by quantitative calculations. For a loss of outer hair cells, however, the frequency selectivity has to be weak (like the basilar membrane selectivity). This effect is actually described not only for outer hair cell damage (Evans and Harrison [9]; Dallos and Harris [4]) but seems also to be reversibly valid for the influence of hypoxia as described by Evans [6], Evans and Klinke [10], and Robertson and Manley [25]. Especially Evans' data show very clearly the reversible change from a normal selective tuning curve with a very sensitive tip, to a low-pass-like frequency response during the effective stage of drugs and again back to normal after recovery. (b) The acoustical echo as measured by Kemp [14] or by Schloth [28] may also be influenced or even produced by a feedback. Since such systems are relatively unstable, i.e. dependent on changes of the boundary conditions such as amplification and phase, the effects measured from outside may vary not only from subject to subject but also for the same subject as a function of time, as indicated in the results of Kemp and Schloth. Under abnormal conditions, feedback systems can produce strong ringing, a case which seems to be described in Schloth's paper. Such ringing would rise to large values without the saturation. The model, however, predicts a limitation to low levels as is found in the data reported. Whether the effect of tinnitus can be described in this way as well may be checked by the audiologists. At least the effect that tinnitus can be cancelled by masking (even of different frequency) can be described by the saturation process, which reduces the feedback for larger input values.

The Zwicker tone may be described by assuming that sounds which produce strong excitation edges along the basilar membrane change the self-regulated feedback system in such a way that it is ringing for several seconds if the sound is suddenly switched off. Such a reaction can take place at higher processing levels as well as at the peripheral part of the hearing system. Peripheral ringing may be provable by acoustical responses, however.

The level, frequency and frequency-distance dependence of difference tones as measured by neu-

rophysiological methods (for recent data see Pfeiffer et al. [22]; Smoorenburg et al. [31]; Buunen and Rhode [3]; Kim et al. [16]) and as measured by psychoacoustical methods (for recent data see Smoorenburg [30]; Zwicker [40, 41]) contains lots of data. To discuss them all would overload this paper, especially since a fruitful discussion needs not only qualitative but also quantitative results. Generally speaking, the model seems to account qualitatively for most of the psychoacoustically measured difference tone effects. For some of the neurophysiologically measured data such as those for quadratic difference tones, however, the model cannot give an explanation. Whether this discrepancy stems from the difference in species (human in relation to cat) or is of essential character is not clear yet. More data have to be collected and the model has to be made more specific so that calculations of produced nonlinear distortions are possible, although they may be relatively complicated.

The value of 40 dB for dynamic ranges in hair cells and fibres or for sensation levels in several psychoacoustical effects seems to be a significant value, which may play an important role in the nonlinearities which characterize the peripheral part of the hearing system. The model – which is thought more as a heuristical model and less as a mathematical model – can describe at least some of the many nonlinear effects measured. It predicts on the other hand a) the same amount of decreasing time delay of action potentials both under conditions of high level stimulation (> 50 dB) as well as under conditions of outer hair cell loss. Without feedback, the filter becomes less sharp and reacts more quickly. b) a lack of nonlinear distortions (cubic difference tone) at medium levels for animals with damaged outer hair cells, c) a weak traveling wave of the Zwicker tone along the basilar membrane for the duration of its audibility. These effects may be measured in order to verify, to improve or to correct the model.

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