Frequency and Intensity Difference Limens and Nonlinearities in the Ear of the Housemouse (*Mus musculus*)*

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Summary. 1. Frequency and intensity difference limens were determined for the house-mouse (*Mus musculus*, outbred strain NMRI) between 1 kHz and 80 kHz and for sound pressure levels (SPLs) between 15 dB and 100 dB re. 0.0002 dyn/cm².

2. The frequency difference limens (Δf_s) decrease linearly with increasing SPL. The slopes (a) of the regression lines are frequency dependent ($|a| = p \cdot f^q$; p and q are constants) with $|a|$ being maximal at 15 kHz. An intensity independent level of the smallest noticeable frequency difference Δf_m is reached at a definite SPL ($L_{\Delta fm}$) which is always 60 dB above the absolute hearing threshold (L_{HS}) at each frequency tested ($L_{\Delta fm} - L_{HS} =$ const.). The relative frequency difference limen $\Delta f_m/f$ was nearly constant and equal to 0.85%.

3. The intensity difference limens (ΔL_s) decrease with increasing SPL. The interdependence can be approximated by a linear or a power function ($\Delta L_s = -0.05 \cdot SL + 7$; $\Delta L_s = 0.04 \cdot SL + 120 \cdot SL^{-1}$; $SL =$ sensation level). The difference limens (ΔL_s) are frequency dependent ($\Delta L_s = d \cdot f^e \cdot SL$) at low sensation levels. The equation $\Delta I = g \cdot I^{0.95}$ ($I =$ sound intensity) shows a near miss of Weber's law. The relative averaged difference limen ($\Delta L_s/SL$) amounts to 6.7% at 60 dB SL.

4. The results agree well with a model of a spectrum-excitation-transformation on the basilar membrane (Maiwald, 1967). In addition, a new frequency dependent nonlinearity of the mammalian ear is defined. It influences frequency and intensity discrimination in the same manner and can be expressed in a power function of the frequency summarized in the proportion: $\Delta f \sim \Delta L_s \sim f^z \cdot L$.

5. Comparative aspects of difference limens in man and other mammals are discussed.

Introduction

A basic characteristic of the ear is the differential sensitivity. There are many psycho-acoustic studies in man on the just noticeable frequency difference Δf_s (Knudsen, 1923; Shower and Biddulph, 1931; Boring, 1940; Harris, 1952) and about the just noticeable intensity difference ΔI or sound pressure difference ΔL_s (Knudsen, 1923; Riesz, 1928; Dimmick and Olson, 1941; Harris, 1963) and their dependence on frequency (f) and sound pressure level (L). The results from these studies on the human ear together with others on masked thresholds have led to a model of a spectrum-excitation-transformation in the cochlea (Maiwald, 1967). Changes in frequency and intensity are thought to have very similar effects on excitation patterns of the basilar membrane and of the sound receptors in general (Maiwald, 1967; Zwicker and Feldtkeller, 1967; Zwicker, 1970). One psycho-acoustically measurable nonlinearity in the spectrum transformation (see Fig. 11)

which is supposed to be of cochlear origin is included in the model (Zwicker, 1956; Maiwald, 1967; Zwicker and Feldtkeller, 1967).

This model or any other has not yet been re-examined for other mammals because related behavioral studies on frequency and intensity discrimination have been lacking. Reliable data for the frequency difference limen (frequency DL) exist only for the cat (Elliott *et al.*, 1960). Results for other species (review in Fay, 1974) are mostly based only on one or two animals. Often only a few frequencies were tested and sometimes information about method and procedure is missing. Cat (Dworkin, 1935; Rosenzweig, 1946; Raab and Ades, 1946; Elliott and McGee, 1965) and rat (Henry, 1938; Terman, 1970; Hack, 1971) are the only mammals of which intensity difference limens have been investigated. The results, however, can hardly be compared with those of the human ear (with the exception of Hack, 1971), because only too few frequencies and sound pressure levels (SPLs) were tested and no systematic variation of parameters was involved.

The intention of the present work is to investigate frequency and intensity discrimination in a small mammal, the laboratory mouse, with behavioral methods to such an extent that a comparison with human data and models derived from them will be possible. At the same time it will be interesting to see whether and how the absolute size of the hearing organs influences their function and characteristics in mammals.

Materials and Methods

1. Animals. Frequency DLs were determined for 9 male white laboratory mice (*Mus musculus*, outbred strain NMRI) aged 16–20 weeks. For the measurement of intensity DLs 5 males aged 5–6 weeks together with the 6 best working animals of the Δf-tests (24–28 weeks) were used.

NMRI-mice represent a genetically rather uniform outbred strain. No deficiencies in hearing or any behavioral disorders are known so far (Heine, pers. comm.).

2. Apparatus. The experiments were conducted in a sound-shielded room (400 cm × 205 cm × 220 cm) at the Zoological Institute of the Technische Hochschule Darmstadt. The inner walls were covered with sound-absorbing rock-wool. Background noise was maximally 24 dB (re. 0.0002 dyn/cm²) measured between 1 kHz and 20 kHz (Bruel and Kjaer sound level meter 2203 with 4131 microphone) and was most probably below that at higher frequencies.

A test grid (10 cm × 10 cm) was situated in the centre of the room. The speakers, either a condenser transmitter (Kuhl *et al.*, 1954) for $f > 5$ kHz or a dynamic speaker (Transco HTF 80/5) combined with a power amplifier (Krohn-Hite DCA-10R) for 1 kHz and 5 kHz, hung at a 30 cm distance from the grid. The unrestricted animals in the tests could move their heads up to 10 cm towards the speaker. The SPL at this distance of 10 cm varied at the most ± 2 dB at all frequencies and intensities tested. Because of the method of tone presentation these variations could not influence the measured DLs.

Fig. 1 shows a block-diagram of the apparatus for the sound pattern production and SPL measurement. Pure tones were produced by an oscillator (Hewlett-Packard 200 AB and (or) Exact 126). The test frequencies could be measured with ± 1 Hz accuracy (Kontron counter-timer 400 A). The output voltage of the oscillators ran through an attenuator (Hewlett-Packard 350 D) either directly or through a two-way switch to a two-channel electronic switch. The electronic switch was adjusted so that signals from channel I or channel II could pass alternately, forming a series. With the two-way switch different series could be selected, either A, A, A, ... (series I) or A, B, A, B, ... (series II). Adjusting the electronic switch and the two-way switch made it possible to present the desired series in random time intervals. Each single tone burst had a duration of 100 msec with an additional rise and fall time of 10 msec. The single tone bursts formed a series with 100 msec intervals
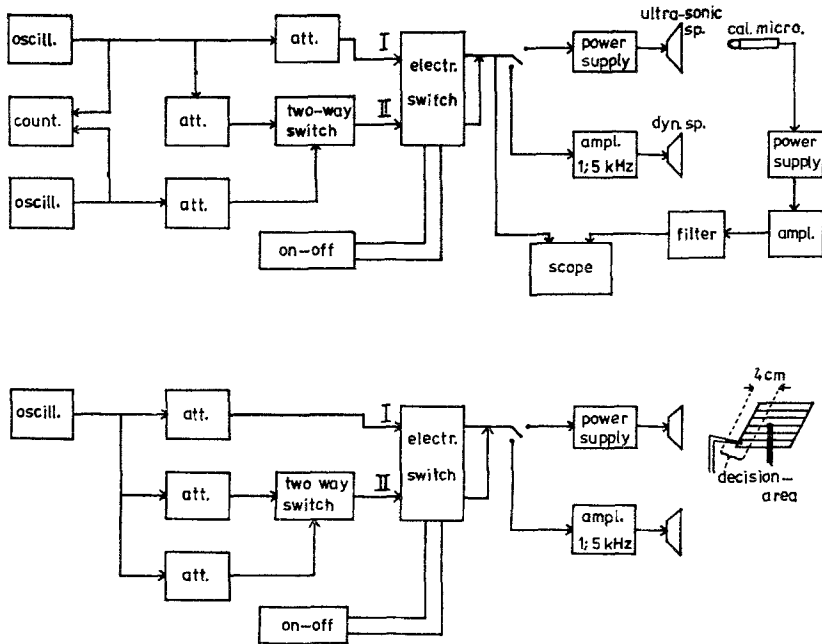
Fig. 1. Block diagram of the apparatus used for sound pattern production and measurement

between the tone bursts or with a modulation frequency of 4.5 Hz respectively. It was assumed that a modulation frequency of about 4 Hz which is optimal for man (Zwicker, 1952, 1956) is also optimal for the mouse. Frequency differences between the tone bursts could be adjusted with ± 1 Hz, intensity differences with ± 0.5 dB accuracy.

The SPL of the pure tones was measured in the decision area of an animal being tested (Fig. 1) with a calibrated 1/4″ microphone (Bruel and Kjaer 4135). The output voltage was amplified (Hewlett-Packard 466 A), filtered (Krohn-Hite 3500) and read onto a storage oscilloscope (Tektronix 564 or 5103 N). The signal waveform was also read out just behind the electronic switch.

3. Conditioning. An operant-reward-conditioning procedure was used. A glass capillary opened into the left front corner of the grid. There the mice could lick water, about 5 drops per reward. They only received water during one test per day and, in the home cage, ad libitum during a period of 15 min following the test session. The mice were trained with burst series II, *i.e.* alternating frequency (10 kHz and 15 kHz at 70 dB SPL) or alternating intensity (50 dB and 70 dB at 10 kHz). Each daily session for a single animal (*S*) required about 10 min in which the *S* received about 20 sound-reward-stimulations. Six days after conditioning started the *Ss* had learned to come to the capillary immediately after the stimulation (series II). Then the series I, always unrewarded, was introduced. Series I and II (each including 6 single bursts) were given successively and without interruption (Thompson, 1959; Elliott *et al.*, 1960; Heffner *et al.*, 1971) so that the difference became directly noticeable. After an additional 14 (frequency difference) and 23 (intensity difference) days of training, a reproducible time criterion for a positive reaction in series II (change in frequency or intensity) became evident: *S* stopped moving, turned immediately and directly to the capillary and started licking at least *3 sec* without immediate reward. Although the reaction in series I was variable it was always clearly different from the observed behavior in series II. The mouse either didn't react, or stopped moving and listened, or turned to the capillary and pushed it, or licked it for a short time (less than 2 sec).

After the termination of the conditioning, four days of test sessions followed. On the fifth day the Ss were retrained. They were immediately rewarded on series II. Some retraining trials with immediate reward were also given during the test sessions.

Seven mice out of 16 at the beginning of the frequency difference conditioning had to be eliminated because of aggressiveness, apathy or insufficient reaction.

Only 5 animals out of 12 at the beginning of the intensity difference conditioning remained for the tests so that the 6 best Ss of the Δf-tests were retrained for ΔL. This selection of animals doubtless contributed to a reduction of threshold variation to a point approaching the absolute limit of hearing capacity in *Mus musculus*.

4. *Test*. a) Frequency DLs: Thresholds were measured at 1, 5, 10, 15, 20, 30, 40, 50, 60, 80 kHz. These were the basic frequencies to which a Δf was added to form the comparison tones. The DLs were determined at various SPLs. The SPLs were selected in such a way that the range from 10 dB above the absolute auditory threshold (Ehret, 1974; see also Fig. 3) was tested generally in 15 dB steps. The number of steps at each frequency depended on the limitations of the apparatus or on the size of the DLs at high SPLs.

At 10 kHz each S was tested twice at each SPL. The mean of the data for all Ss from test 1 and 2 showed so little divergence that only one test was carried out at the other frequencies. The DL for one frequency and intensity was defined as the smallest frequency difference Δf_s at which a S responded positively twice on three signal presentations; if it happened that a Δf was positively responded to three times, and the next smaller only once, the larger Δf was taken as the DL (criterion). Frequency differences in the test tones were varied in such a way that there was a maximum of 5–10 Hz between the largest Δf to which the S responded negatively and the smallest Δf to which the response was positive.

b) Intensity DLs: Thresholds were measured at 1, 5, 10, 15, 20, 30, 40, 50, 60 kHz. As before the reference SPL was presented at intervals of 15 dB beginning 10–20 dB above the absolute threshold. A variable ΔL was added to the reference SPL to form the comparison SPL. In the test ΔL was decreased, starting about 15 dB above the reference intensity, in steps which, near threshold, reached 1 dB. The DL again was defined as the smallest SPL-difference (ΔL_s) at which a S responded twice on three signal presentations; if a ΔL was responded to three times and the next smaller only once the larger ΔL was taken as the DL (criterion).

Results

1. Frequency DLs. Mean and standard deviations for Δf_s were calculated for each frequency and SPL. Fig. 2 shows the dependence of Δf_s on the SPL of the reference frequency with reference frequency as parameter. Δf_s decreases linearly with increasing SPL. The decrease of the regression lines as shown in Fig. 2 is significant $(p < 0.01)$ for each frequency. At 10, 15, and 40 kHz the functions obviously reach a minimum Δf_s. At the intersection of the regression lines with the level of the value of the highest tested SPL the smallest perceptible frequency difference (Δf_m) can be defined for these frequencies. Doing so one gets a definite SPL at Δf_m which may be called $L_{\Delta f_m}$. The same operation was carried out for the other frequencies (without 1 kHz and 80 kHz for which only three SPLs could be tested), although it is not cogent that the highest tested SPL here also marks a Δf_m. There are three reasons indicating that such a fitting of data may be justified: firstly comparative aspects to 10, 15, and 40 kHz where the Δf_m-level is evident, secondly a lower significance of the correlation coefficients of the regression lines if the respective values of the highest tested SPLs are included in calculation, and finally the excellent fit of the obtained $L_{\Delta f_m}$-values in Fig. 3.

A very interesting aspect arises from plotting $L_{\Delta f_m}$ against frequency and comparing the result (Fig. 3) with the curve of the absolute auditory threshold of the mouse (Ehret, 1974). The curves (Fig. 3) have a very similar shape and
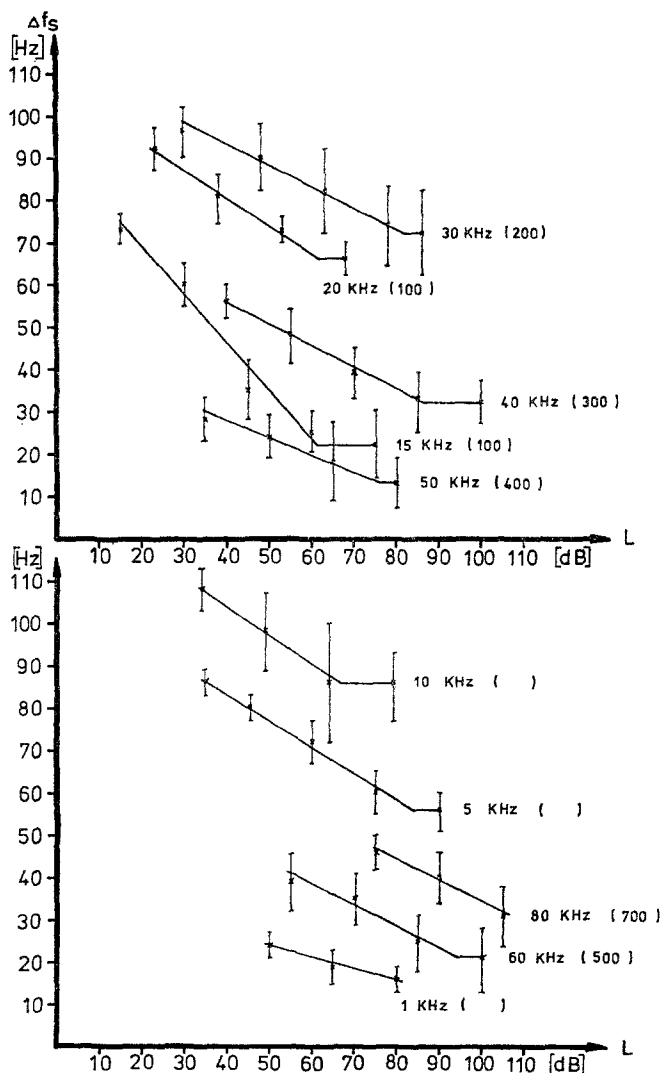
Fig. 2. Frequency difference limens (Δf_s) in dependence of the sound pressure level (L); parameter: frequency. The ordinate scale gives only the tens and units of the Δf_s-values, the hundreds, if appearing, stand in brackets behind the related frequencies and have to be added to the ordinate values

almost coincide if one shifts the ordinate-scale of $L_{\Delta fm}$ for 60 dB so that 0 dB SPL for L_{HS} (absolute threshold level) is equal to 60 dB SPL for $L_{\Delta fm}$:

$$L_{\Delta fm} - L_{HS} = 60 \text{ dB} = \text{const.} \tag{1}$$

or, for intensity:
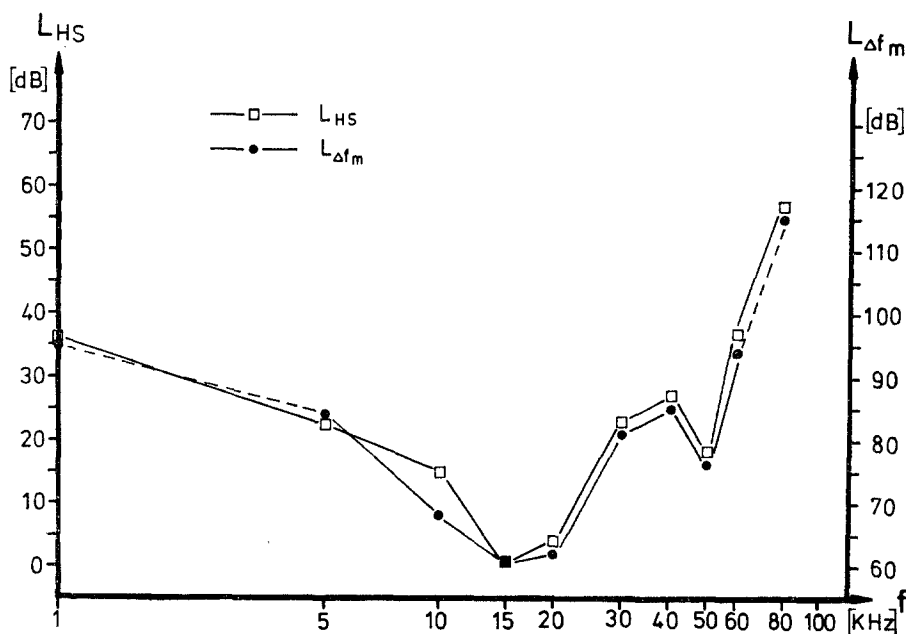
$$I_{\Delta fm} : I_{HS} = 10^6 = \text{const.}$$

Fig. 3. Frequency dependence of the SPL at which the smallest perceptible frequency difference ($L_{\Delta fm}$) compared with the curve of the absolute auditory threshold (L_{HS}) of *Mus musculus* (Ehret, 1974)

It follows that the sound intensity or SPL above the absolute hearing threshold, at which the smallest perceptible frequency difference (Δf_m) is measured, is constant for all frequencies tested.

The data show, therefore, that Δf_m is not intensity dependent but only frequency dependent. Fig. 4 shows a plot of the relative difference limen ($\Delta f_m/f$) against frequency. The curve has a rather constant level for $f > 10$ kHz ($\approx 0.85\%$), an indication for the direct proportionality of Δf_m and f.

The largest value for the slopes ($|a|$) of the regression lines (Fig. 2) is found at 15 kHz, which means that the largest relative increase of frequency discrimination power with increasing SPL takes place at 15 kHz. Fig. 5 shows the frequency dependence of the slopes. The extreme at 15 kHz, which is the precise frequency at which the ear of *Mus musculus* has its maximum sensitivity (Fig. 3), is very clear. In a double-logarithmic plot of the frequency dependence of the ratio $|a/f|$ (Fig. 6) one gets a function with a linear section from about 10 kHz to 80 kHz which follows the equation:

$$\lg \left|\frac{a}{f}\right| = -1.4209 \cdot \lg f + 1.6355 \qquad r = -0.9783 \tag{2}$$

or

$$|a| = 43.2 \cdot f^{-0.4209}. \tag{3}$$

The slopes of the regression lines in Fig. 2 are proportional to a power of the frequency.
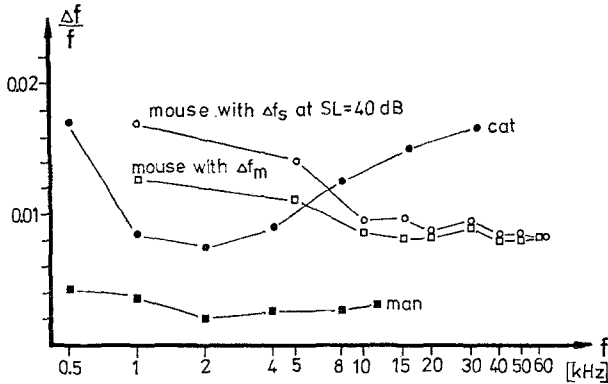
Fig. 4. Frequency dependence of the relative frequency DL ($\Delta f/f$) for *Mus musculus*, cat (Elliott *et al.*, 1960) and man (Shower and Biddulph, 1931). The curves are related to Δf_s at 40 dB SL. For the mouse also the respective Δf_m-curve (60 dB SL) is shown
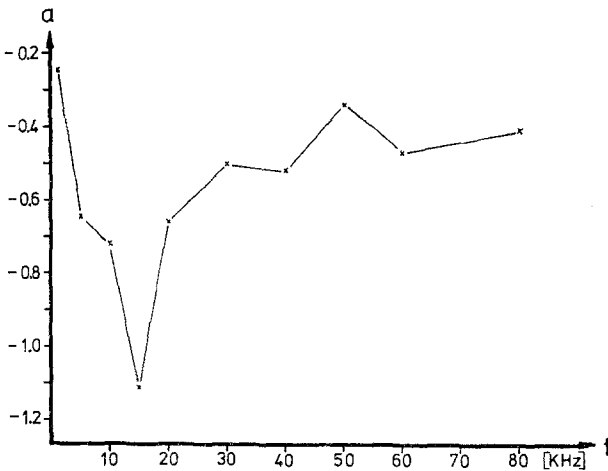

Fig. 5. Frequency dependence of the slopes (a) of the regression lines from Fig. 2

2. Intensity DLs. Mean and standard deviations (s) were calculated for each frequency and SPL. In all cases s was $\leqq \pm 1$ dB. Fig. 7 shows the DLs plotted against the sensation level (SL = SPL above absolute auditory threshold) at each test frequency with frequency as parameter. The intensity DL (ΔL_s) decreases with increasing SL. The decrease is significant ($p \leqq 0.01$) at all frequencies except at 10 kHz. First approximations to the curves are straight lines with the general equation:

$$\Delta L_s = -b \cdot \text{SL} + c \tag{4}$$

or calculated as a mean function for all points in Fig. 7:

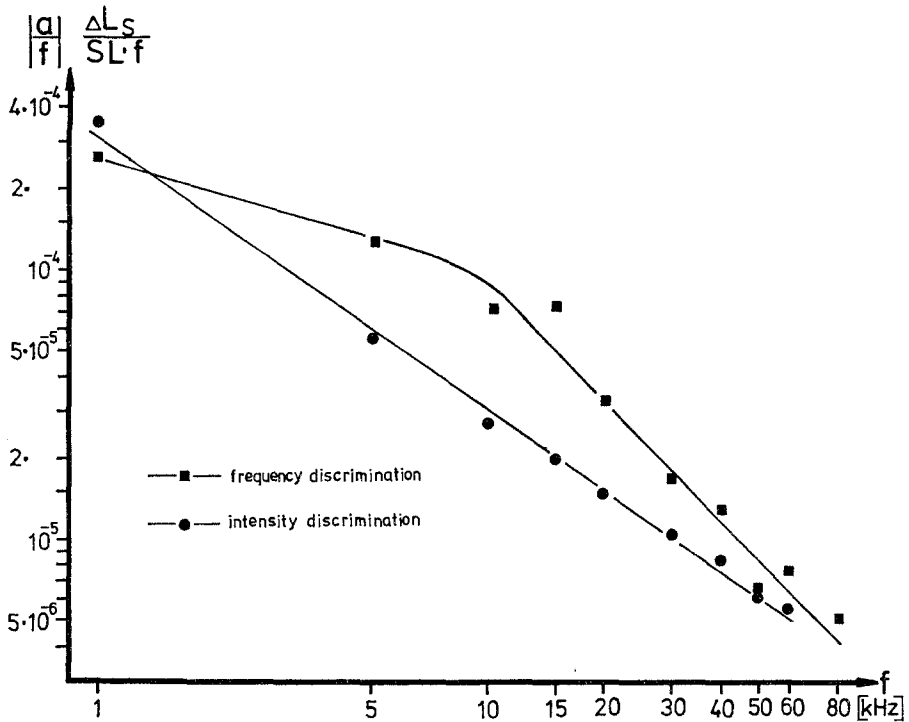$$\Delta L_s = -0.05 \cdot \text{SL} + 7. \tag{5}$$

Fig. 6. Frequency dependent nonlinearities in frequency (Eqs. 2 and 3) and intensity (Eqs. 11 and 12) discrimination. The linear parts of the curves follow power functions of the frequency
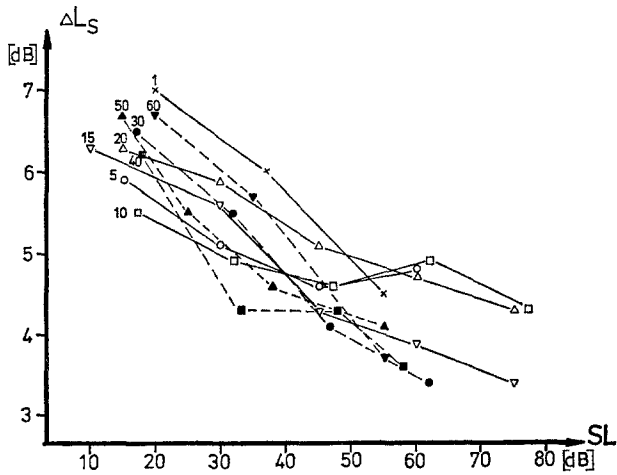

Fig. 7. The dependence of the intensity difference (ΔL_s) on the sensation level (SL)

The following significance limits can be calculated for single correlation coefficients of the linear approximations (Eq. 4): for 10 kHz $p < 0.1$; for 5, 15, 40 kHz $p < 0.05$; for 1, 20, 30, 50, 60 kHz $p < 0.01$.
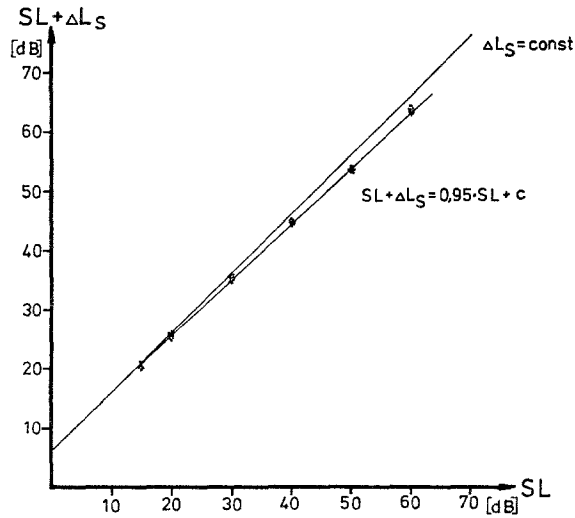
Fig. 8. Interdependence of the just discriminative SPLs: $SL + \Delta L_s$ and SL. The curve is a mean function for all data

A further nonlinear mean function for all data gives a better approximation especially for comparisons with human data (see Fig. 10):

$$\Delta L_s = 0.04 \cdot SL + 120 \cdot SL^{-1}. \tag{6}$$

The results can also be evaluated by plotting the two just discriminative SPLs for all frequencies tested (Fig. 8). The result is a straight line with the equation:

$$SL + \Delta L_s = 0.95 \cdot SL + 7 \qquad r = 0.990. \tag{7}$$

The slope is almost equal to 1. That means a near miss of Weber's law. With a slope of 1 we should get:

$$\Delta L_s = 7 = \text{const.} \tag{8}$$

Eq. (8) expressed in intensities leads to the usual form of Weber's law:

$$\Delta I : I = 4 = \text{const.} \tag{9}$$

Eq. (7) expressed in intensities would be, following (9) and with the slope 0.95 appearing in the exponent:

$$\Delta I = 4 \cdot I^{0.95}. \tag{10}$$

Looking at the frequency dependence of the intensity discrimination one could compare the slopes of the linear approximation functions for Fig. 7. A better picture is gained by plotting the relative intensity DL $\Delta L_s/SL$ against frequency with SL as parameter (Fig. 9). The greatest influence of frequency appears at low intensities (20 dB SL). Above 40 dB SL this influence nearly disappears. At 10 kHz we find the smallest change in discrimination power. The curve at 20 dB
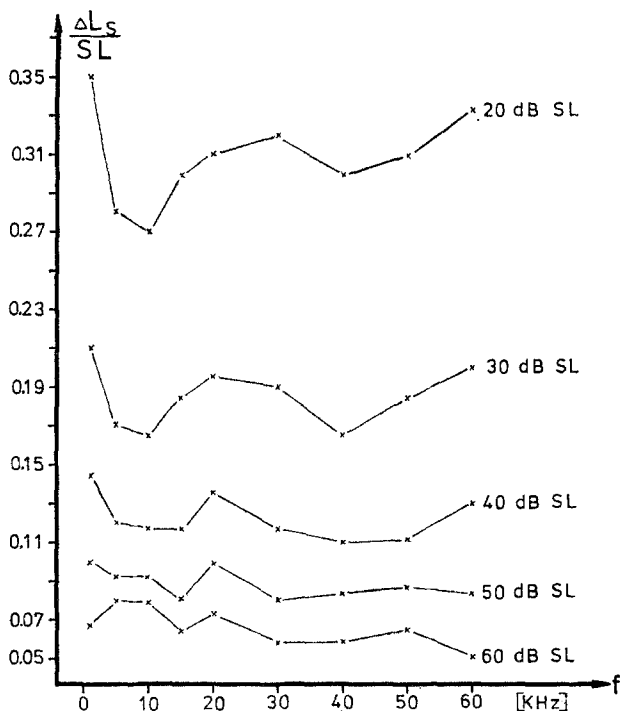
Fig. 9. Frequency dependence of the relative intensity DL (ΔL_s/SL), parameter: sensation
level (SL)

SL can be transformed by plotting ΔL_s/SL $\cdot$ f against f in a double-logarithmic
scale (Fig. 6). The result is a function with the following equation:

$$\lg \frac{\Delta L_s}{\text{SL} \cdot f} = -1.0045 \cdot \lg f - 0.4934 \qquad r = -0.9981 \tag{11}$$

or

$$\Delta L_s = 0.32 \cdot f^{-0.0045} \cdot \text{SL} \tag{12}$$

generally

$$\Delta L_s = d \cdot f^e \cdot \text{SL}. \tag{13}$$

Here as in the case of frequency discrimination the intensity DL is proportional
to a power of the frequency though only for low SLs.

Discussion

1. Comparison of DLs in Man and Other Mammals. In Fig. 4 the relative fre-
quency DLs $\Delta f/f$ are shown for *Mus musculus* (this paper), cat (Elliott *et al.*,
1960), and man (Shower and Biddulph, 1931). Human thresholds are the lowest
with about 0.2%. Cat and mouse reach approximately 0.85% in their respective
optimal f-bands. The values for man and cat, however, were measured for 40 dB
SL and are surely not optimal. So the cat compared with the 40 dB SL curve of
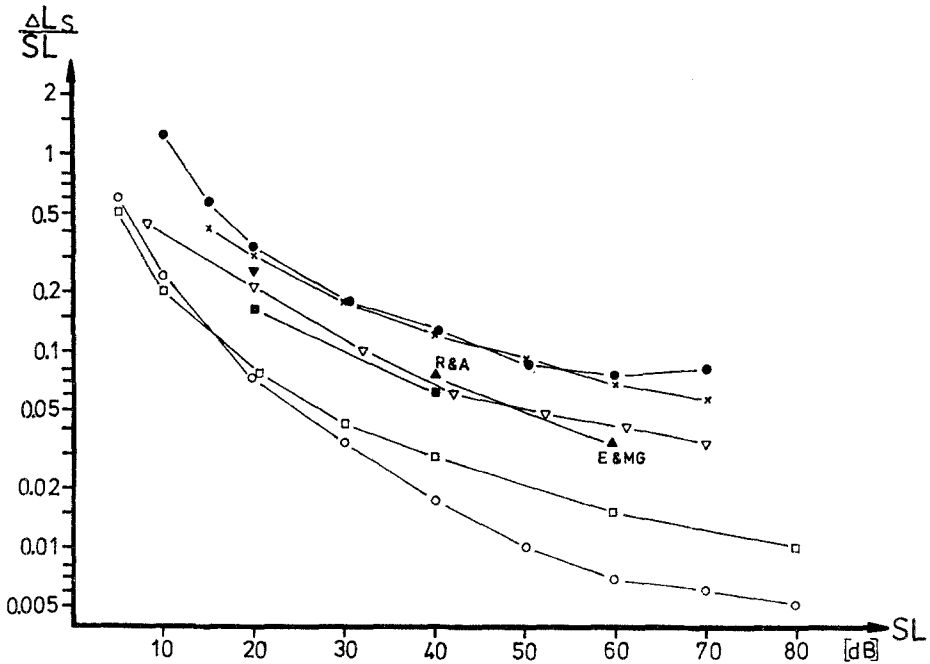
Fig. 10. The relative intensity DLs (ΔL_s/SL) of *Mus musculus*, rat, cat, and man in dependence of the sensation level (SL). All points, except for the mouse, were calculated after data in the related literature. × mouse, mean values; ▲ cat (Raab and Ades, 1946; Elliott and McGee, 1965); ● mouse, (Eq. 6); ○ man (Riesz, 1928); ■ rat (Hack, 1971); □ man (Harris, 1963); ▼ rat (Henry, 1938); ▽ man (Dimmick and Olson, 1941)

the mouse should have somewhat better relative frequency DLs. Heffner *et al.* (1971) and Fay (1974) tabulated frequency DLs of a number of mammals. In the related experiments, however, seldom more than two animals were tested, different conditioning procedures were used, and only low SPLs (30–40 dB SL) were tested so that the threshold values are surely too large (cf. Figs. 2 and 3). Yet in all mammals the ratio $\Delta f/f$ is rather constant over a wide frequency range.

Fig. 10 compares the available data for the relative intensity DLs (ΔL_s/SL). The thresholds for *Mus musculus* are 4–5 times larger than those of man (Riesz, 1928; Harris, 1963) and 2–3 times larger than those of rat (Hack, 1971) and cat (Raab and Ades, 1946; Elliott and McGee, 1965). If one takes, however, the curve of Dimmick and Olson (1941) as standard the DLs of the mouse are only twice as large as man. Conditioning and test procedures and the conditions of sound control and measurement play an important role in these experiments where SPL differences of less than 1 dB are required for accurate determination of thresholds, although the general shape of the curves (Fig. 10) is less influenced by possible inaccuracies of measurement than the absolute values. The curves (Fig. 10) representing human data seem to follow nonlinear functions as calculated for the mouse (Eq. 6) especially at lower SLs.
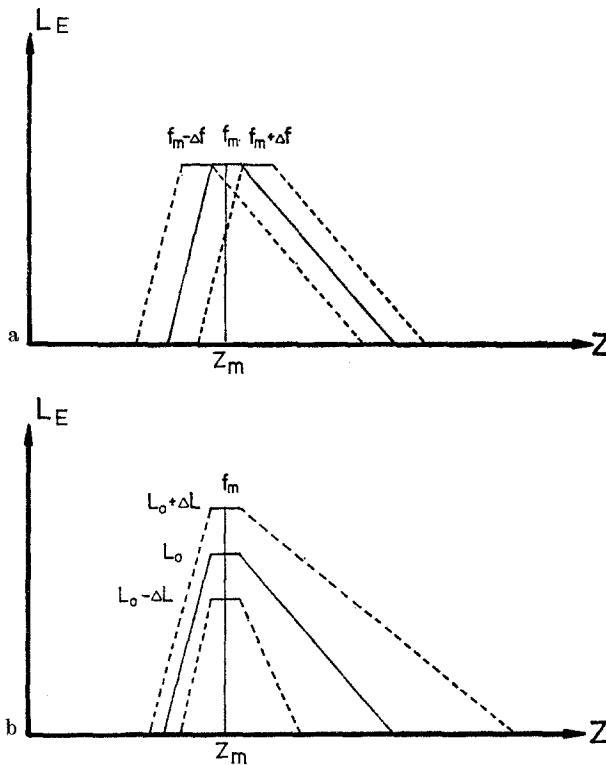
Fig. 11 a and b. Model of a spectrum-excitation-transformation on the basilar membrane after Maiwald (1967), a) for frequency variations, b) for intensity variations. L_E (ordinate) shows the excitation level. Z (abszissa) stands for the "Tonheit", a measure for the longitudinal extension of the basilar membrane. The arrow (abszissa) points in direction to the base of the basilar membrane, *i.e.* to the region which is mainly excited by higher frequencies

2. Spectrum-Transformation-Function in the Cochlea in View of the Difference Limens of Mus musculus. The very similar functions of DLs in all mammals investigated seem to be based on a rather uniform system of sound pattern analysis. One main locus for this analysis is within the cochlea. Maiwald (1967) worked out a model (Fig. 11a, b) in which psycho-acoustical results could be directly related to basilar membrane excitation patterns. The patterns shown (Fig. 11a, b) can be understood as a schematic graphical representation of the absolute value of a momentary displacement of the basilar membrane by a traveling wave. Changes in frequency and intensity induce changes in excitation in sections of the basilar membrane and therefore in the haircells. The change in excitation should be perceived where the product of the slopes of the excitation pyramids and the distance covered on the Z-axis (Fig. 11a, b) reaches a maximum. Fig. 11b shows that the right-side (=upper) slope of the excitation pyramid is intensity-dependent. This nonlinearity in excitation transformation has the effect that intensity variations are perceived at the upper slope, frequency changes at the lower slope.

In this model only one kind of haircell receptor is necessary to detect changes in excitation patterns. Frequency and intensity discriminations can be carried out by correlating the output of several receptors (Maiwald, 1967). Thus a shift of the excitation pattern (FM, Fig. 11a), or a rise and fall of the excitation level (AM, Fig. 11b), may elicit different sensations. With increasing SPL more and more haircells are able to take part in the correlation process with the result that frequency and intensity DLs should become smaller and smaller. The results of the present study show (Figs. 2 and 7) that this obviously also applies to *Mus musculus*. A further increase in discrimination power will not be possible either if all receptors are involved, or if a maximum information flow in the VIII-nerve is attained, or if other effects, *e.g.* inhibitive interactions, take place at high SPLs. These conditions for a Δf_m are independent of the frequency distribution over the basilar membrane because the excitation pyramids can be shifted without changing their shape. Δf_m depends only on the excitation level and therefore on the sound pressure level above the absolute threshold. Eq. (1) shows the experimental confirmation of this relation for the housemouse. The level difference $L_{\Delta fm} - L_{HS}$ is actually frequency independent and constant. 60 dB suprathreshold SPL represents the optimum excitation for frequency discrimination in critical band widths of the acoustic system. These band widths may be indentical with distinct sections on the basilar membrane. In analogy to man (Zwicker and Feldtkeller, 1967) they are called "Tonhöhenstufen" or pitch discrimination steps (T) with $T = 2 \cdot \Delta f_m$. If the pitch discrimination steps really represent equidistant sections on the basilar membrane, then for the mouse about 190 steps can be calculated (Ehret, in preparation). So *Mus musculus* is able to discriminate 380 pure tones ($T = 2 \cdot \Delta f_m$) in a continuous succession. Considering that the length of the basilar membrane of the mouse is 7 mm (v. Békésy, 1960), one can calculate the width of a pitch discrimination step to be 37 μm. In man, for comparison, the width of T is about 52 μm, a distance in which about 6 haircells are excited (Zwicker and Feldtkeller, 1967). Measurements of the haircell density in the normal ear of young adult *Mus musculus* should be made to have a clue to a comparative estimation of resolving power on the level of the haircells.

Due to the nonlinearity of the excitation pattern in the model (Fig. 11b) no ΔL_m can be noticed in intensity difference tests (Zwicker, 1956; Maiwald, 1967). The related results for the mouse show this very clearly (Fig. 7). No curves with a constant level at highest SPLs appear.

Another consequence of the described nonlinearity is the near miss of Weber's law (Eq. 10). Obviously this nonlinearity is less pronounced in the mouse compared with man; the exponent for the mouse (0.95) is closer to the ideal (1.00) than those for man (0.90–0.935, according to Dimmick and Olson, 1941, and McGill and Goldberg, 1968a, b).

The difference in excitation patterns for FM and AM in the model of Maiwald (1967) becomes evident in another experimental result for the mouse. In Figs. 5 and 9 the influence of the frequency on the DLs is shown. The *shift* of the maximum frequency effect from 15 kHz (FM) to 10 kHz (AM) can be explained by the nonlinearity of the model. One only has to consider that SPL-variations of a pure tone of 10 kHz may produce the largest change in excitation in the region of 15 kHz (see extension of the upper slope of the excitation pyramids).

Finally a further and new nonlinear effect can be read from the DLs of the mouse—the frequency dependence in itself (Figs. 5 and 9). The model assumes (Maiwald, 1967) that excitation transformation is the same over all the basilar membrane. Now, if one scans the frequency scale of the mouse with FM and AM discrimination tests, the largest improvements for Δf_s (with increasing SPL) and the relatively lowest thresholds for ΔL_s (at low SLs) can be found in the region of 10–20 kHz. The nonlinear frequency effect at low SPLs follows a power function (Eqs. 3 and 12). If the slope (a) in Eq. (3) is replaced by $\Delta f_u - \Delta f_1 / \Delta L$ (the variation of the difference limen in dependence of a SPL-variation) the general equation follows:

$$\Delta f_u - \Delta f_1 = p \cdot f^q \cdot \Delta L.$$

Integrating from Δf_1 to Δf_u and from $L = 0$ to L, we get:

$$\Delta f = p \cdot f^q \cdot L + C. \tag{14}$$

Δf is equal to the frequency difference between an extrapolated Δf_u at $L = 0$ and $\Delta f_1 = \Delta f_s$ at the sensation threshold.

If now $L = $ SL the Eqs. (13) and (14) coincide to the proportion:

$$\Delta L_s \sim \Delta f \sim f^z \cdot L. \tag{15}$$

The analogous influence of frequency and intensity on the frequency and intensity DLs as shown in the proportion (15) can also be seen in the similar shape of the related curves in Fig. 6.

The results of the investigations of Riesz (1928) on intensity discrimination and Harris (1952) on frequency discrimination for man also include a nonlinear frequency effect, especially at low intensities. No satisfying calculations and interpretations of this effect have been suggested so far. The nonlinearity in the results for man corresponds however with the power function described here for the mouse. Intensity DLs for the rat (Hack, 1971) show a similar effect. The function of the frequency dependence of the DLs has a minimum in a frequency region that is shifted to lower frequencies compared with the optimum of the absolute auditory threshold.

The proportion (15) characterizes the new nonlinearity of the ear very clearly. f^z may be seen as a frequency-specific or, because of the frequency distribution on the basilar membrane, place-specific transient displacement factor, and the sound pressure level L stands for the intensity of the influence. This interpretation projects the described nonlinearity into the displacement patterns of the basilar membrane. Kim et al. (1973) developed a model of nonlinear differential equations to approximate nonlinear basilar membrane motion. This model includes non-linear effects like combination tones (e.g. $2f_1 - f_2$), two-tone suppression, and the nonlinearity of the excitation pyramids of the model of Maiwald (1967). Two-tone suppression (Kiang, 1965) and combination tones (Goldstein and Kiang, 1968) can be recognized in single-unit responses of the VIII-nerve, so these effects must be generated in the cochlea. Probably the nonlinearity described in the present work may be represented by a term in the equation of Kim et al. (1973). Nonlinearities in the basilar membrane motion were detected by Rhode (1971) and Robles and Rhode (1974) using the Mössbauer technique. The nonlinearities

they found were pronounced in the frequency region of best hearing and in this respect they are in common with the nonlinearity found in the present work.

Further studies about the hydromechanical and bioelectrical transformation in the cochlea are needed to clear the processes involved in spectrum-excitation-transformation. The present work has shown that behavioral testing of acoustical discrimination power in a small mammal leads to very similar conclusions as derived from biophysical, psycho-acoustical, and electrophysiological experiments in man and cat. The results seem to fit together in one model of nonlinear basilar membrane displacement.

References

Békésy, G. v.: Experiments in hearing. New York: McGraw-Hill Book Company 1960

Boring, E. D.: The size of the differential limen for pitch. Amer. J. Psychol. 53, 450–455 (1940)

Dimmick, F. L., Olson, R. M.: The intensive difference limen in audition. J. acoust. Soc. Amer. 12, 517–525 (1941)

Dworkin, S.: Pitch and intensity discrimination by cats. Amer. J. Physiol. 112, 1–4 (1935)

Ehret, G.: Age-dependent hearing loss in normal hearing mice. Naturwissenschaften 61, 506 (1974)

Elliott, D. N., McGee, T. M.: Effect of cochlear lesions upon audiograms and intensity discrimination in cats. Ann. oto-rhino-laryng. 74, 386–408 (1965)

Elliott, D. N., Stein, L., Harrison, M. J.: Determination of absolute-intensity thresholds and frequency-difference thresholds in cats. J. acoust. Soc. Amer. 32, 380–384 (1960)

Fay, R. R.: Auditory frequency discrimination in vertebrates. J. acoust. Soc. Amer. 56, 206–209 (1974)

Goldstein, J. L., Kiang, N. Y. S.: Neural correlates of the aural combination tone $2f_1 - f_2$. Proc. IEEE. 56, 981–992 (1968)

Hack, M. H.: Auditory intensity discrimination in the rat. J. comp. physiol. Psychol. 74, 315–318 (1971)

Harris, J. D.: Pitch discrimination. J. acoust. Soc. Amer. 24, 750–755 (1952)

Harris, J. D.: Loudness discrimination. J. Speech Hearing Dis. Suppl. 11 (1963)

Heffner, R., Heffner, H., Masterton, B.: Behavioral measurements of absolute and frequency-difference thresholds in guinea pig. J. acoust. Soc. Amer. 49, 1888–1895 (1971)

Henry, F. M.: Audition in the white rat. J. comp. Physiol. 26, 45–62 (1938)

Kiang, N. Y. S.: Discharge patterns of single fibers in the cat's auditory nerve. MIT Press, Cambridge, Mass., Res. Monograph 35 (1965)

Kim, D. O., Molnar, C. E., Pfeiffer, R. R.: A system of nonlinear differential equations modeling basilar-membrane motion. J. acoust. Soc. Amer. 54, 1517–1529 (1973)

Knudsen, V. O.: The sensibility of the ear to small differences of intensity and frequency. Phys. Rev. 21, 84–102 (1923)

Kuhl, W., Schodder, G. R., Schröder, F. K.: Condenser transmitters and microphones with solid dielectrics for airborne ultrasonics. Acustica 4, 19–32 (1954)

Maiwald, D.: Ein Funktionsschema des Gehörs zur Beschreibung der Erkennbarkeit kleiner Frequenz- und Amplitudenänderungen. Acustica 18, 81–92 (1967)

McGill, W. J., Goldberg, J. P.: Pure-tone intensity discrimination and energy detection. J. acoust. Soc. Amer. 44, 576–581 (1968)

McGill, W. J., Goldberg, J. P.: A study of near-miss involving Weber's law and pure-tone intensity discrimination. Perception Psychophysics 4, 105–109 (1968)

Raab, D. H., Ades, H. W.: Cortical and midbrain mediation of a conditioned discrimination of acoustic intensities. Amer. J. Psychol. 59, 59–83 (1946)

Rhode, W. S.: Observations of the vibration of the basilar membrane in squirrel monkeys using the Mössbauer technique. J. acoust. Soc. Amer. 49, 1218–1231 (1971)

Riesz, R. R.: Differential intensity sensitivity of the ear for pure tones. Phys. Rev. 31, 867–875 (1928)

Robles, L., Rhode, W. S.: Nonlinear effects in the transient response of the basilar membrane. In: Facts and models in hearing. (E. Zwicker and E. Terhardt, eds.) Berlin-Heidelberg-New York: Springer 1974

Rosenzweig, M.: Discrimination of auditory intensities in the cat. Amer. J. Psychol. **59**, 127–136 (1946)

Shower, E. G., Biddulph, R.: Differential pitch sensitivity of the ear. J. acoust. Soc. Amer. **3**, 275–278 (1931)

Terman, M.: Discrimination of auditory intensities by rats. J. exp. Anal. Behav. **13**, 145–160 (1970)

Thompson, R. F.: The effect of training procedure upon auditory frequency discrimination in the cat. J. comp. physiol. Psychol. **52**, 186–190 (1959)

Zwicker, E.: Die Grenzen der Hörbarkeit der Amplitudenmodulation und der Frequenzmodulation eines Tones. Acustica **2**, Beih. 3, 125–133 (1952)

Zwicker, E.: Die elementaren Grundlagen zur Bestimmung der Informationskapazität des Gehörs. Acustica **6**, 365–381 (1956)

Zwicker, E.: Masking and psychological excitation as consequences of the ear's frequency analysis. In: Frequency analysis and periodicity detection in hearing. (R. Plomp and G. F. Smoorenburg, eds.). Leiden: Sijthoff 1970

Zwicker, E., Feldtkeller, R.: Das Ohr als Nachrichtenempfänger. Stuttgart: Hirzel 1967

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