

Temporal auditory summation for pure tones and white noise in the house mouse (*Mus musculus*)



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The dependence of the absolute auditory threshold on signal duration was measured by means of behavioral methods in the house mouse (*Mus musculus*). Twelve frequencies between 1 kHz and 120 kHz and white broadband noise were tested while seven pulse durations between 1 and 3000 msec were used. In any case temporal summation follows the function $I \cdot t^b = \text{const}$ until, at a critical duration t_c , a constant value is reached where thresholds become independent from signal duration. The critical durations are frequency-dependent following the general function: $t_c = p \cdot f^q$ (with $q < 0$). This frequency-dependent nonlinearity could also be extracted from available data on human hearing. The present results and respective data of the human ear are discussed with reference to a critical-band-related summation theory assuming fixed critical bands even for very short signal durations.

Subject Classification: [43]65.68, [43]65.75, [43]65.35; [43]80.50.

INTRODUCTION

Signal duration is an important parameter in sound perception and recognition. The relation between duration and auditory threshold of a tone has been investigated in detail for man. It was found that with increasing signal duration the auditory threshold decreased until a constant level was reached. Hughes (1946) formulated a simple function:

$$I = I_\infty [1 + (\tau/t)] \quad (1)$$

or

$$t(I - I_\infty) = I_\infty \tau = \text{const}, \quad (2)$$

where I is the threshold intensity at the duration t , I_∞ the threshold intensity for $t = \infty$, and τ is a time constant. I_∞ is equal to the minimum effective sound intensity for the ear. If t is equal to τ , I becomes $2I_\infty$. Equation (2) was quite suitable for the description of further results (e.g., Garner, 1947; Garner and Miller, 1947), as far as only a middle frequency range (about 200 Hz to 4 kHz) and no extremely short (<10 msec) signals were used. Feldtkeller and Oetinger (1956) derived an exponential function from their data on absolute and masked thresholds:

$$I = I_\infty \frac{1}{1 - e^{-t/\tau}} \quad (3)$$

For $t \ll \tau$ Eqs. (1) and (3) coincide so that the main difference between Eq. (1) and (3) appears when t approaches ∞ .

Zwislocki (1960) developed a theory of temporal acoustical summation on the basis of neural excitation. His calculations led to Eq. (3) with a time constant $\tau = 200$ msec. The calculations agreed well with results from his own experiments. At the same time he gave an explanation for the differences of Eqs. (1) and (3). The exponential function considers adaptation of neural elements. This adaptation shall play no role at the absolute threshold and there one can expect the direct proportionality and Eqs. (1) and (3).

There are some uncertainties about the amount of influence of frequency and critical bands in the above

mentioned functions. In most investigations time constants τ are found to decrease with increasing frequency and critical bands seem to widen with decreasing duration although there are some studies showing no time effect on the bandwidth of critical bands (for references, see Watson and Gengel, 1969; Scharf, 1970).

Only two behavioral investigations on temporal summation in mammals are available. Johnson (1968) tested one individual dolphin (*Tursiops truncatus*) at different frequencies and signal durations, and Henderson (1969) got some data from two chinchilla at 2 kHz. It is obvious that no mammal (besides man) has been tested with a sufficient number of individuals and with an extensive variation of parameters.

The present study on *Mus musculus* wants to extend the well known auditory thresholds of the house mouse (Markl and Ehret, 1973; Ehret, 1974) for short signal durations, and intends to present enough material for a detailed discussion with human data on this subject especially in view of frequency dependence and critical band influence.

I. MATERIALS AND METHOD

A. Animals

Altogether 15 male mice (*Mus musculus*, outbred strain NMRI) aged eight to ten weeks were tested. In eight mice thresholds were taken for pure tones, in seven mice for white broadband noise.

B. Apparatus

The experiments were conducted in a sound shielded room (400×205×220 cm) the inner walls of which were covered with sound-absorbing rock wool. Total background noise was maximally 24 dB (≈ 0.0002 dyn/cm²) measured between 1 kHz and 20 kHz (Brüel & Kjaer sound-level meter 2203 with 4131 microphone) and was most probably below that at higher frequencies.

Pure tones were generated in an oscillator (Philips PM 5160) and went through an attenuator (Hewlett-Packard 350D) to an electronic switch. White noise

was generated in a broad-band noise generator (Rohde and Schwarz, SUF BN 4150),¹ ran through a filter (Krohn-Hite 310 CR), attenuator (Hewlett-Packard 350D), and amplifier (Hewlett-Packard 466A) to the electronic switch. In the experiments pure tones or noise were switched on respectively. In the electronic switch signals were shaped into transient-free pulses of selectable definite durations (flat top) with additional rise and fall times (linear slope). Passing the electronic switch the signals went on to a condenser transmitter after Kuhl *et al.* (1954). Sound pressure levels (SPL's) were measured by a calibrated $\frac{1}{4}$ -in. microphone (Brüel & Kjaer 4135). The microphone output was amplified (Hewlett-Packard 466A), filtered (Krohn-Hite 3500) and read on a storage oscilloscope (Tektronix 564 or 5103N). From the microphone output voltage sound pressure was calculated in dB *re* 0.0002 dyn/cm². For white noise the intensity is expressed as the spectrum level (I_{WN}).

The response of the loudspeaker was flat within ± 2.5 dB from 15 to 80 kHz, and flat within ± 1 dB between 15 and 20 kHz which seems to be the decisive frequency range in the house mouse for hearing noise at the absolute threshold (see discussion). Below 15 kHz the response decreased with a slope of 8 dB per octave and above 80 kHz with a estimated slope of 12 dB per octave.

For 1, 100, and 120-kHz tones a power amplifier (Krohn-Hite DCA 10R) had to be introduced between electronic switch and speaker to generate the desired SPL's.

The test procedure did not allow use of two different speakers (electrostatic for ultrasonic frequencies and dynamic for frequencies below 20 kHz). So it had to be accepted that the electrostatic speaker produced distorted signals at low frequencies. Distortion measurements were made at 1, 5, 10, and 15 kHz at 66 dB SPL. The emitted signal, a continuous tone, was picked up by a calibrated $\frac{1}{4}$ -in. microphone (Brüel & Kjaer 4135), amplified (Hewlett-Packard 466A), high-pass filtered (Krohn-Hite 3500, cutoff at 500 Hz), and recorded by a Philips instrumentation recorder (Analog 7) with 30 ips (± 1 -dB flat frequency response from 500 Hz to 100 kHz). The signal was played back with reduced speed to fit the frequency range of a sound spectrograph (Kay 7029A). Spectrograms were made and the relative amplitude of distortion products measured. At 1 kHz the first two harmonics were about 7 dB down (relative to the level at 1 kHz), the third 24 dB, harmonics up to the tenth at least 33 dB. Higher harmonics could not be measured. At 5 kHz the first harmonic was about 35 dB down, higher harmonics could not be identified. At 10 and 15 kHz the first harmonic was about 45 dB down. The possible influence of distortion products on measured thresholds are discussed later.

SPL's were always measured with ± 1 -dB accuracy for every 1 cm in the area in which the animal could move its head. So in the test the position of the animal's head was related to a definite SPL. The averaged distance between speaker and head was 30 cm.

C. Conditioning

Two different conditioning procedures were used (for details, see Markl and Ehret, 1973). The results, therefore, have a broader methodological basis.

1. Conditioned eyelid reflex

The Ss worked in a cage (13×3×4 cm) made out of metal bars. Through the bottom an electroshock (UCS) of 40 V A.C. and 0.5-sec duration was administered. On every shock the Ss reacted with closing the eyes (eyelid reflex, UCR). The Ss were trained with tone-shock pairs (10-kHz, 70-dB tone of 1-sec duration, terminated by the electroshock) until they invariably produced the reflex (CR) on tone stimulation (CS) alone. Training sessions lasted for 10 min in which about 20 tone-shock pairs were presented. Intertrial intervals varied between 3 and 60 sec depending on the behavior of the animal. For getting good and reproducible responses it was most important that the animals were sitting motionless in the cage when the CS was presented. Only animals with reliable and steady responses (4 Ss) were used in the threshold tests.

2. Operant reward conditioning

Here the animals worked on a metal grid (10×10 cm). The Ss could lick water at a glass capillary that reached into one corner of the grid (towards the speaker). They got their daily water ration during and up to 15 min following the training session. The Ss received five drops per reward, after the signal (10 kHz, 70 dB SPL, 1-sec duration) was presented. The Ss were trained to come to the capillary immediately after the onset of the tone and to lick there at least 3 sec before being rewarded. With this time criterion a positive reaction could be easily differentiated from any other possible negative reaction. Finally here also 4 Ss with reliable responses were tested.

Only eyelid conditioning was used in mice of which thresholds to noise stimuli were measured.

In any case conditioning lasted for eight days with one training session of about 10 min per day.

D. Test

The tests were conducted at the absolute auditory threshold without background masking. Thresholds were taken at 1, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 120 kHz and with white broad-band noise (bandwidth 10–100 kHz). Signal durations (the respective additional rise and fall times) of 3 sec (100 msec), 1 sec (100 msec), 500 msec (50 msec), 100 msec (10 msec), 50 msec (5 msec), 10 msec (5 msec), and 1 msec (2 msec) were presented. At 1 kHz, the duration of 1 msec was not tested. Harris (1957) showed that a variation of rise and fall times had no influence on auditory thresholds in man which seem to be determined by peak energy if one works near the absolute threshold of hearing. If this also holds for the mouse, then rise and fall times, used to avoid switching transients, do not play a role in the present experiments.

Each S was tested at each frequency or bandpass

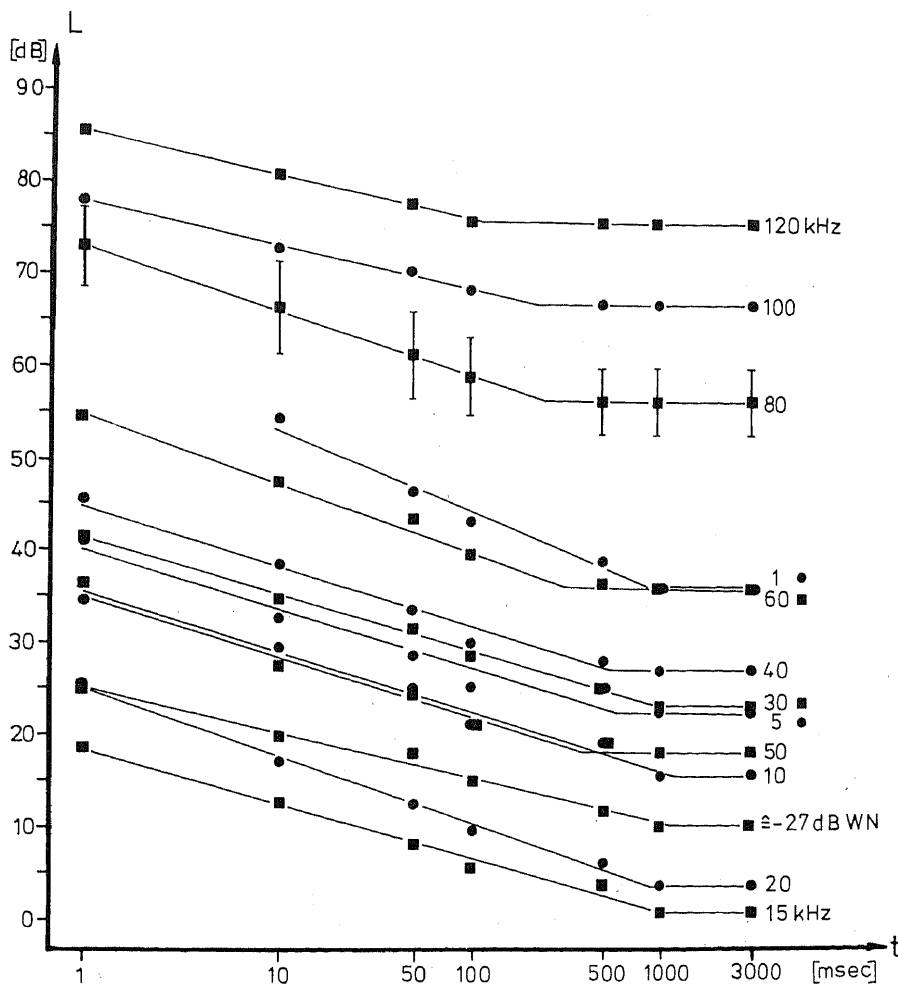


FIG. 1. Relation between the absolute auditory threshold (ordinate) and signal duration (abscissa) for all test-frequencies and white broadband noise (bandwidth from 10 to 100 kHz).

noise, respectively, in three sessions. A modified method of limits was used. In each test session thresholds were measured for all pulse durations. In the respective first session, the SPL was decreased in 10 dB, near threshold in 5-dB steps from about 30 dB above the known absolute threshold for 3-sec tones (Markl and Ehret, 1973) down to 5 dB below threshold, starting with the shortest duration. In the second and third session the SPL was increased from below threshold in 5-dB steps up to 5 dB above threshold. Now the longest duration was tested first. As the threshold at one frequency (bandpass noise) and pulse duration the lowest SPL was defined to which a S responded positively at least twice out of three sequential signal presentations; if a SPL was positively responded to three times and the next 5 dB smaller one only once, the larger SPL was taken as the threshold (criterion).

Thus for each subject, frequency, and pulse duration three measurements were carried out, altogether 24 per frequency and pulse duration and 21 per noise-pulse duration.

II. RESULTS

The thresholds measured with the eyelid reflex or with the operant reward conditioning did not differ significantly so they were averaged for each frequency and pulse duration. In Fig. 1 all mean thresholds are

plotted against pulse duration. For 80 kHz standard deviations are exemplarily shown, in the other curves they are of the same magnitude but are omitted for clearness. Level differences d with $d \geq 10$ dB (partly with $d \geq 6$ dB, e.g., at 100 kHz) within each curve are significantly different (rank test, $p < 0.01$). It is evident that the measured SPL increase with shortening of pulse duration is significant for each pure tone (except 120 kHz) and for bandpass noise.

The curves are plotted as broken lines. At the intersection of the regression lines with the constant level for longer durations the critical duration t_c can be defined for each frequency and bandpass noise.² t_c divides each curve into a part where temporal summation influences thresholds ($t < t_c$) and into another part of constant thresholds ($t \geq t_c$). All curves can be described (for $t \leq t_c$) by regression lines with the general equation:

$$L = L_{t_c} + |a| \log(t_c/t), \quad (4)$$

where L_{t_c} is equal to the absolute auditory threshold of *Mus musculus* (see also Ehret, 1974) and $|a|$ indicates the slopes of the regression lines. For all curves the regression coefficient $|r|$ ranges between 0.96 and 0.99. This means a significance level of $p < 0.01$ in any case.

Table I presents the slopes of the regression lines,

TABLE I. Characteristic values of the curves in Fig. 1.

f (kHz)	$ a $	t_c (sec)	L_{t_c} (dB)
1	8.559	0.953	36.0
5	5.936	0.706	22.5
10	6.285	1.255	15.0
15	5.854	1.067	0.5
20	7.236	0.974	4.0
30	6.073	0.974	23.0
40	6.670	0.468	27.0
50	6.652	0.450	18.0
60	7.262	0.371	36.0
80	6.702	0.266	56.5
100	4.605	0.233	67.0
120	4.785	0.115	76.0
noise	4.698	1.230	-27.0

t_c and L_{t_c} for all tested frequencies and noise.

Figure 1 and Table I indicate that the critical duration t_c depends on frequency. Figure 2 shows a double-logarithmic plot of the ratio t_c/f against f . Between 10 and 100 kHz one gets a straight line function following the equation

$$\log(t_c/f) = -1.78 \log f + 3.33, \quad r = -0.992, \quad (5)$$

solved for t_c :

$$t_c = 2140 f^{-0.78}, \quad (6)$$

and generally,

$$t_c = p f^q, \quad q < 0. \quad (7)$$

The critical duration is proportional to a power of frequency.

In contrast to the critical duration the slopes of the regression lines [Eq. (4)] are independent from frequency in a wide range (Table I). A mean slope of 6.5 dB per pulse shortening for one log unit can be calculated (mean of values from 5 to 80 kHz). Deviations to larger values appear at 1 kHz to smaller values at 100 and 120 kHz and noise.

III. DISCUSSION

A. Comparative aspects and critical bands

The results for *Mus musculus* can be described by the general function [Eq. (4)] that is defined for $t \leq t_c$. Expressed in intensities it corresponds to Eq. (2):

$$\begin{aligned} L - L_{t_c} &= \log(t_c/t)^{|a|}, \\ \log(I/I_{t_c}) &= \log(t_c/t)^{(|a|/10)}, \quad \text{making } |a|/10 = b, \\ I &= I_{t_c} (t_c/t)^b, \quad \text{with } (t_c)^b = t_c', \end{aligned}$$

which follows

$$I t^b = I_{t_c} t_c'$$

and, finally,

$$I t^b = \text{const.} \quad (8)$$

Equation (2), considering only the part above the constant level I_{∞} , can be written as

$$I t = I_{\infty} \tau = \text{const.} \quad (9)$$

If $b = 1$ (or $a = 10$) Eqs. (8) and (9) are identical.

The temporal summation in the ear of the house mouse can be generally described by the proportionality between I and t , the application of the exponential function [Eq. (3)] is not necessary. This result could be predicted according to Zwislocki (1960) because measurements were made at the absolute threshold (see Introduction).

Differences between the present study and data from other authors concern the value for the exponent b in Eq. (8) or the value for the respective slopes in Eq. (4). If $|a| = 10$ and by that $b = 1$, signal duration and sound intensity are equivalent in their effects on threshold. If $|a| < 10$ ($b < 1$) the system is not able either to integrate over the whole signal duration or to make use of the whole sound intensity. Finally, if $|a| > 10$ ($b > 1$) an overproportional summation appears which may be explained by additional influences (see below). In the available literature only Feldtkeller and Oetinger (1956) explicitly found a slope of $|a| = 10$. From the data of Hughes (1946), Garner and Miller (1947), and Zwislocki (1960) a slope of $|a| = 10$ can also be read. Some authors (Johnson, 1968; Henderson, 1969; Watson and Gengel, 1969) use Eqs. (1), (2), or (3), the application of which presupposes that $|a| = 10$ ($b = 1$), but from the plot of their data it is evident that $|a| \neq 10$ ($b \neq 1$) for at least some frequencies. Garner (1947), Plomp and Bouman (1959), and Hempstock *et al.* (1964) draw attention to this effect. Plomp and Bouman (1959) proposed a correction for Eq. (3) in

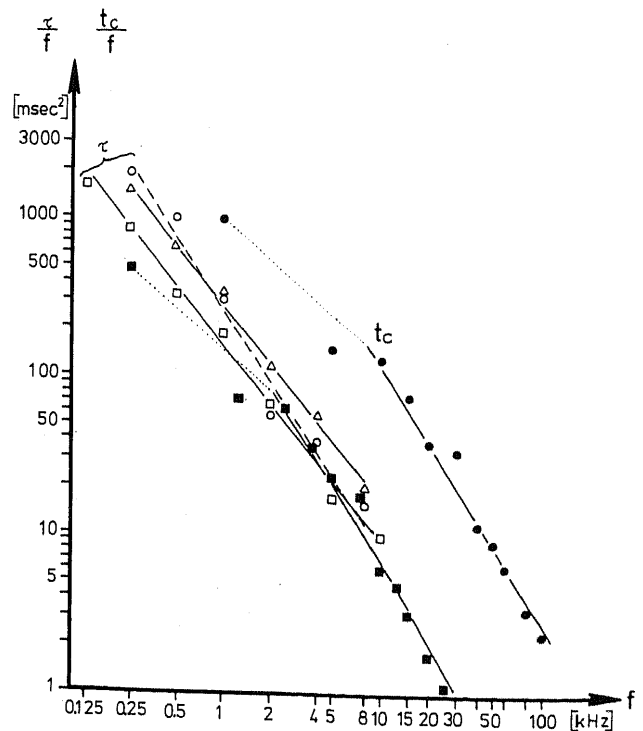


FIG. 2. Frequency dependence of the ratio τ/f for man and t_c/f for the house mouse. In the critical case t_c becomes 2τ . Open triangle: Plomp and Bouman (1959); open circle: Watson and Gengel (1969); open square: Tempest and Bryan (1971); filled circle: *Mus musculus* measured values; and filled square: *Mus musculus* calculated values (see text).

which they considered the summation of energy in fixed bandwidths of the acoustic system. Hempstock *et al.* (1964) presented a complicated correction for the frequency influence on the slope. Green *et al.* (1957) evaluated their data on the basis of signal detection theory. Their results could be best approximated by three functions indicating that the exponent b (slope a) strongly depended on signal duration.

In all corresponding results the tendency exists that with increasing frequency the slope $|a|$ becomes smaller than 10 ($b < 1$), or on the other hand, with shortening of signal duration slope values larger than 10 ($b > 1$) can be measured. The smallest values always appear at highest frequencies and broadband noise, the largest values at low frequencies and very short signals. These results can be explained by means of the concept of critical bands.

The critical bandwidth expressed in Hertz increases with increasing frequency (e.g., Zwicker *et al.*, 1957; Zwicker, 1961). Fourier analysis of short tone signals lead approximately to an inversed proportionality between bandwidth in Hz of the signal and signal duration (Garner, 1947; Blodgett *et al.*, 1958). Because the critical bands in Hertz are rather small at low frequencies a good deal of sound intensity, considering a short t , may fall out of the critical band marked by the frequency in the tone pulse. With lengthening pulse duration the intensity concentrates more and more within the critical band and relatively large decreases in threshold (with sometimes $|a| > 10$) can be measured. The shorter the tone the faster the threshold increase, because this increase is necessary to compensate not only for the loss of total energy of the tone pulse but also for the extension of the frequency spectrum beyond the critical bandwidth (Garner, 1947).

Now, if one looks at the present results for *Mus musculus* the slope $|a|$ varies only little over a wide frequency range and remains constant even for the shortest pulse durations.³ Thus along the basilar membrane of the mouse (without the extreme basal and apical part, representing 100, 120, and 1 kHz) equal suprathreshold amounts of sound energy per time unit are integrated (with $t < t_c$). *Mus musculus* has large critical bandwidths in Hertz even at low frequencies (Ehret, 1975b),⁴ so that no effect of band exceeding is measurable in this species and no variation of slopes within the curves (Fig. 1) appear. The smallest slope for broadband noise can also be explained by this critical-band-related summation theory. Here for each pulse duration a constant amount of sound energy falls outside the decisive critical band around 15 kHz.⁵ No variation with pulse duration should be possible. A strong indication that only the critical band around 15 kHz takes part in temporal summation of noise near threshold is given by the fact that the critical durations for broadband noise and the 15-kHz pure tone are very similar (Table I).

The experimental results for man and mouse can be well interpreted by considering the critical band concept, provided that the critical band width is constant for very short signal durations as well. Zwicker

(1965) suggested that excitation, for example by a narrow-band noise, occurs almost instantaneously. So excitation is not increasing from a zero level within a rise time but is immediately added as a ΔE to a basic excitation E_0 within critical bands. For $t < t_c$ ΔE then would be proportional to t^b . Results on the dependence of frequency difference limens on tone durations (Turnbull, 1944; Oetinger, 1959; Chih-an and Chistovich, 1961) give further evidence for frequency selectivity of the ear at very short signals. Difference limens could be measured even at durations of 1–4 msec. So discrimination capacity must extend at least up to these durations. The relation between difference limen (Δf) and signal duration (t) could be generally expressed by the equation (transformed after Chih-an and Chistovich, 1961):

$$\Delta f t^b = K t_c^b = \text{const.} \quad (10)$$

This function corresponds to Eq. (8). Shortening of signal duration leads in the same manner either to an increase of threshold intensity or to an increase of just-noticeable frequency differences. Assuming fixed critical bandwidths the first case can be explained by a band exceeding intensity distribution for short signals. The second case then is a consequence of the first because the size of the difference limens depends on the intensity of the test signal (Ehret, 1975a). These considerations lead to the conclusion that the acoustic system cannot use the whole spectral sound intensity in temporal summation but is fairly able to integrate over the total time of signal duration.

B. Frequency dependence of the critical duration t_c

In investigations covering a larger frequency range in man (Plomp and Bouman, 1959; Watson and Gengel, 1969; Tempest and Bryan, 1971) a frequency dependence of the time constant τ , or the critical duration t_c has been found. A definite function as presented by Eqs. (5) and (6) has not yet been established. If one treats, however, the time constants of Plomp and Bouman (1959), Watson and Gengel (1969), and Tempest and Bryan (1971; based on Hempstock *et al.*, 1964) in the same way as done for t_c in the present study, they all fit in Eq. (5) with the related graphs in Fig. 2. The following functions result:

$$\begin{aligned} \text{Plomp and Bouman: } & \log(\tau/f) = -1.25 \log f + 3.20, \\ \text{Watson and Gengel: } & \log(\tau/f) = -1.43 \log f + 3.71, \\ \text{Tempest and Bryan: } & \log(\tau/f) = -1.12 \log f + 2.88, \\ \text{mouse: } & \log(t_c/f) = -1.78 \log f + 3.33. \end{aligned}$$

These functions can be expressed as a power function of frequency according to Eqs. (6) and (7). So as in the mouse it can be derived from data on man that the critical durations (time constants) follow a power function of frequency at least in the main frequency range.

Tests of frequency and intensity discrimination in *Mus musculus* (Ehret, 1975 a) have already shown that the difference limens also follow a power function of frequency. It has to be investigated now, which processes in the sound spectrum excitation transformation may be responsible for this nonlinearity.

Figure 2 shows that the function for *Mus musculus*, although the slope is similar to those of man, is displaced to the right. The displacement can be explained as follows:

(1) Looking at the definitions of Eqs. (1) and (4), t_c must be equal to 2τ . So all ordinate values for the mouse decrease by a factor of 2.

(2) The next step is a shift in the frequency domain. This shift is deduced from the frequency interval between the sensitivity optimum in the absolute threshold curve of the house mouse (at 15 kHz; Ehret, 1974; see also L_{tc} values) and man [3.7 kHz; ISO—Rec. 226—1961 (E)]. The threshold curve of the mouse has to be shifted by a factor of about 0.25 so that the sensitivity optima coincide. A displacement of the data of the mouse by a factor of 0.25 on the abscissa in Fig. 2 together with the above mentioned decrease leads to the filled squares (Fig. 2) which fit quite well to the functions for man.

This calculation shows, together with others (Ehret, 1975b; Ehret, unpublished), that the basilar membranes of man and mouse seem to be scale models of each other. It can be concluded that in temporal summation the quotient of time constants to frequency is equal in man and mouse for comparable frequencies.

Finally the frequency dependence of the critical duration shall be considered in the general functions [Eqs. (1) and (3)] describing temporal summation of the ear:

$$I = I_{\infty} \left(1 + \frac{m}{f^n t} \right) \quad (11)$$

and

$$I = I_{\infty} \left(\frac{1}{1 - e \exp(-t f^n / m)} \right). \quad (12)$$

Values for m and n can be calculated for man (averaged from Plomp and Bouman, 1959; Watson and Gengel, 1969; Tempest and Bryan, 1971): $m = 2460$ and $n = -0.27$. The respective values for the house mouse were $m = 2140$ and $n = -0.78$.

These expanded functions [Eqs. (11) and (12)] are not yet actually complete because the expressions in brackets should have an exponent which is, as the experimental results for man and mouse indicate, in many cases not equal to 1. As mentioned earlier this may be due to effects of summation within fixed critical bands even for very short tones.

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²The critical durations by this definition are not identical with the time constants in Eqs. (1)–(3); in the critical case t_c becomes 2τ .

³Distortion products of the speaker could have little influence on thresholds. One has to consider that the measurements were done at the absolute auditory threshold and, comparing the intensity of the distortion products with the threshold for the longest signals (L_{tc} values, Table (I), harmonics except at 1 kHz (first and second harmonic) were inaudible. It may be that the real slope $|a|$ at 1 kHz is a little steeper and the t_c value larger than the measured.

⁴For example: critical bandwidth (measured as the critical ratio) amounts to 3200 Hz from the lower frequency limit of hearing up to about 8 kHz (Ehret, 1975b).

⁵At 15 kHz *Mus musculus* has its sensitivity optimum in hearing (Markl and Ehret, 1973; Ehret, 1974).

- Blodgett, H. C., Jeffress, L. A., and Taylor, R. W. (1958). "Relation of masked threshold to signal-duration for various interaural phase-combinations," *Am. J. Psychol.* **71**, 283–290.
- Chih-an, L., and Chistovich, A. (1961). "Frequency-difference limens as a function of tonal duration," *Sov. Phys. Acoust.* **6**, 75–80.
- Ehret, G. (1974). "Age-dependent hearing loss in normal hearing mice," *Naturwiss.* **61**, 506.
- Ehret, G. (1975a). "Frequency and intensity difference limens and nonlinearities in the ear of the house mouse (*Mus musculus*)," *J. Comp. Physiol.* **102**, 321–336.
- Ehret, G. (1975b). "Masked auditory thresholds, critical ratios, and scales of the basilar membrane of the house mouse (*Mus musculus*)," *J. Comp. Physiol.* **103**, 329–341.
- Feldtkeller, R., and Oetinger, R. (1956). "Die Hörbarkeitsgrenzen von Impulsen verschiedener Dauer," *Acustica* **6**, 489–493.
- Garner, W. R. (1947). "The effect of frequency spectrum on temporal integration of energy in the ear," *J. Acoust. Soc. Am.* **19**, 808–815.
- Garner, W. R., and Miller, G. A. (1947). "The masked threshold of pure tones as a function of duration," *J. Exp. Psychol.* **37**, 293–303.
- Green, D. M., Birdsall, T. G., and Tanner, W. P., Jr. (1957). "Signal detection as a function of signal intensity and duration," *J. Acoust. Soc. Am.* **29**, 523–531.
- Harris, J. D. (1957). "Peak vs total energy in thresholds for very short tones," *Acta Oto-Laryngol.* **47**, 134–140.
- Hempstock, T. I., Bryan, M. E., and Tempest, W. (1964). "A redetermination of quiet thresholds as a function of stimulus duration," *J. Sound Vib.* **1**, 365–380.
- Henderson, D. (1969). "Temporal summation of acoustic signals by the chinchilla," *J. Acoust. Soc. Am.* **46**, 474–475.
- Hughes, J. W. (1946). "The threshold of audition for short periods of stimulation," *Proc. R. Soc. B* **133**, 486–490.
- Johnson, C. S. (1968). "Relation between absolute thresholds and duration-of-tone in the bottlenosed porpoise," *J. Acoust. Soc. Am.* **43**, 757–763.
- Kuhl, W., Schodder, G. R., and Schröder, F. K. (1954). "Condenser transmitters and microphones with solid dielectrics for airborne ultrasonics," *Acustica* **4**, 19–32.
- Markl, H., and Ehret, G. (1973). "Die Hörschwelle der Maus (*Mus musculus*). Eine kritische Wertung der Methoden zur Bestimmung der Hörschwelle eines Säugetiers," *Z. Tierpsychol.* **33**, 274–286.
- Oetinger, R. (1959). "Die Grenzen der Hörbarkeit von Frequenz- und Tonzahländerungen bei Tonimpulsen," *Acustica* **9**, 430–434.
- Plomp, R., and Bouman, A. (1959). "Relation between hearing threshold and duration for tone pulses," *J. Acoust. Soc. Am.* **31**, 749–758.
- Scharf, B. (1970). "Critical bands," in *Foundations of Modern Auditory Theory*, edited by J. V. Tobias (Academic, New York).
- Tempest, W., and Bryan, M. E. (1971). "The auditory thresholds for short-duration pulses," *J. Acoust. Soc. Am.* **49**,

1901-1902.

Turnbull, W. W. (1944). "Pitch discrimination as a function of tonal duration," *J. Exp. Psychol.* **34**, 302-316.

Watson, C. S., and Gengel, R. W. (1969). "Signal duration and signal frequency in relation to auditory sensitivity," *J. Acoust. Soc. Am.* **46**, 989-997.

Zwicker, E. (1961). "Subdivision of the auditory frequency range into critical bands (Frequenzgruppen)," *J. Acoust. Soc.*

Am. **33**, 284.

Zwicker, E. (1965). "Temporal effects in simultaneous masking and loudness," *J. Acoust. Soc. Am.* **38**, 132-141.

Zwicker, E., Flottorp, G., and Stevens, S. S. (1957).

"Critical band width in loudness summation," *J. Acoust. Soc. Am.* **29**, 548-557.

Zwislocki, J. (1960). "Theory of temporal auditory summation," *J. Acoust. Soc. Am.* **32**, 1046-1060.