Comparative Psychoacoustics: Perspectives of Peripheral Sound Analysis in Mammals

Günter Ehret

Fachbereich Biologie der Universität, D-7750 Konstanz

Psychophysical data on hearing in mammals are summarized. The data are then correlated to the anatomy and physiology of the ear. Common mechanisms of sound transfer and analysis in the acoustic system, with stress on the auditory periphery, are discussed.

The ear of man and mammals is a fascinating sensory system because of its sensitivity to membrane displacements smaller than the diameter of an H atom, its energy threshold coming close to thermal noise, and its subtle differential sensitivity for pitch and intensity that becomes evident in musical perception. Investigations on basic mechanisms of hearing make use of various anatomical, histological, physical, electrophysiological, and psychophysical techniques. Obviously mammals are ideal subjects for extensive electrophysiological and physical studies, whereas man serves in highly sophisticated psychoacoustic experiments.

The terms psychophysics and psychoacoustics are used here both for man and mammals in the sense that sensory thresholds are determined on the basis of behavioral responses to physical stimuli. A great advantage of psychophysical tests compared with recordings of neural activity is that recordings of nerve-cell activity do not allow statements about the true thresholds of sensitivity of the whole system (reception, processing, reaction), which, however, can be gained by measuring the behavioral output of an intact subject. Nerve-cell responses always lead to speculations about their significance in further processing and recognition processes, whereas behavioral responses demonstrate what is in fact realized in the subject. It follows that the lowest behavioral thresholds must be regarded as the best approximations to the true, however unknown, threshold of sensitivity.

In this paper an attempt is made to bring basic psychoacoustic data from man and mammals in a logical line with the anatomy, physiology, and biophysics of the ear. This comparative approach is based on man and those five mammals, including bat and dolphin, for which sufficient data are available.

Psychophysically Measured Thresholds

Absolute Auditory Thresholds to Pure Tones

The absolute threshold can be defined as the lowest intensity at a given frequency that elicits any behavioral response in the animal. It is obvious that behavioral thresholds depend heavily on methods of conditioning and testing. Despite this, as can be seen in Figure 1, absolute threshold curves of a selection of

Fig. 1. Absolute auditory threshold curves for man [1], cat [2], guinea pig [3], house mouse (*Mus musculus*) [4], dolphin (*Tursiops truncatus*) [5], and horseshoe bat (*Rhinolophus ferrumequinum*) [6]. The curves are adjusted on the frequency axis so that the sensitivity optima coincide at 3.7 kHz, which is f_{opt} for man. The adjustment factors (m) are also presented. The sound-pressure level (ordinate, L_T) is expressed in dB re. 0.0002 dyn/cm² (also in respective, subsequent Figures)

mammals have similar shapes, especially for frequencies above the best frequency (f_{opt}). The only exception is the horseshoe bat, which has a very narrowly tuned third maximum of sensitivity at about 83 kHz and a narrow audible field. The curves are adjusted on the frequency axis to the one for man. The adjustment is done so that the frequencies of best hearing in each mammal become equal to 3.7 kHz, which is f_{opt} for man [1]. By this adjustment, the curves can be easily compared. Adjustment factors (m) are presented in Figure 1. Characteristic values of the curves are given in Table 1 together with the lengths of the basilar membranes. Table 1 shows the following trends: (1) the number of octaves between f_{opt} and f_u (upper frequency limit of hearing) is relatively constant in land mammals; (2) the audible ranges in octaves are not proportional to the lengths of the respective basilar membranes.

Excluding the 83 kHz maximum in the bat, the *shape* of all absolute threshold curves (Fig. 1), which is the *relative* sensitivity along the frequency scale, seems to be determined by resonant features of the external ear, impedance of the middle ear, and input impedance to the inner ear [14–18]. The sensitivity maxima of the threshold curve at 3.7 and 12 kHz (man) reflect exactly the gain in sound-pressure level (SPL) by

resonances within the external ear [17]. It has been demonstrated for the cat [15] that the inverse middle ear transfer function (see Fig. 7) follows the shape of the function of the absolute threshold [2] except for very low frequencies. At low frequencies the high-pass characteristic of the helicotrema plays a role and a respective correction brings both functions into coincidence [14]. The sharp third sensitivity peak at 83 kHz in the audiogram of the horseshoe bat [6] can be related to anatomical specializations of the cochlea, i.e. a rapid increase in thickness of the basilar membrane at about 4.5 mm from the basal end [13].

The lower frequency limit of hearing has two main structural correlates that work as high-pass filters: the tympanic membrane and the helicotrema (cf. Table 2). The smaller the eardrum the higher is the acoustic impedance at low frequencies and the higher the absolute threshold. This relation is responsible for the differences in the lower frequency limits between man, cat and guinea pig, mouse, and bat. The bat, with a very small eardrum (Table 2), has a very high lower frequency limit. On the other hand a small helicotrema (values see Table 2) allows the traveling waves to reach a point nearer to the apex of the cochlea and thereby improves the reception of low

Table 1. Characteristic values of absolute threshold curves (Fig. 1) and units of basilar membranes in some mammals. f_{opt} frequency of best hearing, f_u upper frequency limit of hearing, f_l lower frequency limit of hearing, p audible range in octaves between f_u and f_l , p' range between f_{opt} and f_u in octaves, q length of basilar membranes, n number of CR bands that can maximally simultaneously be established along the basilar membranes, s width of one CR band; f_u and f_l are determined as the frequencies at which the threshold becomes 65 dB higher than the threshold for f_{opt}

	f_{opt} [kHz]	f_u [kHz]	f_l [kHz]	p	p'	q [mm]	p/q	n	s [mm]
man	3.7 [1]	17	0.025	9.2	2.2	32 [7]	0.286	54 [34]	0.60
cat	8 [2]	65	0.045	10.0	2.7	22 [8]	0.455	33 [42, 33]	0.67
guinea pig	8 [3]	50	0.040	10.2	2.6	20 [9, 10]	0.510	—	—
mouse	15 [4]	100	0.5	7.5	2.7	6.8 [10, 11]	1.07	10 [33]	0.68
dolphin	65 [5]	145	0.7	8.8	1.2	39 [12]	0.226	61 [41]	0.64
horseshoe bat	20 [6]	105	3.0	4.5	2.4	16.1 [13]	0.281	—	—

Table 2. Some anatomical constants of cochleae and tympanic membranes. w width of basilar membranes, h thickness of basilar membranes, u averaged width for one outer hair cell, u' averaged width for one inner hair cell, r radius of the helicotrema, r' radius of the tympanic membrane

	w [mm]		h [mm]		u [μm]	u' [μm]	r [mm]	r' [mm]
	base	apex	base	apex				
man	0.1	–0.5 [19, 20]	—	—	8.3 [7, 23]	9.1 [23]	0.32 [19]	4.72 [19]
cat	0.08	–0.37 [20]	—	—	7.2 [8]	8.3 [8]	0.22 [14]	4.0 [16]
guinea pig	0.07	–0.25 [21, 22]	0.0074–0.0013 [21]	—	8.3 [24]	10.4 [24]	0.084 [14]	3.3 [16]
mouse	0.04	–0.16 [11]	0.014	–0.002 [11]	8.0 [11]	8.9 [11]	0.13 [11]	1.3 [16]
dolphin	0.025–0.35 [12]	—	—	—	8.45 [25]	10.8 [25]	—	—
horseshoe bat	0.08	–0.15 [13]	0.034	–0.002 [13]	—	—	—	0.89 [26]

frequencies. This helicotrema effect plays a role in the comparably good low-frequency sensitivity of the guinea pig [14].

High-frequency sensitivity and the upper frequency limit of hearing are influenced mainly by two factors: the low-pass characteristic of the osseous chain in the middle ear [27] and the structure of the basilar membrane near the stapes (base) [28, 29]. At high frequencies the tympanic membrane contributes negligibly to sound transmission and reacts only as a baffle for the osseous chain, which is driven directly by the incoming sound [30]. Light ossicles in a rigid chain and a stiff connection to the cochlea favor transfer of high frequencies. Middle ears of bats are specialized in this direction [27]. Also in the dolphin the middle ear forms an extremely stiff and rigid connection between a massive bony bulla and the cochlea [17].

Frequency representation on basilar membranes (locus of peak displacement for a given frequency) depends on the function of change in thickness and width along the basilar membrane; e.g., a thick, narrow basilar membrane, as it appears near the base, leads to a peak displacement for high frequencies. Values for width and thickness of basilar membranes are shown in Table 2, and the relation between narrow and relatively thick basilar membranes at their bases and high-frequency hearing in dolphin, bat, and mouse becomes evident.

Finally the differences in absolute sensitivities among species have to be discussed. Here cats lead by far (Fig. 1). A -18 dB threshold at 8 kHz (re. 0.0002 dyn/cm²) represents an energy of about $2.4 \cdot 10^{-11}$ erg impinging on the tympanic membrane for 1 s. For comparison: the translation energy of a single molecule at 27°C is equal to $6.2 \cdot 10^{-14}$ erg [31]. External and middle-ear transfer may contribute only little to a high absolute sensitivity [15, 18]. From a comparison of the innervation density of hair cells in man and cat with respective absolute threshold curves, it has been suggested [8] that the excellent absolute sensitivity in cats corresponds to the larger number of ganglion cells in the spiral ganglion. Data from dolphin and guinea pig [25, 32], however, do not fit well into this picture; thus no final conclusions can yet be drawn.

Masked Thresholds and Critical Bands

The absolute threshold for pure tones is nearly always a laboratory threshold because natural conditions are usually noisy, and the detection of tones having absolute threshold intensity is unlikely. Thresholds of tones that are determined in a situation

including background noise are called masked thresholds. Whenever masked thresholds come into discussion, one has to be sure that the acoustic system analyzes complex sounds, i.e., sounds that have more than one frequency component. Logically, masking experiments can throw light on mechanisms of complex-sound analysis.

In measuring masking effects on pure tones, one can use a great variety of noise combinations. The simplest one is continuous white broad-band noise. This noise, per definition, has an equal and constant intensity or SPL for every frequency and time interval. This is the reason why noise intensity or SPL is usually *not* expressed as the *total* intensity or *total* SPL of the noise. Instead the spectrum intensity or spectrum level of noise is used, which is defined as the intensity or SPL falling at every single frequency—at every single 1-Hz band—within the noise band width. In other words, the spectrum level of noise is exactly equal to the SPL of every frequency within the noise band width.

When broad-band noise passes the external and middle ear, every frequency of the noise band is subjected to approximately the same transfer mechanism as a pure tone would be. The originally flat noise spectrum changes into an amplitude-adjusted spectrum according to the transfer function of every frequency (see Fig. 7). Because of the independent transfer of frequencies through the external and middle ear, mechanisms leading to masking effects can first be expected at the level of the inner ear.

Thresholds for pure tones that are masked by white broad-band noise (spectrum level = 0 dB) are presented in Figure 2 for mouse and man. Compared with absolute thresholds (Fig. 1) these thresholds are relatively high and independent of frequency. This can be explained as follows: Taking the masked threshold curve for man, a spectrum level of 0 dB leads to a threshold increase of 20 dB at 2 kHz. Noise-spectrum level means intensity in dB per 1 Hz. Therefore, if only the intensity falling within a 1-Hz band would

Fig. 2. Masked threshold curves at 0-dB spectrum level of noise for mouse [33] and man [34]. Ordinate: level of masked thresholds (L_{MT}), abscissa: frequency (f)

be effective in masking, the masked threshold, e.g., for 2 kHz and 0 dB spectrum level, should be just equal to the absolute threshold at 2 kHz, which is 0 dB (Fig. 1). This is not the case. The masked threshold of 20 dB (Fig. 2) can be explained by an intensity summation in a frequency band around 2 kHz leading to a summated masking effect and thereby to an increase of the masked threshold level compared with the absolute threshold. Therefore the ratio between the intensity of a pure tone at its masked threshold (I_{MT}) and the spectrum intensity of the masking noise (I_{WN}) is a measure of the band width over which intensity is summed and is called critical ratio (CR) [35] (Eq. (1)). This intensity ratio can also be expressed as the difference between the masked threshold level (L_{MT}) and the spectrum level (L_{WN}) of noise (Eq. (2)).

$$\text{CR band [Hz]} = I_{MT} \left[\frac{W}{\text{cm}^2} \right] : I_{WN} \left[\frac{W}{\text{cm}^2 \cdot \text{Hz}} \right] \quad (1)$$

$$\text{CR band [dB]} = L_{MT}[\text{dB}] - L_{WN}[\text{dB}]. \quad (2)$$

In practice, the width of summing bands (CR bands) is determined by measuring masked thresholds for pure tones and then subtracting the spectrum level of the masking white broad-band noise according to Equation (2). The resulting band width in dB can be transformed into Hz [33]:

$$\text{CR band [Hz]} \cong 10 \exp \frac{\text{CR band [dB]}}{10}. \quad (3)$$

These considerations seem to be very theoretical. How do they help to understand the phenomenon of masking and complex sound analysis? Well, the results and conclusions from masking experiments indicate that when a complex sound spectrum excites the acoustic system of a mammal (only mammals have been psychophysically tested so far), this spectrum is divided into frequency bands of summated sound evaluation. Depending on the method of measurement the summing bands are called critical ratios (CR bands) or critical bands (*Frequenzgruppen*) [7, 36–38]. The critical-band mechanism can be seen as a filter bank of independently working band-pass filters (for filter characteristics see [37–40]). The number of filters that can maximally simultaneously be established is a measure of the frequency resolution of the ear of a mammal (see below).

It is very interesting to look for differences in frequency resolution among species. In Figure 3 the frequency dependence of the width of CR bands is shown for some mammals. In all species the width of CR bands is relatively constant at comparably low frequencies and then increases linearly with increasing frequency. Smallest CR bands appear in man and

Fig. 3. Frequency dependence of the width of CR bands and of the just noticeable frequency difference (Δf_m) for man [34, 47], cat [42, 48], mouse [33, 49], and dolphin [41, 50]

cat. The maximal number of CR bands that can simultaneously be formed within the audible range of each species [33] can be derived from the curves in Figure 3. One has to select the mid-frequency of the first CR band so that the width covers the frequency band from the lower frequency limit of hearing to a frequency determined by the CR band width. The mid-frequency of the second CR band has to be selected so that the width covers the frequency band from the end-frequency of the first CR band to a respective frequency, etc. Numbers of CR bands of mammals are presented in Table 1. One can compare these values with the respective lengths of basilar membranes (Table 1). In man CR bands have equal widths expressed in mm along the basilar membrane; the scale is linear [36, 37]. So far there are no indications that CR bands in mammals behave in another way; thus one can generally calculate the width in mm for a CR band by dividing the length of the basilar membrane by the number of CR bands. The result is shown in Table 1. In view of the different methods and procedures used to obtain all the measurements, it can be stated that the widths of CR bands in the preceding mammals and man are, averaged, the same and equal to 0.65 mm.

This result is important because it indicates a *common* filter mechanism for complex sound in mammals. The filter seems to be established within the cochlea. Electrophysiological and anatomical data accentuate the significance of this conclusion. First, it has been shown that the effective band width of fibers of the VIIIth nerve agrees with the width of CR bands in the cat [43]. Second, the outer spiral fibers (afferents from the outer hair cells) in cat [44], rat [45], and guinea pig [32] run spirally over a distance of about 0.65 mm, which, as demonstrated above, exactly equals the averaged width for a CR band in mammals. This astonishing numerical identity between psychoacoustical, electrophysiological, and anatomical results must now be confirmed in further measurements.

Once one has experimentally determined the frequency dependence of CR bands or critical bands (Fig. 3), a way is open to construct the function of frequency representation along the basilar membrane. Considering that CR bands in mammals are equal in width (expressed in mm), the corners of the CR bands have fixed distances in mm. Starting at the lower frequency limit of hearing, CR bands have to be plotted in a continuous sequence along the basilar membrane, whereby the corner frequencies automatically determine the frequency representation. Frequency-representation functions can be approximated by the equation [37]

$$f = A \cdot (10^{ax} - 1). \quad (4)$$

The factors A and a are species-dependent constants, x is the distance on the basilar membrane in mm from the helicotrema. Frequency scales constructed after Equation (4) are presented in Figure 8.

Discrimination Thresholds

To mark out the field it should be premised that differential thresholds in frequency and intensity for pure tones cannot be influenced by mechanisms of the external and middle ear. This is evident from the very small differences in question. External-ear resonances and middle-ear impedances are not as sharply tuned to lead to different transfer functions for two slightly different tones. Looking at Figure 7, correlates for difference limens can be expected first from the displacement patterns of the basilar membrane, that is, from a point where hydromechanical excitation is transformed into excitation of receptors. Frequency discrimination should not be confused with frequency resolution. In the first case frequency-modulated or sequential pure tones must be discriminated; in the latter case one must discriminate be-

tween simultaneous tones in a complex sound [46]. Frequency resolution is related to critical bands and has already been discussed.

In Figure 3 absolute frequency-difference limens (frequency DLs) are plotted against frequency for man, cat, mouse, and dolphin. The curves follow generally the same functions, that is:

$$\text{At comparably low frequencies } \Delta f_m = \text{const.} \quad (5)$$

$$\text{At higher frequencies } \Delta f_m / f = \text{const.} \quad (6)$$

The transition zone between the validity of the two Equations (5), (6) is around 1 kHz in man and cats, around 5 kHz in dolphins, and 10 kHz in mice. Above these frequencies, averaged relative DLs ($\Delta f_m / f$) amount to 0.0023 in man, 0.01 in cats, 0.005 in dolphins, and 0.0085 in mice. Relative DLs provide information about the slope of the curves in Figure 3 but say little about the absolute differential sensitivity that can be reached. It is obvious (Fig. 3) that the cat, despite the fact that it has the largest relative DLs, has by far better absolute difference limens than the mouse at low frequencies where Equation (5) is relevant.

Extensive behavioral measurements of intensity-difference limens (intensity DLs) exist only for man and mouse. In Figure 4 absolute DLs (averaged across frequencies) are plotted against the sensation level (superthreshold stimulus level in dB). The curves run nearly parallel and can be approximated for sensation levels (SLs) greater than 20 dB by a linear function [49]:

Fig. 4. The dependence of the intensity-difference limen (ΔL_m) on the sensation level (SL) for man [52], mouse [49], rat [53], and cat [54, 55]. The values are averaged across frequencies. Sensation level means superthreshold stimulus level in dB

$$\Delta L_m = -b \cdot SL + c. \quad (7)$$

Equation (7) can be expressed in intensities leading to the ordinary form:

$$\Delta I = d \cdot I^g, \quad (8)$$

g (man) = 0.91 [56], g (mouse) = 0.95 [49].

A near miss of Weber's law is indicated by g unequal to 1, which can be attributed to a nonlinearity of the ear (see Fig. 6). The absolute lowest intensity difference to be discriminated is about 0.5 dB in man [52] and 3 dB in the mouse [49]. The few behavioral data from rat [53] and cat [54, 55] indicate intermediate difference limens (Fig. 4).

CR bands and frequency DLs show similar functions plotted against frequency (Fig. 3). The respective DL and CR band curves for a species are parallel; that is to say, the width of CR bands is a multiple of the just noticeable frequency difference Δf_m . The following relations hold:

$$\text{man: CR band (Hz)} = 24 \Delta f_m = 12 \cdot T \quad (9)$$

$$\text{cat: CR band (Hz)} = 17 \Delta f_m = 8.5 \cdot T \quad (10)$$

$$\text{mouse: CR band (Hz)} = 38 \Delta f_m = 19 \cdot T \quad (11)$$

T stands for a pitch-discrimination step (*Tonhöhenstufe* according to [7]) and is defined as $T = 2 \cdot \Delta f_m$. Equations (9)–(11) indicate how many times the analytical capacity of the ear is better for modulated pure tones than it is for complex sounds.

It is very exciting to search for the mechanisms of frequency and intensity discrimination. The auditory system generally has two possibilities for coding the frequency of a tone: (1) The discharge rate of a single fiber (up to about 200 Hz) or of a group of cochlear fibers ('volley principle' up to about 5 kHz) is phase-locked to the frequency of the pure tone [43]. This 'periodicity pitch' seems to be limited to frequencies below about 5 kHz, and it is obvious (see frequency ranges of absolute threshold curves in Fig. 1) that another mechanism must be responsible for pitch perception, at least for higher frequencies. (2) Frequency information is coded in the activity of cochlear fibers originating from the place of maximal excitation for this frequency on the basilar membrane. This 'place-pitch' concept can be used throughout the audible frequency range. Examples and evidences for place and periodicity pitch shall not be discussed here, but it should be mentioned that place information alone is sufficient to explain, e.g., frequency discrimination [57].

Because of the regular spatial distribution of the hair cells and afferents within the cochlea [44], followed by tonotopic organization in higher centers of the

acoustic pathway up to the primary cortex [58], spatial information is an inherent factor of the auditory system. Along this line, the following model for frequency and intensity discrimination is based on place information (displacement pattern of the basilar membrane to different frequencies), and tries to explain the difference limens as variations of excitation rates of groups of hair cells or their afferents. The model is a modified version of Maiwald's [59]. Figures 5 and 6 show the variation of excitation patterns (excitation level L_E against the longitudinal extension of the basilar membrane) in the case of frequency and intensity discrimination. The triangle excitation patterns are derived from the instantaneous displacement of the basilar membrane by a traveling wave [60], which is shown in the insert to Figure 5. It is assumed that + and - displacement takes part in excitation; thus the envelope of the absolute value of displacement (triangle) is taken as the excitation pattern.

In Figure 5 the excitation triangle is shifted back and forth the basilar membrane, demonstrated for two different excitation levels (L_{E1} , L_{E2}). The shift corresponds to a frequency difference Δf . Assuming equal absolute thresholds of excitation in the sound receptors (hair cells + afferents) and equal relative thresholds (d') to detect changes in excitation, then in the case of L_{E1} three sound receptors (6, 7, 8) at the left-side slope of the triangle are able to detect the variation of excitation due to a Δf . The receptors change their response levels, i.e., they change their discharge rates. Note that the variations at the right-side slope of the triangle are

Fig. 5. A model of excitation variation on the basilar membrane and in the sound receptors due to a frequency variation Δf (further explanations, see text). The insert shows an instantaneous displacement pattern of the basilar membrane by a traveling wave and the derivation of the triangle excitation pattern (envelope)

Fig. 6. A model of excitation variation on the basilar membrane and in the sound receptors due to an intensity variation ΔL_E (further explanations, see text)

Fig. 7. Scheme of sound transfer through the external and middle ear, the cochlea, and higher centers up to the behavioral output. For each level a characteristic function (*left side*) is shown together with a short description of the stimulus transfer (*middle part*) and the overall filter characteristics (*right side*)

The shift of perceptible excitation variation toward the base of the basilar membrane with increasing sound-pressure level is discussed in detail elsewhere [7]. Differences in intensity-discrimination power between species (Fig. 4) can be related to the same factors mentioned for frequency discrimination. In addition the magnitude of the nonlinearity plays a role. The greater the nonlinearity the better is the differential sensitivity. Comparing intensity DLs of man and mouse (Fig. 4) to the respective nonlinearities (g -values in Eq. (8)), the differences in DLs can, at least partly, be related to different magnitudes of nonlinearity.

If one compares the outputs of relevant receptors in the models for frequency and intensity discrimination (Figs.5 and 6), the envelope functions of the discharge-rate distributions are different, and in the case of intensity DLs, the envelope is highly asymmetric. This difference in envelope functions can finally be assumed to be a decisive factor in the ability of the nervous system to detect a frequency difference or an intensity difference between two pure tones that sequentially stimulated the auditory periphery.

Equivalent Scales of Basilar Membranes

The data accumulated in the previous Sections allow the construction of equivalent scales of the basilar membranes of dolphin, man, cat, and mouse. The scales are presented in Figure 8. Note that for reasons

Fig. 8. Equivalent scales of the basilar membranes of the dolphin, man, cat, and house mouse (further explanations, see text)

of legibility the scales for the mouse are enlarged by a factor of 2.

The first scales show the extension of the basilar membrane in mm from the helicotrema (0 mm) to the basal end.

The second scales indicate the frequency distribution on the basilar membranes. According to Equation (4) the frequency representation can be described by the following functions:

$$\text{man [39]: } f = 165.4 \cdot (10^{0.06x} - 1) \quad (12)$$

$$\text{cat [39]: } f = 418.6 \cdot (10^{0.095x} - 1) \quad (13)$$

$$\text{mouse [33]: } f = 3350 \cdot (10^{0.21x} - 1) \quad (14)$$

dolphin calculated from [36]:

$$f=1745 \cdot (10^{0.05x} - 1). \quad (15)$$

The functions for man and cat are supported by anatomical evidence [10, 8].

The third scales show the CR band distributions. The scales are linear and, as mentioned, the CR bands have about equal widths in mm in all species. If the frequency of a tone is shifted one CR band, the focus of excitation is shifted about 0.65 mm.

An example shall illustrate the importance of the *number* of CR bands for complex-sound analysis. The mouse is maximally able to form 10 CR bands simultaneously. If one takes the simple case that the input to each of the CR band filters is CR band-wide noise of equal superthreshold intensity, then the stage of each filter can be characterized as empty or filled. The total output of the whole filter bank depends on the respective number of filters being in one of the two possible stages. Using Formula (16) one can calculate the maximal number of different filter-bank configurations in a system of n filters. r is the number of filled filters, $n-r$ the number of empty filters in Formula (16). In the mouse where $n=10$, the sum becomes 903 (Eq. (17)).

$$\sum_{r=0}^n \frac{n!}{r!(n-r)!} \quad (16)$$

for the mouse:

$$\sum_{r=0}^{10} \frac{10!}{r!(10-r)!} = 903. \quad (17)$$

It follows that the mouse, based on mechanisms of CR-band filtering, is virtually able to preceive and discriminate 903 different filter combinations, i.e., 903 different noise combinations of equal superthreshold intensities. If one stimulates with more complex sounds such as natural calls, the input energies to the filters are unequal and a much greater number of filter stages occur, which finally lead to astronomical values of potentially discriminative sounds. The numbers derived from Formula (16) only indicate possible discriminations according to peripheral filtering (CR bands). On this basis one can only speculate about central signal processing, filtering, and recognition of different peripheral filter-output patterns that are established to different incident sound patterns. In a recent conference problems of pattern recognition and feature detection in the acoustic system were discussed in detail [62].

The fourth scales represent pitch-discrimination steps. The scales are linear. Man, e.g., is able to discriminate 636 pure tones in steps (T) or 1272 pure tones in a continuous sequence of Δf_m . One step equals about 102 μm in the dolphin, 50 μm in man, 78 μm in the cat, and 36 μm in the mouse.

The fifth scales indicate the number of hair cells for one row on the respective basilar membranes. The values are averaged over the three rows of outer and the one row of inner hair cells. Averaged values in μm per hair cell are shown in Table 2. For simplicity linear scales are drawn. The true hair cell distributions, however, deviate from linearity at least in the mouse [11].

Three of the five scales are closely related to each other. The ratio of the lengths of basilar membranes 39:32:22:6.8, the ratio of the number of CR bands 61:53:33:10, and the ratio of the number of hair cells 4250:3500:2950:840 are proportional to each other by the following factors:

- 0.65 between length of basilar membranes and number of CR bands,
- 0.0083 between length of basilar membranes and number of hair cells,
- 0.013 between number of CR bands and number of hair cells.

The relations can also be expressed in another way. Taking the values for the mouse (length of basilar membrane, number of CR bands and hair cells) as 1, those for cat, man, and dolphin follow the proportion (averaged values):

mouse: cat: man: dolphin
1: 3.32: 4.70: 5.66

Being aware of the dangers of this kind of rough calculation, I think the evidence is strong enough to state that the length of basilar membranes is clearly correlated to the maximal number of CR bands that determine the peripheral quality of the ear in analyzing complex sound. Within one CR band about equal numbers of hair cells are present, whereby the course of the afferents to the outer hair cells reflects the width in mm of the CR bands.

As already shown, the audible ranges in octaves are not proportional to the lengths of basilar membranes. The frequency distributions on the basilar membranes, however, follow the same basic functions (Eq. (4)).

No simple correlation can be established between pitch-discrimination steps and any other measure in Figure 8. This, however, is not astonishing. If one takes into account the three peripheral determinants for frequency-discrimination power (see p. 468)—receptor density, slope of traveling-wave displacement, threshold of total discharge-rate change to a variation of excitation—and the task of higher centers to extract the envelope function of the discharge-rate distributions (Figs. 5 and 6), a simple relation to anatomical constants of the cochlea is not probable.

Conclusions

In psychoacoustic (behavioral) tests data are collected by measuring the output of the whole acoustic pathway (periphery and higher centers). This output is a change in behavior and can be expected to be very susceptible to disturbances of any kind. It has been demonstrated in the preceding Sections that, despite these difficulties, behavioral data on acoustic thresholds have their direct correlates in special properties of different levels of the acoustic pathway. In some cases one can go so far as to predict anatomical constants and electrophysiological data from the knowledge of psychophysically measured thresholds. Passing through the stages of filtering (Fig. 7) an astonishing amount of analysis can be related to mechanisms peripheral to the auditory nerve. Within the spatial organization of the cochlea the absolute limits of sound analysis are marked out. Mechanisms

determinating these limits are generally the same in mammals and are the basis for the correlations between behavioral and anatomical data (Figs. 5, 6, 8; Tables 1, 2; Eqs. (1), (4)). Higher centers of the pathway are responsible for recognition and classification of the enormous variety of patterns (Eq. (16)) that arrive through the acoustic nerve [62].

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