Masking Patterns and Filter Characteristics of Auditory Nerve Fibers in the Green Treefrog (*Hyla cinerea*)

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Summary. 1. Absolute thresholds to tone and noise bursts were measured for 177 single auditory fibers in the eighth nerves of 8 adult green treefrogs (*Hyla cinerea*). The lowest tonal thresholds were found between 300 and 600 Hz (at about 30 dB SPL) and lowest noise thresholds between 500 and 1,200 Hz (at about 10 dB spectrum level, noise bandwidth 20–10,000 Hz).

2. Masking effects of continuous broad-band noise on the response to tone bursts were studied using rate-intensity and latency-intensity curves and PST-histograms. The dynamics of masking can be described by two noise levels, one at which a fiber starts responding to background noise (in the presence of tone bursts), and the other at which the response of a fiber is totally dominated by noise (the response to the tone bursts is masked). This 'dynamic range of masking' varies around 20 dB measured in rate-intensity curves and around 10 dB in latency-intensity curves.

3. The fibers are divided into four response types according to their response rate change in the masking paradigm. The differences can be explained by different influences of summation, adaptation and suppression in the four groups of fibers.

4. Masked thresholds of the fibers were used for calculation of the masking susceptibility, which is equal to the bandwidth of the critical ratio (CR-band) filter of a fiber. Fibers with best excitatory frequencies (BEFs) below 700 Hz have CR-bandwidths mostly between 10 and 100 Hz, those with higher BEFs have CR-bands mostly between 50 and 1,000 Hz. CR-bands were found in nerve fibers originating in both hearing organs (amphibian and basilar papilla) in treefrogs.

5. The neural CR-bandwidths are significantly related to the sharpness of tuning (Q_{10} -values) and they agree well with the 3 dB bandwidths of the tuning curves of the respective fibers.

6. The mean neural CR-bandwidths near 900 and 3,000 Hz mid-frequency are very similar to those behaviorally measured at these frequencies. This similarity suggests that the mechanism of the CR-band (critical band) filter is of peripheral origin and may be identical with the filtering process leading to the frequency tuning curve of a single fiber in the auditory nerve.

Introduction

The green treefrog *Hyla cinerea*, as do most other anurans, relies on species-specific vocalizations for communication (Gerhardt 1974, 1976). In a natural environment, in which many other species may be present, these calls generally are embedded in a background of noise, so that the intended receiver must somehow filter out those communication signals of interest from the unwanted ambient noise. A first step in this detection process involves the evolution of selective frequency tuning in the ear itself. Anurans are a prime example of this peripheral specialization (Capranica 1976, 1977): a number of electrophysiological studies have verified that the amphibian and basilar papillae in their inner ears are tuned to species-specific frequency ranges which underlie reception of conspecific vocal signals. However, such studies of the matched sensitivity of the peripheral auditory system to the vocal signal characteristics have generally involved measurements of thresholds and frequency sensitivity in which background noise levels were deliberately suppressed. Since animal communication occurs, instead, in a noisy environment, we became in-

Abbreviations: BEF best excitatory frequency; CR-band critical ratio band; PST-histogram post-stimulus-time histogram; SPL sound pressure level

terested in the selectivity of auditory nerve fibers to excitatory signals in the presence of masking noise. Such peripheral processing obviously represents the first stage of filtering upon which further central processing must build.

Behavioral measurements of threshold detection of tones masked by white noise have been reported for a variety of vertebrates (Fay 1974; Ehret 1975; Pickles and Comis 1976; Saunders et al. 1978; Ehret and Gerhardt 1980) including humans (Zwicker and Feldtkeller 1967; Scharf 1970). But it is not entirely clear whether the behavioral detection of a tonal stimulus in noise requires additional filtering in the central auditory nervous system or whether, instead, it can be accounted for entirely by the frequency selectivity of auditory fibers in the eighth nerve. This question reflects on the relative importance of central vs. peripheral filtering in processing complex sounds, which is rather poorly understood at the present time. For example, it has been reported that the effective bandwidths of the filters necessary to explain a cat's behavioral detection of signals in noise are considerably broader than the filter bandwidths of single fibers in its auditory nerve (Pickles and Comis 1976; Pickles 1979). These results lead to the implication that there is a degradation in frequency filtering as one ascends from the peripheral auditory system through the central auditory system to the eventual behavioral output. This is actually a rather surprising conclusion. One might have expected that evolutionary pressure in animal signalling would preserve the selective filtering in the periphery and, if anything, actually sharpen this filtering by subsequent operations in the central auditory system.

Masking experiments indicate an important basis for frequency discrimination in noise, namely the existence of critical bands or critical ratios (CR-bands). Behavioral tests have verified that the auditory system of vertebrates divides the sound spectrum into a series of different frequency bands, each with its own selective – the critical – bandwidth. Sound energy in any particular critical band or CR-band is summed and processed independently from that in the other channels. The CR-bands thus act as a set of bandpass filters (e.g. Scharf 1970; Patterson and Green 1978) and their output array serves, e.g., in the detection of a tone in noise. Larger critical bandwidths represent poorer frequency resolution, which in turn requires a higher tonal level for detection in a constant background noise.

We became interested in learning to what extent the filter mechanism underlying behavioral performance is of peripheral origin in the anuran's auditory system. To explore this question we calculated CR-bands from masking experiments for single auditory

nerve fibers in the green treefrog and then compared them with behaviorally determined CR-bands (Ehret and Gerhardt 1980). We also explored the relationship between sharpness and tuning of individual auditory nerve fibers and the values of CR-bandwidths derived from masking studies (since an interrelationship between these two measures has previously been suggested for mammals; Evans and Wilson 1973). We feel that studies of anuran species can provide valuable insight into mechanisms underlying critical bands because of the uniqueness of having two separate hearing organs (amphibian papilla and basilar papilla) which differ markedly in structure from the cochlea of more advanced vertebrates.

Materials and Methods

We recorded from 177 auditory fibers in the VIIIth nerve of 8 adult green treefrogs using 3 M KCl-filled micropipettes (impedance 30–60 M Ω). Each animal was immobilized by intramuscular injection of d-tubocurarine chloride (6 mg/kg) and placed in an audiometric room (Industrial Acoustics Corporation). Its body was kept moist by a light covering of wet gauze and the room temperature was maintained at 23 ± 2 °C. The nerve was exposed through a small hole in the lateral parasphenoid-exoccipital region of the roof of the mouth and the electrode was advanced from the ventral to the dorsal surface of the nerve by a hydraulic microdrive (Kopf 607). Acoustic stimuli were presented through a PDR-10 earphone (Permoflux) in a special housing which was sealed around the outer margin of the animal's tympanic ring. A condenser microphone (Brüel and Kjaer 4134) within the housing monitored the sound pressure level (SPL) at the eardrum.

Pure tones from an audio oscillator (Hewlett-Packard 200 CDR) were passed through an attenuator (Hewlett-Packard 350D), shaped into phase-locked bursts of 300 ms duration with 10 ms rise and fall times and 300 ms intertone intervals (Grason Stadler timing modules, 1200 series), and then passed through an electronic adder, master attenuator and voltage follower to the earphone. White noise was produced by a noise generator (Grason Stadler 1285), passed through an attenuator (Hewlett-Packard 350D), two bandpass filters in series (Krohn-Hite 3500) and a low-noise voltage amplifier (Ithaco 255), and then either through timing modules (Grason Stadler, 1200 series) to produce bursts or else directly into the electronic adder and combined with the tonal signal. The filters were adjusted so that the bandwidth of the noise was always 20 to 10,000 Hz. All tonal sound pressure levels are expressed in dB re 20 μ Pa; the noise levels are specified by their spectrum level (i.e., noise intensity in dB per 1-Hz band). The frequency response of the overall earphone stimulus system was measured with a recording wave analyzer (General Radio 1900 A) and all SPL values were corrected accordingly. The noise spectrum was flat within ± 3 dB.

Spike responses from single fibers were passed through a high-impedance unity-gain follower mounted on the electrode drive. The output of the follower was amplified by a low-noise preamplifier and then simultaneously displayed on an oscilloscope (Tektronix 564), broadcast over a loudspeaker monitor, and recorded on channel I of a multichannel tape recorder (TEAC 2340). Reference pulses corresponding to the on and off transitions of the tone bursts were stored on channel II; a third channel III provided general commentary and protocol documentation. A DEC Lab-8E computer was used for compiling post-stimulus-time and latency histograms and in generating spike rate functions.

When a single fiber was isolated, its threshold at its best excitatory frequency (BEF) was determined as the just audible (audio monitor) and visible (oscilloscope) increase in spike rate against any spontaneous level. Then the threshold for noise bursts was measured. These threshold measurements for auditory nerve fibers in response to excitatory stimuli are very reliable in anurans because most of the fibers exhibit little or no spontaneous activity.

After the absolute threshold of a fiber was measured, tone bursts were presented at 1 dB above excitatory threshold at the fiber's BEF and continuous noise was added in 10 dB steps from subthreshold values up to about 80 dB spectrum level. After a pause of 30 s, the level of the tone was increased to 10 dB above threshold and the same intensity sequence of continuous masking noise was again added to the tone. The responses to 10 tone bursts and 10 intertone intervals (noise alone) were evaluated at every tone and noise level. After a 60-s recovery pause for the fiber, the excitatory tuning curve was taken. Finally, in 96 fibers the rate of any ongoing spontaneous activity in the absence of acoustic stimulation was also measured.

Results

1. General

Auditory fibers in the VIIIth nerve in anurans are usually divided into three classes: low frequency fibers (which show tone-on-tone suppression), and mid frequency fibers, both originating in the amphibian papilla, and high frequency fibers from the basilar papilla. Low frequency fibers in *Hyla cinerea* have best frequencies up to about 700 Hz, mid frequency fibers up to about 1,300 Hz and high frequency fibers between 2,800 and 3,800 Hz (Moffat and Capranica 1974; Capranica 1976). In the present study we also recorded fibers with BEFs between 1,300 and 2,800 Hz (Fig. 1), however only in one frog. Thus these fibers do not seem representative and therefore are not classified separately.

Figure 1 shows the thresholds of all fibers for tones at their BEF (A) and for broad-band noise (B). Fibers with BEFs between 300 and 600 Hz showed the lowest tone thresholds while fibers with BEFs between 500 and 1,200 Hz had lowest noise thresholds. Low frequency fibers are relatively less sensitive to noise than to tones compared with mid and high frequency fibers. In general, however, all the fibers are more sensitive to broad-band noise (expressed in spectrum level) than to tones.

The sharpness of the frequency tuning curve of a fiber is generally expressed as the Q_{10} -value (BEF divided by the bandwidth of the tuning curve 10 dB above threshold). The Q_{10} -values increase (the sharpness of tuning increases) with increasing frequency to a peak around 500 Hz and, on the average, stay constant at a lower level at higher frequencies (Fig. 2A). Q_{10} -values are not clearly correlated with absolute sensitivity to tones (Fig. 2B) although very

Fig. 1. A Absolute thresholds in response to tone bursts (tone level, L_T) at the best excitatory frequency (BEF) plotted against BEF for 177 auditory nerve fibers. B Absolute thresholds in response to broad-band noise bursts (bandwidth 20–10,000 Hz). The noise intensity is expressed as the spectrum level (l_{wn})

sensitive fibers do not have Q_{10} -values below 2 and very insensitive fibers do not have values above 1.5.

The spontaneous activity of almost all fibers was less than 6 spikes/s with the majority below 1 spike/s. Only 10 fibers of the low and mid frequency range had spontaneous rates between 6 and 16 spikes/s.

2. Responses to Tone Bursts in Background Noise

Adding continuous white noise to tone bursts changes the responses of the fibers significantly as can be seen in Figs. 3 and 4. The representative post-stimulus-time histograms (PSTs) show (Fig. 3) that when noise of increasing spectrum level is added a) the "on"-response peak to the tones is reduced (fibers 87-4, 132-6, 117-5), and b) the fibers increasingly respond in the intertone intervals to the noise and a 'flat' PST occurs at high noise levels, which means that the average spike rates during tone and intertone intervals become very similar. All fibers showed this kind of change in their response pattern. However, differences among the three groups of fibers were

Fig. 2A, B. Q_{10} -values (BEF divided by the bandwidth of the tuning curve 10 dB above the absolute tonal threshold) plotted against BEFs. **B** Relationship between Q_{10} -value and absolute tonal threshold for each fiber

found in the way in which the number of spikes during the tone bursts varied with the intensity of the continuous noise. This is demonstrated in representative rate-intensity curves in Fig. 4 and is quantified for all fibers in Table 1. Since fibers with BEFs below

Table 1. Number of fibers showing a spike rate increase (+) or decrease (−) or no change (0) during tone intervals when continuous noise is added to tone bursts. Tone levels are either 1 dB or 10 dB above tone threshold. The general response behavior is significantly different among the four groups of fibers. low_1 : fibers with BEFs up to 340 Hz; low_2 : BEFs up to 700 Hz; mid: BEFs up to 1,300 Hz; high: BEFs between 2,800 and 3,800 Hz (compare text)

Fibers	Tone level 1 dB above tone threshold			Tone level 10 dB above tone threshold		
	+	0	−	+	0	−
Low_1	17	12	7	5	12	16
Low_2	24	5	0	16	10	1
Mid	37	1	0	32	2	3
High	31	4	0	17	11	5

350 Hz often differed in their rate-intensity curves from other low frequency fibers, we divided the low frequency fibers into two subgroups, low_1 for fibers with BEFs below 350 Hz and low_2 for those with BEFs between 350 and 700 Hz.

All fibers were classified into three categories according to the variation in their spike rates during tone bursts when noise was added: fibers which increased their spike rate by more than 20% compared with no noise (+ in Table 1), fibers with a change in spike rate within $\pm 20\%$ (0 in Table 1), and fibers which decreased their spike rates by more than 20% (Table 1). A chi-square contingency analysis showed that low_1 frequency fibers behave significantly differently from all other fibers ($P < 0.01$) inasmuch as they tend to decrease their rate during tone bursts when noise is added. This decrease occurs in significantly

Fig. 3. Post-stimulus-time histograms of four representative fibers at their BEFs. The BEFs are 180 Hz, 400 Hz, 1,200 Hz and 3,400 Hz, respectively. Thus fiber 47-3 is a low_1 , fiber 87-4 a low_2 , fiber 132-6 a mid, and fiber 117-5 a high frequency fiber according to the classification made (compare Table 1). Continuous noise is added from 'no noise' (top) to a noise level at which the response to the tone bursts is masked and the PST becomes 'flat'. Respective noise levels are indicated. Tone level 10 dB above tone threshold in each case. Tone duration is indicated by the horizontal line at the bottom of each series. Bin width in PSTs always 10 ms

Fig. 4A–C. Rate-intensity curves for the same fibers as in Fig. 3 at tone levels of 1 dB (A) and 10 dB (B) above tone threshold. Relative spike rates are plotted expressed in % of the maximum rate of a fiber in the respective masking test. Spike rates during tone (closed circles) and intertone intervals (open circles) change when the noise level is increased. 'No' means no noise present. At high noise levels the spike rates during tone and intertone intervals reach the same values regardless whether the spike rate curves show an increase or a decrease or stay on a constant level. C Latency-intensity curves for the same fibers at tone levels of 10 dB above tone threshold. With increasing noise level latencies show a sharp drop to very small values. Arrows: 'masking starts' and 'masking complete' levels (see text). The difference between these two levels is called 'dynamic range for masking'

($P < 0.01$) more fibers when the tone level is 10 dB above threshold than when it is 1 dB. There is also a trend among high and low₂ frequency fibers to keep their spike rate constant at the 10 dB tone level. In high frequency fibers (Table 1) the ratio at 10 dB tone level (17/11/5) is significantly different ($P < 0.01$) from that at 1 dB tone level (31/4/0). Mid frequency fibers do not change their response behavior as the tone level is increased from 1 dB to 10 dB. Thus our data indicate that the auditory nerve fibers in the treefrog are inhomogeneous in their response to tone-noise combinations. In addition, in two fiber groups (low₁ and high) the response patterns to this kind of stimulus change with tone intensity (measured up to 10 dB above tone threshold).

The rate-intensity curves in Fig. 4 show the differences among the fiber groups very clearly. All fibers, however, have in common that the spike rates to noise (i.e. during the intertone intervals) increase with increasing noise level and eventually reach the spike rates during the tone bursts (tone+noise) which correspond to the occurrence of a 'flat' PST histogram (Fig. 3). At high noise levels the responses of the

fibers are totally dominated by the noise and all the response characteristics to the tone bursts are lost, i.e., the responses to the tone bursts are masked. We defined this masked threshold as the noise level at which the spike rate to noise alone (during the intertone interval) reached 80% of the spike rate during the tone bursts (tone+noise) and we assume that at this masking level the response to noise alone does not differ significantly from the response to the tone burst in noise. This assumption seems justified on the following grounds: a) the nine most spontaneously active fibers in our sample had spontaneous rates which were $73 \pm 6.5\%$ of the firing rates to BEF tones at our threshold criterion, and therefore an averaged 80% firing rate represents the limit which reliably began to exceed any ongoing background activity; b) at high noise levels where the spike rates to the masked tone and to the noise alone appeared to be about the same there nevertheless remained differences in these rates of $21 \pm 5\%$ for the 30 fibers with the largest differences. Thus again, 80% seems to be a reasonable limit above which differences in spike rates presumably fall within the same response category.

Fig. 5 A, B. Dynamic ranges for masking (measured 10 dB above tone threshold) from rate-intensity curves (A) and latency-intensity curves (B) plotted against the BEFs of the respective fibers

ry. Previous investigators have likewise adopted a criterion of 80% as the basis for assuming similarity in response categories (e.g. Sachs and Kiang 1968; Möller et al. 1978).

With the same criterion we defined not only the level for total masking but also the noise level at which a fiber began to respond to continuous noise while also responding to tone bursts. This is the level at which the spike rate to noise (intertone interval) is 20% higher than the spontaneous activity or, when no activity in intertone intervals occurred, the noise level increasing the probability for one spike in one intertone interval to 0.5 (i.e., 5 spikes in 10 intertone intervals).

Both noise levels, 'masking starts' and 'masking complete', are indicated by arrows in Fig. 4. The range between the two noise levels can be called the 'dynamic range' of the masking process. This figure shows that not only the spike rates to tone bursts are affected by adding noise but also the latencies of the fibers to the onset of the tone (evaluated for tone levels 10 dB above threshold). Figure 4 clearly shows that the latencies drop often in one step, when the noise intensities exceed a particular level. At higher noise levels the probability of short latencies increases since the fibers lose their regular time relationship in their discharges to the onset of the tone, and instead fire irregularly in response to the noise. In this case, therefore, we defined the noise level corresponding to the end of the rapid decrease in latency as the masked threshold. We used the 20% criterion however to define the level at which masking starts when the latencies begin to decline rapidly (Fig. 4).

The range in dB between 'masking starts' and 'masking complete' again indicates a dynamic range for the masking process.

In Fig. 5 the dynamic ranges for masking are plotted. Those derived from spike rate curves 10 dB above tone threshold (A) show a larger variation among fibers than those from latency functions (B). In addition, values from latency functions are generally smaller.

The differences between the tone level at the masked threshold (when masking is complete) and the spectrum level of noise necessary for complete masking is a measure of the susceptibility of a fiber, responding to tone bursts, to masking by continuous white noise.

$$MS = L_{MT} - I_{WN} \quad (1)$$

where MS = masking susceptibility, L_{MT} = tone level at the masked threshold (masking complete), I_{WN} = spectrum level of noise necessary to mask the tone completely.

The masking susceptibility is smallest when the difference is smallest, i.e., when the spectrum level of the noise necessary for complete masking is high and comes close to the tone level.

Figure 6 (A-C) shows a complete evaluation of the masking susceptibility of all fibers derived from spike rate curves (A, B) and latency measurements (C). The three plots agree in that low frequency fibers are generally less susceptible to masking than mid and high frequency fibers; the mean difference is about 10 dB in each plot. Only a very few low frequency fibers withstand masking unless the spectrum level of the noise is equal or almost equal to the tone level. On the other hand there are some mid and high frequency fibers which are completely masked already when the spectrum level of noise is more than 30 dB lower than the tone level.

Discussion

1. Masking Characteristics

All the fibers we studied showed masking in the sense of stimulus dominance, i.e., the relative intensities of tone and noise determine whether a fiber responds to the rhythm of the tone bursts or randomly to the continuous noise. The more effective stimulus determines the mean spike rate and the temporal patterns (e.g., latency relative to tone onset) of the discharge. The post-stimulus-time histograms (Fig. 3) clearly show that response characteristics to tone bursts, such as a phasic onset response and post-

Fig. 6. A–C Masking susceptibilities (right ordinate) and CR-bandwidths (left ordinate) in dB and Hz plotted against the BEFs. (A from rate-intensity curves 1 dB, and B, 10 dB above tone threshold; C from latency-intensity curves 10 dB above threshold). D Calculated 'effective bandwidth' of the fibers (equal to the difference between tone and noise threshold, see text and Eq. 2). Effective bandwidths (D) should be equal to the CR-bandwidths (A–C), if the filter characteristics of the fibers near threshold are linear

stimulus depression of spontaneous activity disappear when sufficiently intense noise is added. At high noise levels the fibers respond to the continuous noise only and totally 'ignore' the tone bursts as shown by the 'flat' PST histogram and the decrease to short latencies (Fig. 4). This resembles the behavior of auditory nerve fibers in the cat (Kiang et al. 1965), squirrel monkey (Rhode et al. 1978), and mongolian gerbil (Smith 1979), and of units in the cochlear nucleus of cats (Goldberg and Greenwood 1966; Greenwood and Goldberg 1970). Masking tests in mammals have usually been conducted at high tone levels to which the responses of the fibers were already saturated (Kiang et al. 1965; Evans 1974; Smith 1979). In these mammalian studies background noise of increasing level led to a decrease in spike rate during the tone

bursts. Smith (1979) explained this decrease in terms of saturation and adaptation of the fibers to the masking stimulus (noise). In the present study tone levels of only 1 dB and 10 dB above the threshold of a fiber were used. All fibers had dynamic ranges of at least 15 dB in response to tone or noise bursts alone, so that a decrease in spike rate due to saturation is generally unlikely. Table 1 indicates that a decrease in spike rate during tone presentation (i.e., within tone intervals) mainly occurred in low₁ frequency fibers. These fibers showed very little adaptation to 300 ms tone bursts (Fig. 3); therefore adaptation seems also unlikely to be the reason for the spike rate decrease in these fibers.

The decrease of the spike rate to tone bursts in low₁ frequency fibers while adding noise can be explained, however, by suppression. In general the firing rate of low frequency fibers in anurans can be suppressed by adding sound energy in the mid frequency region (Liff and Goldstein 1970; Feng et al. 1975; Capranica 1976; Ehret et al., in preparation). Suppression is not found in mid and high frequency fibers. Some of the low₁ frequency fibers can be totally suppressed by mid frequency tones whose intensities are only a few dB above the intensity of the excitatory tone. Suppression of low₂ frequency fibers requires a higher SPL of the suppressor tone. Thus the broad-band noise contributed sound energy in the excitatory and suppressive frequency range of low₁ frequency fibers at the same time. Because the suppressive frequency band is much wider than the excitatory one in these fibers (Ehret et al., in preparation), relatively more energy is introduced into the suppressor band than into the excitatory one, when the noise level is increased. This means that effects of suppression become dominant with the result a) of a decrease in spike rate to masked tone bursts, and b) of a much lower spike rate to high intensity noise than to a low intensity tone at BEF (Figs. 3, 4).

A summation of excitation (nerve fiber discharges) elicited by tone and noise energies near tone threshold described for some fibers of the squirrel monkey (Rhode et al. 1978), can be seen in high, mid, and some low frequency fibers in the treefrog, especially at 1 dB above tone threshold (Table 1). Generally, the effect is larger in the frog than in the monkey. For many fibers the spike rates in tone intervals more than doubled with addition of noise of increasing level until finally the response to the tone was masked completely (Fig. 4). The pronounced summation effect of tone and noise energies in the treefrog may at least partly be attributed to the broader tuning curves of frogs compared with those of mammals at the same frequencies. The Q_{10} -values do not exceed

2.5 in most fibers of the treefrog (Fig. 2A) but are generally higher in mammals at comparable frequencies (Kiang et al. 1965; Evans 1975). In the frog, therefore, a larger noise band falls within the tuning curve of a fiber and can contribute to the total excitation.

No simple explanation can be offered for fibers showing neither increase nor decrease in spike rate (Table 1). In low₁ frequency fibers summation processes and suppression effects may just compensate, in the other groups adaptation is often seen (Fig. 3) and may play a role in reducing summation effects.

All fibers responded to increasing noise levels with increasing activity during the intertone intervals. We defined a dynamic range for masking as the noise level difference between 'masking complete' and 'masking starts'. Within this range an auditory nerve fiber is able to discriminate between two different signals, a continuous noise and tone bursts. It is remarkable that despite the different masking patterns (Fig. 4) the dynamic ranges for masking show nearly the same means and variation in all groups of fibers (Fig. 5A, B). The large variation in dynamic ranges for masking among fibers with the same BEF (up to about 30 dB) is puzzling; it corresponds, however, to the variation of dynamic ranges in response to pure tones, which has been found in many mammalian primary auditory fibers (Kiang et al. 1965; Evans 1975). The dynamic masking ranges neither show a regular relationship to the sharpness of tuning (Q_{10} -values) nor to the absolute thresholds for tones or noise. It is evident, however, that the dynamic ranges from latency functions (Fig. 5B) are generally smaller than those from spike rate curves and show a smaller degree of variation. This means that, on the average, temporal analysis of tone-noise complexes may yield a smaller transition between the dominance of one or the other stimulus, which could sharpen the boundaries for detection of either stimulus. On the other hand, a spike rate analysis (the integration of discharges over time intervals), opens the possibility of detecting a weak noise signal, which may be about 30 dB less in intensity, in a dominating tone signal including the same frequency components. Thus both methods of analysis are valuable.

The susceptibilities to masking (Eq. 1), calculated from rate-intensity curves 1 dB or 10 dB above tone threshold or from latency measurements (Fig. 6A-C) are very similar. The susceptibility is smallest for low frequency fibers; in some of these fibers the spectrum level of noise can get very close to the tone level without masking the tone completely. In some mid and high frequency fibers, however, tones can be masked by spectrum levels as low as 30 dB below the tone level. Since the dynamic ranges for masking

on the average are the same in all fiber groups (Fig. 5A, B) this difference in susceptibility to masking indicates that 'masking starts' at higher noise levels in low frequency fibers compared with the others.

2. Frequency Selectivity and Critical Ratios (CR-Bands)

The frequency selectivity of a primary auditory fiber is generally expressed as the Q_{10} -value of its tuning curve (BEF divided by the bandwidth 10 dB above the absolute threshold). The tuning curves of VIIIth nerve fibers in mammals are interpreted as filter curves which are the result of three stages of filtering: the outer and middle ear, and the basilar and tectorial membranes as mechanical filters, and a third (often called 'second filter' of the cochlea) physiologically vulnerable filter that sharpens the response of the basilar membrane into the final tuning curve (Evans 1975). It has been suggested that the tuning curve represents the output of a linear filter, although only near its tip. Evans et al. (1970) and Evans and Wilson (1973) tested this hypothesis.

If at the output of a linear rectangular bandpass filter the power of a tone centered in the filter is equal to the *total* power of a broad-band noise, then the noise band that is passed is equal to the 'effective bandwidth' ('half power' or 3 dB down bandwidth) of the filter. Under these assumptions one way to calculate the 'effective bandwidth' of a nerve fiber is to subtract the threshold spectrum level in response to a broad-band white noise (I_{AWN}) from the threshold tone level (L_{AT}) at its best frequency.

$$10 \cdot \log_{10} \text{ effective bandwidth} = L_{AT} - I_{AWN}. \quad (2)$$

Evans et al. (1970) and Evans and Wilson (1973) measured the absolute thresholds to tones and noise for a number of auditory nerve fibers in cats, calculated the effective bandwidths (Eq. 2), and compared the results with the actual "half power" bandwidth of the tuning curves. The differences between measured and calculated values grouped reasonably closely around zero. From this comparison they therefore concluded that the tips of the tuning curves in the cat seem to be the result of a linear filtering.

To see whether this filter hypothesis applies to the treefrog we calculated the effective bandwidth from the thresholds to tones and noise (Fig. 1A, B). These threshold differences, which actually are the bandwidths expressed in dB, are shown in Fig. 6D. Then we compared these calculated bandwidths with the '3 dB down' bandwidths of the tuning curves. The 3 dB bandwidths are only an approximation to the

Fig. 7A–C. Differences between the CR-bandwidths and the 3 dB bandwidths of the tuning curves of each fiber (A, B). A CR-bands from rate-intensity; B from latency-intensity curves. C Differences between the 'effective bandwidths' (calculated from Eq. 2) and the 3 dB bandwidths of the tuning curves of each fiber (see text)

true halfpower bandwidths of the tuning curves since the tuning curve shape only approximates the filter characteristic of a linear filter. Figure 7C shows that for most of the fibers the effective bandwidths calculated from threshold measurements are larger than those measured in tuning curves. The largest deviations are consistently found in mid and high frequency fibers and at least for these the tuning curve filter seems to differ from a linear one.

The masking susceptibility defined in the present study (Eq. 1) is a measure for the ability of a single auditory fiber to discriminate tone bursts from a continuous background noise. The corresponding behavioral measure (related to the response of the whole intact animal) is the critical ratio (CR-band; Fletcher 1940; Scharf 1970; Ehret 1975), which is defined as

$$\text{CR-band (dB)} = L_{\text{MT}} - l_{\text{WN}} \quad (3)$$

or as

$$10 \cdot \log_{10} \text{CR-band (Hz)} = L_{\text{MT}} - l_{\text{WN}} \quad (4)$$

L_{MT} = tone level at the behavioral masked threshold,

l_{WN} = spectrum level of white noise necessary to just mask a tone of a given SPL completely.

The comparison of the Eqs. 1 and 3 shows that both express the same relation, Eq. 1 on a single unit level, Eq. 3 on the level of the whole animal; therefore masking susceptibility and CR-band are equivalent measures. Thus, instead of using the term masking susceptibility, we may speak of CR-bands of single auditory nerve fibers (Fig. 6A–C). The CR-band represents that noise band around a tone which is effective in masking. It is thus equal to the bandwidth of a bandpass filter which filters out of the broadband noise the effective spectrum for masking a tone in the center of the filter. The CR-band is commonly used as a measure for frequency resolution of the ear of vertebrates (e.g. Scharf 1970; Ehret 1975; Patterson and Green 1978). Small CR-bands mean small passbands of the filters, which indicates a high frequency resolution or selectivity.

CR-bands can be related to the effective bandwidth of single fibers defined by Eq. 2. If we assume that the absolute threshold to a tone (L_{AT}) actually is equal to a masked threshold (the masker would be the spectrum level of noise at the absolute noise threshold, l_{AWN}), then Eqs. 2 and 4 become equal and the CR-bandwidth expressed in Hz is equal to the effective bandwidth of a fiber. This, however, is true only if both, CR-band and effective bandwidth, are the result of a linear filtering process.

It can be concluded that the three measures, masking susceptibility, CR-band, and effective bandwidth, which are independently defined from response characteristics of single auditory nerve fibers or from the whole animal, may describe the same filter mechanism if the assumptions made above hold. Further masking experiments including single fiber studies in frogs and mammals will have to show whether peripheral filtering is, in fact, the only determinant for the behaviorally measured CR-band (see also next chapter).

The CR-bandwidth related to single fibers from the two kinds of data evaluation (spike rates and latencies) agree very well. Low frequency fibers have small CR-bands ranging mostly between 10 and 20 dB which is about 10–100 Hz. Mid and high frequency fibers have larger CR-bands, mostly between 17 and 30 dB (about 50–1,000 Hz).

We compared the CR-bandwidths of the fibers with the 3 dB bandwidths of the tuning curves (Fig. 7A, B). This time the values group better around zero (which would be equality of the two bandwidths) and deviations are less systematic than in Fig. 7C, where absolute thresholds were involved. Figure 7A, B suggest that, on the average, in the treefrog the filter which sets up the tip of the tuning curves of single fibers seems to be the filter forming the CR-bands.

Fig. 8. Comparison of the sharpness of tuning (Q_{10} -values) with the widths of the CR-band filters. This relation is shown separately for the fibers of the four different groups because the regression lines have different slopes. The sharper the tuning (large Q_{10} -values) the smaller the CR-bandwidths

The correspondence between the CR-bands and the sharpness of tuning curves is confirmed by the relation of Q_{10} -values and CR-bandwidths (Fig. 8). The higher the Q_{10} (the sharper the tuning) the smaller is the CR-band. This correlation is statistically significant in low_1 and low_2 and high frequency fibers ($P < 0.01$) and weakly significant in mid frequency fibers ($P < 0.05$).

3. Comparison of Neural and Behavioral CR-Bands

Since CR-bands were originally defined as a measure of frequency selectivity of the whole intact animal in behavioral tests, it is of interest to compare behavioral and neural CR-bandwidths. In Fig. 9 mean CR-bandwidths of the fibers are plotted together with two mean behavioral values at 900 Hz and 3,000 Hz (Ehret and Gerhardt 1980). The behavioral measurements were done at 55 dB and 65 dB SPL of the tones. Since most of the fibers with BEFs around 900 Hz and 3,000 Hz have their thresholds in this range of sound pressure levels (Fig. 1A), both behavioral and neural CR-bandwidths were measured at comparable tone levels. Both mean behavioral and mean neural CR-bandwidths agree very well. Also the ranges of neural CR-bandwidths at 900 Hz center frequency (Fig. 6A-C) and behavioral CR-bandwidth at 900 Hz (Ehret and Gerhardt 1980) are very similar. This suggests that the performance of the whole animal in a behavioral masking test seems to be deter-

Fig. 9. Mean neural CR-bandwidths (filled symbols) compared with mean behavioral CR-bands (open circles) measured at 900 Hz and 3,000 Hz (from Ehret and Gerhardt 1980). Neural means are based on 100 Hz bins for fibers with BEFs below 1,000 Hz and on 500 Hz bins for fibers with BEFs above 1,000 Hz. Triangles: from rate-intensity curves 1 dB above tone threshold; circles: from rate-intensity curves 10 dB above tone threshold; squares: from latency-intensity measurements 10 dB above tone threshold

mined by the CR-band filters in single fibers of the VIIIth nerve.

This result of our present study in the treefrog does not agree with similar measurements in cats. Pickles and Comis (1976) and Pickles (1979) report that the CR-bands of most auditory nerve fibers in the cat are smaller than the ones behaviorally measured (Watson 1963; Pickles 1975). On first view this indicates a loss of frequency resolution in the acoustic pathway of the cat, whereas the frequency resolution of the periphery is preserved in the treefrog. These differences between the two vertebrates are not easy to understand. Pickles and Comis (1976) used a criterion different from ours to estimate masked thresholds and by that CR-bandwidths of single fibers. They judged the masked threshold by ear, which turned out to be equal to a difference of about 10–15 spikes/s between stimulation by tone-noise compared to noise alone. The 20% difference in spike rates which we used to define the masked threshold is equal to a difference of 10–15 spikes in many fibers of the treefrog. Therefore the different criteria in the electrophysiological studies are probably not the source for the discrepancy.

One possible reason for the disagreement of behavioral and neural data in the cat is that the behavioral masked thresholds in the cat have been judged too high and as a result their CR-bands are too large. A comparison of different methods of auditory threshold determinations in the house mouse (Markl and Ehret 1973) showed large differences in threshold values derived from different methods of testing. Since the determination of absolute auditory capabilities in a behavioral test requires a) optimal attention of the animal, b) optimal sensory processing, and

c) optimal motor reaction (behavior) the results of a behavioral test may not reach the ultimate performance inferred from recording from a sufficient number of auditory nerve fibers. If the behavioral thresholds in the cat were not measured by a method approaching optimal conditions, which can only be decided in further experiments, then the difference between neural and behavioral results in the cat are of methodological origin. On the other hand, the behavioral tests in the treefrog used a highly adaptive natural reaction to the mating call which presumably has been optimized through evolutionary natural selection.

On the other hand, the differences in the data from cat and treefrog may have their origin in true differences of auditory signal processing. An assumption of this kind, however, is difficult to test, so all possible methodological reasons for the differences should first be ruled out before differences in mechanisms are proposed.

4. CR-Bands and Call Detection

By a CR-band analysis in the inner ear the green treefrog has an array of filter outputs at hand which represent an effective strategy for detection of biologically significant sounds in its natural environment such as the harmonics in its mating call in a fluctuating background noise. The auditory system has simply to compare the filter outputs and determine which of the outputs are higher than the average, or which show a temporal pattern, distinct from the average. The problem of call detection is reduced to a detection of energy differences or temporal differences in the bank of CR-band filters. One can predict the widths of the CR-bands which optimally match the analysis of the harmonic components in the species-specific mating call. The CR-bands should be sufficiently narrow that every harmonic falls into a different CR-band, and the bands should be wide enough so that small frequency and intensity modulations of the harmonics or of the background spectrum do not strongly influence the output of a CR-band and thus do not complicate the detection. The fundamental frequency of the harmonics in the green treefrog's mating call is about 300 Hz (Gerhardt 1974). Fibers with very small CR-bands of only a few Hz (some low frequency fibers, Fig. 6A-C), however, would not be suitable for harmonic call analysis despite their low susceptibility to masking. But the principle energy in the mating call falls into the frequency range of mid and high frequency fibers, where most filters have bandwidths of more than 100 Hz. By that an accurate discrimination of the appropriate harmonic structure can be realized.

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References

- Capranica RR (1976) Morphology and physiology of the auditory systems. In: Llinás R, Precht W (eds) Frog neurobiology. Springer, Berlin Heidelberg New York, pp 551-575
- Capranica RR (1977) Auditory processing of vocal signals in anurans. In: Taylor DH, Guttman SI (eds) The reproductive biology of Amphibians. Plenum Press, New York London, pp 337-355
- Ehret G (1975) Masked auditory thresholds, critical ratios, and scales of the basilar membrane of the house mouse (*Mus musculus*). *J Comp Physiol* 103:329-341
- Ehret G, Gerhardt HC (1980) Auditory masking and effects of noise on responses of the green treefrog (*Hyla cinerea*) to synthetic mating calls. *J Comp Physiol* 141:13-18
- Evans EF (1974) Auditory frequency selectivity and the cochlear nerve. In: Zwicker E, Terhardt E (eds) Facts and models in hearing. Springer, Berlin Heidelberg New York, pp 118-129
- Evans EF (1975) Cochlear nerve and cochlear nucleus. In: Keidel WD, Neff WD (eds) Handbook of sensory physiology, vol V/2. Springer, Berlin Heidelberg New York, pp 1-108
- Evans EF, Wilson JP (1973) The frequency selectivity of the cochlea. In: Möller AR (ed) Basic mechanisms in hearing. Academic Press, New York London, pp 519-551
- Evans EF, Rosenberg J, Wilson JP (1970) The effective bandwidth of cochlear nerve fibers. *J Physiol (London)* 207:62-63 P
- Fay RR (1974) Masking of tones by noise for the goldfish (*Carassius auratus*). *J Comp Physiol Psychol* 87:708-716
- Feng AS, Narins PM, Capranica RR (1975) Three populations of primary auditory fibers in the bullfrog (*Rana catesbeiana*): Their peripheral origins and frequency sensitivities. *J Comp Physiol* 100:221-229
- Fletcher H (1940) Auditory patterns. *Rev Mod Phys* 12:47-65
- Gerhardt HC (1974) The significance of some spectral features in mating call recognition in the green treefrog (*Hyla cinerea*). *J Exp Biol* 61:229-241
- Gerhardt HC (1976) Significance of two frequency bands in long distance vocal communication in the green treefrog. *Nature* 261:692-694
- Goldberg JM, Greenwood DD (1966) Response of the neurons of the dorsal and posteroventral cochlear nuclei of the cat to acoustic stimuli of long duration. *J Neurophysiol* 29:72-93
- Greenwood DD, Goldberg JM (1970) Response of neurons in the cochlear nuclei to variations in noise bandwidth and to tone-noise combinations. *J Acoust Soc Am* 47:1022-1040
- Kiang NYS, Watanabe T, Thomas EC, Clark LF (1965) Discharge patterns of single fibers in the cat's auditory nerve. *Res Monograph No 35*. M.I.T. Press, Cambridge
- Liff HJ, Goldstein MH (1970) Peripheral inhibition in auditory fibers in the frog. *J Acoust Soc Am* 47:1538-1547
- Markl H, Ehret G (1973) Die Hörschwelle der Maus (*Mus musculus*). Eine kritische Wertung der Methoden zur Bestimmung der Hörschwelle eines Säugetieres. *Z Tierpsychol* 33:274-286
- Moffat AJM, Capranica RR (1974) Sensory processing in the peripheral auditory system of treefrogs (*Hyla*). *J Acoust Soc Am* 55:480
- Möller J, Neuweiler G, Zöllner H (1978) Response characteristics of inferior colliculus neurons of the awake CF-FM bat *Rhinolophus ferrumequinum*. *J Comp Physiol* 125:217-225

- Patterson RD, Green DM (1978) Auditory masking. In: Carterette EC, Friedman MP (eds) Handbook of perception, vol IV. Academic Press, New York London, pp 337-361
- Pickles JO (1975) Normal critical bands in the cat. *Acta Otolaryngol* 80:245-254
- Pickles JO (1979) Psychophysical frequency resolution in the cat as determined by simultaneous masking and its relation to auditory nerve resolution. *J Acoust Soc Am* 66:1725-1732
- Pickles JO, Comis SD (1976) Auditory-nerve-fiber bandwidths and critical bandwidths in the cat. *J Acoust Soc Am* 60:1151-1156
- Rhode WS, Geisler CD, Kennedy DT (1978) Auditory nerve fiber responses to wide-band noise and tone combinations. *J Neurophysiol* 41:692-704
- Sachs MB, Kiang NYS (1968) Two-tone inhibition in auditory nerve fibers. *J Acoust Soc Am* 43:1120-1128
- Saunders JC, Denny RM, Bock GR (1978) Critical bands in the parakeet (*Melopsittacus undulatus*). *J Comp Physiol* 125:359-365
- Scharf B (1970) Critical bands. In: Tobias JV (ed) Foundations of modern auditory theory, vol 1. Academic Press, New York London, pp 159-202
- Smith RL (1979) Adaptation, saturation, and physiological masking in single auditory-nerve fibers. *J Acoust Soc Am* 65:166-178
- Watson CS (1963) Masking of tones by noise for the cat. *J Acoust Soc Am* 35:167-172
- Zwicker E, Feldtkeller R (1967) Das Ohr als Nachrichtenempfänger. Hirzel, Stuttgart