Behavioral Determination of Frequency Resolution in the Ear of the Cricket, *Teleogryllus oceanicus*

Günter Ehret, Anne J.M. Moffat, and Jürgen Tautz

Fakultät für Biologie, Universität Konstanz, Postfach 5560, D-7750 Konstanz, Federal Republic of Germany

Accepted May 3, 1982

Summary. 1. We used the flying phonotactic behavior of tethered female Australian field crickets, *Teleogryllus oceanicus*, to measure frequency filtering (determined from CR-bands, critical bands, and “effective” bandwidths) in the auditory system at frequencies of 4.5, 20, 40 and 70 kHz. Till now such measurements have been made only in vertebrates.

2. In CR-band determinations the spectrum level of the noise at the masked threshold increased monotonically with increasing tone level (Fig. 2). At 20, 40 and 70 kHz the regression lines had slopes very close to 1 indicating that, at least over the intensity range tested (5–20 dB above tone threshold), the masking process is linear. At 4.5 kHz, however, the slope of the regression line was only 0.56 showing a strong non-linearity in the masking process at this frequency. Such a non-linearity has not been found in vertebrates.

3. At 4.5 kHz the three measures of filter bandwidths, CR-band, critical band and “effective” bandwidth, were not significantly different from each other, whereas at 40 kHz the “effective” bandwidth was significantly smaller than CR-band and critical band.

4. The width of the CR-band filter around 4.5 kHz increases with tone intensity, an effect which has not been observed in vertebrates.

5. Both CR-bands and critical bands indicate that the cricket auditory system is sharply tuned around 4.5 kHz, may show some tuning at 40 kHz, and is completely untuned at 20 and 70 kHz.

6. These results are discussed with respect to frequency tuning at the single unit level in crickets.

Introduction

In vertebrate psychophysics auditory masking tests have proved to be a powerful tool for studying the frequency selectivity or resolution of the auditory system. The bandwidths of filters processing acoustic signals can be derived from thresholds for pure tones masked by either broad-band white noise or by band-passed noise of different bandwidths (Fletcher 1940; Greenwood 1961; Zwicker and Feldtkeller 1967; Scharf 1970; Fay 1974; Patterson 1974; Pickels 1975; Margolis and Small 1975; Ehret 1976; Saunders et al. 1978; Dooling and Searcy 1979). Filter bandwidths calculated from the ratio of tone and noise intensities at the masked threshold are called critical ratio bands (CR-bands), while those determined directly from the shape of masking functions are called critical bands. At least for man it has been shown that critical bands are basic units of sound perception. Sound energy within a critical band is perceived differently from that outside the band. Perceived sound quality changes with changes in the amount of sound energy falling in any of the array of critical bands which can be formed in the frequency range of hearing.

Although the physiological bases of critical bands are not yet understood, they depend on the fact that peripheral auditory nerve fibers are tuned (Evans 1975; Ehret and Capranica 1980). Thus CR-bands and critical bands determined in behavioral tests provide estimates of the acuity of tuning in the auditory system.

In this paper we attempt to answer the following questions: First, does the critical band concept apply to insects. The answer to this question has consequences for the formulation of the critical band theory itself. Second, if CR-bands and critical bands can be measured, what do they tell us about

Abbreviations: CR-bands critical ratio bands; *I* sound intensity; *SPL* sound pressure level

frequency filtering in the insect auditory system. Third, since natural environments are usually noisy, it is important to know how well an animal can detect and orient to communication signals in the presence of background noise. We selected female *Teleogryllus oceanicus* for this study because, when flying, they show a very reliable phonotactic response (Moiseff et al. 1978; Pollack and Hoy 1979, 1981; Pollack and Plourde 1982) and because their peripheral auditory system has been studied in some detail (Loftus-Hills et al. 1971; Patton et al. 1977; Hutchings and Lewis 1981).

Materials and Methods

Young adult female *Teleogryllus oceanicus*, suspended in a wind stream usually begin flying. When sounds are presented to the flying animals they make steering movements with their abdomen, the direction of the movement depending on the sound frequency (Moiseff et al. 1978). This is the reaction we used.

We tested 39 adult virgin female *T. oceanicus*, taken from a laboratory colony, between one and three weeks after the imaginal molt. A holder was glued to the pronotum and animals were suspended in a wind stream in a sound proof and anechoic (above 200 Hz) room. A video system allowed the animals to be monitored from outside the room. Sound stimuli were presented through two identical loudspeakers suspended independently of the animal and positioned 30 cm to the left and right of its long body axis. For frequencies between 2 and 10 kHz dynamic speakers (Dynaudio, D 28) with a frequency response flat within ± 3 dB were used. Frequencies from 10 to 100 kHz were presented through electrostatic speakers (Machmerth et al. 1975), which had flat ± 2 dB response characteristics. Sound pressure levels (SPLs) at the position of the animal were measured with a calibrated $\frac{1}{4}$ inch microphone (Brüel and Kjaer, 4135) and sound level meter (Brüel and Kjaer 2606, rms impulse, time constant 35 ms) and are given in dB re. 20 μ Pa. Noise levels are given as spectrum levels (dB/Hz).

Test stimuli were variable frequency tone pulses the temporal pattern of which matched that of the *T. oceanicus* calling song (Bentley and Hoy 1972). Tones were synthesized with a digital frequency synthesizer (Rockland 5100), shaped with additional electronic pulse formers, and the resulting pulse train attenuated (Hewlett-Packard, 350D) before being mixed with the noise in an electronic adder. The adder output was amplified (Exact, 170) and attenuated (Hewlett-Packard 350D) and then sent to one of the speakers. Continuous white noise from a noise generator (General Radio, 1390-B) was filtered (96 dB/octave initial slope) by two digital bandpass filters in series (Rockland 852 and Kemo VBF-8) and attenuated (Hewlett-Packard, 350D) before being added to the tone pulses. In the CR-band measurements the noise band was from 2–10 kHz for 4.5 kHz tone pulses and from 10–100 kHz for 20, 40 and 70 kHz tone pulses. In the critical band measurements noise bands of different widths were centered arithmetically around the tone frequency.

All thresholds were determined using a modified method of limits with a final step size of 5 dB. We first determined the animals' absolute thresholds for tones of different frequencies in the absence of noise. Animals responded to 4.5 kHz¹

with a fairly long latency but then sustained displacement of the abdomen towards the sound source. Switching the sound to the other speaker caused the animal to steer towards the new sound location. Tone intensity was decreased in 5 dB steps until the animal no longer "followed" changes in the location of the sound source and threshold was considered to be half way between the lowest intensity at which following occurred and the next lower intensity.

The response to 20, 40 and 70 kHz tone pulses was a short latency "twitch" away from the sound source followed by a return to the starting position. In this case the tone was switched off after the animal had responded and then, after 30 s, switched on again. For a response to be considered positive the animal had to respond to at least 3 of 5 stimulus presentations. Threshold was taken as between the lowest intensity at which the criterion was satisfied and the next lower intensity. Animals usually responded more consistently to high frequency tones from one side than from the other. This side preference was noted during the threshold determinations and in the masking tests stimuli were presented from only the "preferred" side.

Broad-band masking tests were done with tone pulses 5, 10 and 20 dB above tone threshold. Since continuous noise caused the animal to "twitch" away from the speaker (in fact, this response was used to determine noise thresholds), in the masking tests we first switched on the noise and allowed the animal to adapt to its effects. For 4.5 kHz tones we then added the tone pulses to the noise and after the animal responded we switched the entire signal (tone pulses + noise) to the other loudspeaker. Noise intensity was increased until the animal no longer followed changes in the stimulus location. The masked threshold was taken as being between the highest noise intensity at which a response still occurred and the next higher. For high frequency tones our procedure was to allow the animal to adapt to any effects of noise coming from its preferred speaker, then switch, with the noise being on continuously, the tone on and off. The noise intensity was increased until the animal no longer responded to at least 3 of 5 tone stimuli.

Masking tests with bands of noise of variable widths (critical band measurements) were also conducted, using a procedure very similar to that applied in mammals and birds. In a second set of animals we first determined absolute tone thresholds for 4.5 and 40 kHz and masked thresholds for broad-band noise (2–10 and 10–100 kHz) at a tone level of 10 dB above absolute tone threshold using the procedure just described. Keeping the tone intensity constant, we then determined the masked threshold for a narrower noise band centered around the tone frequency. Determinations were repeated with ever narrower noise bands (always centered around the tone frequency) until for at least two noise bands the spectrum levels at the masked thresholds were markedly above that for the broad-band noise. We thus obtained ethometric functions for each animal showing the dependence of the noise level at the masked threshold on the bandwidth of the noise for a constant tone level. Figure 1 shows two examples of such functions. They can be characterized by two lines, a monotonically decreasing line representing the decrease of noise levels at the masked threshold with increasing noise bandwidths, and one parallel to the abscissa representing the constant masked thresholds for rather wide noise bands. The point of intersection of the two lines is equal to the bandwidth of the filter which separates the noise spectrum into components which do not influence tone perception because they are outside the filter band and components which contribute to masking the tone in the center of the filter. The critical bandwidths at the two center frequencies (4.5 and 40 kHz) were determined for each animal from the intersection of the regression lines in plots similar to those shown in Fig. 1.

¹ In preliminary experiments we found that our *T. oceanicus* females showed the most reliable positive phonotactic steering response at 4.5 kHz

Fig. 1 A, B. Masking functions for individual animals at 4.5 kHz A and 40 kHz B. Noise spectrum levels at the masked thresholds are high for narrow noise bands and decrease with increasing noise bandwidth. For rather broad noise bandwidths a constant low level is reached. All points within ± 1.5 dB of the spectrum level for the broadest noise band were included for determining the horizontal line

Results

The mean absolute thresholds for the different tone frequencies and noise bands used are shown in Table 1; data are presented separately for the first and second group of experimental animals. Animals in both groups were most sensitive to 40 kHz, where the threshold was significantly lower than at the other frequencies tested ($P < 0.02$, rank-test, two-tailed). In the first group of animals the threshold at 4.5 kHz was significantly lower than at 20 or 70 kHz ($P < 0.05$ and $P < 0.02$ respectively). The thresholds for the two noise bands (expressed in spectrum level) were also significantly different ($P < 0.02$).

Figure 2 shows the relation between the tone level and the spectrum level of noise at the masked threshold for the different tone frequencies tested. In all cases the spectrum level at the masked threshold increased significantly ($P < 0.01$) with increasing tone level. The regression lines had slopes very close to 1 (0.93, 1.14, 1.14) for 20, 40 and 70 kHz tones and 0.56 at 4.5 kHz. A slope of 1 indicates linearity of the masking process i.e. to maintain masking any change in tone level (in the tested range) must be accompanied by an equal change in spectrum level of noise. This linearity obviously does not hold for the 4.5 kHz tone where a 10 dB change in tone level required only about

a 6 dB change in noise level to maintain masking. Masked thresholds measured in the second group of animals were not significantly different from those in the first group ($P > 0.1$).

From masked thresholds of tones in broadband noise one can calculate the bandwidths of the filters which filter out that part of the noise band which is effective in masking the tone in the center of the filter. In making this calculation it is assumed that a) at the masked threshold tone and effective noise energies are equal and b) the filter is linear. Under these assumptions, at the masked threshold the following equation holds:

$$I_{\text{tone}} = I_{n(\text{total})} \quad (1)$$

where

$$I_{n(\text{total})} = I_{n(\text{spectral})} \cdot \text{effective bandwidth} \quad (2)$$

and therefore

$$I_{\text{tone}} / I_{n(\text{spectral})} = \text{effective bandwidth (Hz)} \quad (3)$$

I_{tone} = tone intensity, $I_{n(\text{total})}$ = total noise intensity, $I_{n(\text{spectral})}$ = spectral intensity of the noise, all

at the masked threshold.

The effective noise bandwidth calculated from the tone intensity and the spectral intensity of the noise at the masked threshold is equal, under the assumptions made, to the effective filter bandwidth. The ratio $I_{\text{tone}} / I_{n(\text{spectral})}$ is called the critical ratio and the bandwidth of the filter the critical ratio band (CR-band). In addition to the intensity ratio [Eq. (3)] the difference between the tone and noise level can also be used to calculate the effective filter bandwidth:

$$SPL_{\text{tone}} - SPL_{n(\text{spectral})} = \text{effective bandwidth (dB)}. \quad (4)$$

Equations (3) and (4) both express the same relationship and can be transformed into each other (e.g. Zwicker and Feldtkeller 1967).

Table 1. Mean absolute thresholds for tones and noise bands tested, with standard deviations (s.d.), ranges of values and numbers (N) of animals tested. Tone thresholds are in dB SPL, noise thresholds in dB spectrum level (i.e. dB/Hz)

	First group				Second group			
	$\bar{x}$	s.d.	range	N	$\bar{x}$	s.d.	range	N
4.5 kHz	51.9	3.5	45–58	14	52.5	4.4	48–65	11
20 kHz	55.8	5.0	49–63	9	—	—	—	—
40 kHz	48.2	5.0	40–58	12	50.8	5.1	43–58	10
70 kHz	57.0	3.7	52–62	10	—	—	—	—
2–10 kHz	25.4	3.5	21–30	14	—	—	—	—
10–100 kHz	13.8	5.8	5–20	5	—	—	—	—

Fig. 2A–D. Dependence of the spectrum level of noise on tone level at the masked threshold for tones of 4.5 A, 20 B, 40 C and 70 D kHz. Plotted are the mean values and ranges. In D only values at 5 and 10 dB above threshold are plotted since we could test only the 5 most sensitive animals at 20 dB above threshold (the intensities required for the others were above the upper limit of our system). Correlation coefficients are all significant ($P < 0.01$). Triangles indicate thresholds for 2–10 kHz noise A and for 10–100 kHz noise C

Table 2. Mean $\pm$ standard deviation of bandwidths in dB and mean bandwidths in kHz for critical ratio bands (CR-bands), “effective” bandwidths and critical bands ($\bar{x}_i$ =means from the individual animals, $\bar{x}_m$ =from mean ethometric functions, see Fig. 3). CR-band data at 70 kHz 20 dB above tone threshold could be obtained only from 5 of 10 animals. th.=threshold

		CR-bands				“Effective” bandwidth	Critical bands	
		First group			2nd group		$\bar{x}_i$	$\bar{x}_m$
		th. + 5 dB	th. + 10 dB	th. + 20 dB	th. + 10 dB			
4.5 kHz	dB	25.9 ± 6.8	27.6 ± 5.7	32.4 ± 6.7	29.1 ± 4.0	27.3 ± 3.5	30.4 ± 1.2	31.5
	kHz	0.389	0.581	1.72	0.813	0.537	1.1 ± 0.3	1.4
20 kHz	dB	56.9 ± 4.4	57.8 ± 4.2	58.0 ± 3.8	—	—	—	—
	kHz	488	599	631	—	—	—	—
40 kHz	dB	46.9 ± 4.7	44.8 ± 4.4	44.6 ± 6.0	44.5 ± 4.1	35.5 ± 5.8	46.1 ± 1.1	47.3
	kHz	49.2	29.9	28.7	28.2	3.55	40.4 ± 12.6	53.7
70 kHz	dB	58.9 ± 5.6	58.2 ± 3.8	(59.4 ± 3)	—	—	—	—
	kHz	776	660	(871)	—	—	—	—

Mean CR-bands at all frequencies and intensities tested are given in Table 2. The smallest filter bandwidths were measured for the 4.5 kHz tone. At this frequency CR-bandwidths varied significantly with intensity, ranging from 389 Hz at 5 dB above threshold to 1720 Hz at 20 dB above threshold ($P < 0.05$). For 20, 40 and 70 kHz tones the CR-bandwidths were intensity independent ($P > 0.1$). At 20 and 70 kHz the calculated filter bandwidths (average 573 and 718 kHz) were much wider than the actual noise band used in the masking test (90 kHz). At 40 kHz the mean CR-bandwidth was 36 kHz. There was no significant difference between CR-bands measured in the two groups of animals ($P > 0.05$).

Under the assumption of a linear filter mechanism we can use the absolute thresholds for tones

and for the two noise bands to calculate the “effective” filter bandwidths, which approximate the bandwidths at the 3-dB points. This is done by substituting the tone and noise intensities at the absolute threshold into Eqs. (3) and (4). If the lowest tone threshold between 2 and 10 kHz is close to 4.5 kHz and that between 10 and 100 kHz close to 40 kHz (reasonable assumptions based on Moiseff et al. 1978), then we can calculate the “effective” bandwidths of the filters with 4.5 and 40 kHz center frequencies. These values are also shown in Table 2. CR-bandwidths agree very well with the “effective” bandwidths at 4.5 kHz; at 40 kHz, however, the “effective” bandwidth is much smaller.

CR-bands and “effective” bandwidths are indirect measures of frequency resolution since they

Fig. 3 A, B. Mean masking functions for tones at 4.5 kHz A and 40 kHz B. Mean spectrum levels at the masked thresholds are high for narrow noise bands and decrease with increasing noise bandwidth until they reach a constant level for broad-band noise. Correlation coefficients of the decreasing lines are significant at $P < 0.001$. All points within ± 1.5 dB of the spectrum level for the broadest noise band were included in determining the horizontal line. The point of intersection of the two lines defines the critical bandwidth (CB)

are derived from intensity ratios. However, frequency resolution can also be determined directly by measuring critical bands as described in Materials and Methods. The mean critical bandwidths derived from individual masking functions at 4.5 and 40 kHz are listed in Table 2 ($\bar{x}_i$). One can also calculate mean masking functions (Fig. 3) and determine critical bandwidths from the intersection of the regression lines; the results of these calculations are also given in Table 2 ($\bar{x}_m$). The critical bandwidths determined from mean masking functions (Fig. 3) have values very similar to those obtained from the means of the individual masking functions (Fig. 1). The slopes of the decreasing regression lines in Fig. 3 have values of -4.25 dB/octave (Fig. 3 A) and of -4.68 dB/octave (Fig. 3 B).

The mean critical bandwidths derived from individual masking functions can be compared statistically with the mean widths of the CR-bands (measured 10 dB above tone threshold in the same animals). These measures are not significantly different at either 4.5 or 40 kHz, although critical bands expressed in kHz are wider by a factor of 1.32 or 1.43 than the CR-bands. The critical band at 4.5 kHz is not significantly different from the "effective" bandwidth ($P > 0.1$), while at 40 kHz the difference is significant ($P < 0.01$).

Discussion

A. Absolute Thresholds

The threshold curve for flight phonotaxis given by Moiseff et al. (1978) shows two sensitivity peaks, one around 5 kHz, which corresponds to the carrier frequency of the conspecific calling song (range 4.5–5.4 kHz; Hill et al. 1972) and a second rather broad peak between 30 and 70 kHz. Animals showed different responses in the two ranges, steering toward the low frequency tones (positive pho-

notaxis) but away from the high frequency tones (negative phonotaxis). It is unfortunately rather difficult to compare directly thresholds of our animals with those of Moiseff et al. (1978) since they measured peak intensity and we measured average intensity (rms) over 35 ms (necessary in our case, so that tone and noise intensities could be compared). Differences between the two readings are approximately 9 dB. Taking this into account, our animals were in general somewhat less sensitive at low frequencies but more sensitive at higher frequencies. While part of this difference may be attributed to intercolony variability some of the difference at high frequencies may be due to the fact that we used as a response a brief twitch away from the loudspeaker while Moiseff et al. (1978) used a sustained deflection of the abdomen.

Animals showed negative phonotactic responses to both continuous noise bands (2–10 and 10–100 kHz). This is surprising inasmuch as the animals respond to pure tones in the range of 3–10 kHz with a positive phonotaxis (Moiseff et al. 1978; Oldfield 1980). This suggests that they treat continuous broad-band noise differently (negatively) than tone pulses even if the noise band is within the range where tone pulses cause positive phonotaxis.

The noise thresholds expressed in spectrum level (dB/Hz) are very much lower than tone thresholds (Table 1) which suggests that the cricket auditory system (like the vertebrate auditory system) sums energy over a certain frequency band to reach noise threshold. While the noise thresholds for the two bands were significantly ($P < 0.01$) different from each other when expressed in spectrum level, this was not the case when the total SPL of the noise bands was considered (thresholds 64.4 dB SPL for 2–10 kHz and 63.3 dB SPL for 10–100 kHz; $P > 0.1$). Thus it seems that to elicit negative phonotaxis there must be about 64 dB SPL of total noise energy present; the frequency

band covered by the noise, however, is relatively unimportant.

The behavioral tone thresholds we found at 4.5 kHz are in good agreement with mean neural thresholds (at this frequency) of both primary units (Hutchings and Lewis 1981) and neurones in the prothoracic ganglion (Loftus-Hills et al. 1971; Casaday and Hoy 1977) of laboratory raised animals. Hill and Boyan (1977) and Ball and Hill (1978) found, however, that in wild caught animals neural thresholds can be 10–15 dB lower than in laboratory raised crickets. Hutchings and Lewis (1981) found rather broadly tuned neurons responding best at 20 kHz and having thresholds close to those we measured behaviorally. Although they could not measure above 40 kHz their data suggest that some broadly tuned units may respond best near 40 kHz with thresholds in the range of our behavioral ones.

B. Masking

The determinations of masked thresholds showed that, at the noise intensities used, the negative phonotactic reaction to noise habituates and that dishabituation by sufficiently intense tone stimuli occurs leading either to positive (4.5 kHz) or negative (20, 40 and 70 kHz) phonotaxis. The signal-to-noise ratio was the decisive parameter for eliciting a tone response and the frequency of the tone determined the response direction.

The spectrum level of the noise at the masked threshold increased monotonically with tone level (Fig. 2). At 20, 40 and 70 kHz an increase in tone level required an equal increase in noise level to maintain masking, indicating that the masking mechanism is linear at these frequencies at least between 5 and 20 dB above tone threshold. However, a nonlinearity is evident at absolute threshold since the noise threshold is higher than the noise level necessary to mask a 40 kHz tone at 5 dB above tone threshold. In other words, a noise band 7.5 dB below absolute noise threshold masks a tone 5 dB above threshold. If linearity extended to the absolute threshold the noise threshold for a band centered around 40 kHz should fall on the regression line at the point of the tone threshold. A better agreement between predicted and measured noise threshold is found at 4.5 kHz. At this frequency, however, the slope of the regression line is only 0.56 which means that any change in tone level requires only about half as much change in noise level to maintain masking. Apparently the steering response of *T. oceanicus* is more susceptible to disturbing background noise in the fre-

quency range of the conspecific calling song than in the high frequency range which is used, for example, by echolocating bats to detect flying insects. This makes biological sense in that we would expect an "escape" response which may preserve an animal's life and mating chances to be less susceptible to interference from background noise than a "mating" response.

A nonlinearity near threshold has been found in masking experiments in man (Zwicker and Feldtkeller 1967; Scharf 1970; Weber 1977). At moderate intensities above threshold, however, masking by broad-band noise is linear (slope=1) for all vertebrates tested so far, including fish, birds, mammals and man (e.g. Scharf 1970; Fay 1974; Ehret 1975; Dooling and Saunders 1975). None of them show the sort of nonlinearity we found at 4.5 kHz in *T. oceanicus*. This nonlinearity does not occur when 20, 40 and 70 kHz tones are masked by broad-band noise which suggests that there may be two different mechanisms for processing tones in noise in the nervous system of *T. oceanicus*, one covering the frequency range of positive phonotaxis, and the other the range of negative phonotactic behavior.

C. CR-Bands, Critical Bands, Frequency Filtering and Resolution

When calculating CR-bands from masked thresholds we made the assumptions that tone and noise energies at the masked threshold are equal and that the filter which filters out that part of the broad-band noise which is then effective in masking the tone is linear. The nonlinearity found at 4.5 kHz suggests a changing energy ratio of tone and noise with intensity or a nonlinear filter or both. There is an explanation for this nonlinearity which takes into account what we know about frequency tuning in the peripheral auditory system of other animals. It has been shown that masking of tone responses in auditory nerve fibers in the house mouse is nonlinear with intensity (Ehret and Moffat, to be published), i.e. the farther away from the tone threshold masking tests are done the broader are the calculated CR-band filters. This nonlinearity in masking may be explained on the basis of tuning curve shapes. Since the tuning curve of an auditory nerve fiber broadens with intensity at higher tone intensities relatively more noise energy falls within the bandwidth of the tuning curve and thus contributes to masking. In vertebrates the central nervous system must compensate for this nonlinearity in masking based on the tuning curve shape inasmuch as the behavioral response

is linear. This compensation, which may be related to higher frequency selectivity in the central nervous system seems not to be present in *T. oceanicus*. A comparison of primary auditory fiber tuning in *T. oceanicus* (Hutchings and Lewis 1981) with the tuning of a descending auditory interneuron in a closely related species (*T. commodus*; Boyan 1979) shows that the frequency tuning is not altered, i.e. V-shaped tuning curves, which broaden with intensity, are also found in neurons which may be close to the generation of the motor response. In fact, the motor response itself (the phonotaxis) shows a V-shaped frequency tuning characteristic (Hill 1974).

The sharpness of tuning of primary auditory neurons in *T. oceanicus* can be estimated from the tuning curves shown by Hutchings and Lewis (1981). The tuning curve bandwidth of unit To107PN1 (best frequency at 4.8 kHz) is about 400 Hz 5 dB above threshold and 1,200 Hz 20 dB above threshold. Comparable bandwidths have also been found in other crickets (e.g. Hill and Boyan 1977; Esch et al. 1980). These values agree well with the CR-bands measured in the present study (Table 2). It seems that CR-bands and "effective" bandwidths at 4.5 kHz center frequency in *T. oceanicus* are a direct measure of peripheral frequency resolution while in vertebrates a further step of central linearization is involved, making behaviorally measured filters intensity independent.

The extremely wide CR-bands at 20 and 70 kHz indicate a total lack of tuning around these frequencies. This explains why CR-bandwidths are constant with intensity. When the range over which noise energy can be effective in masking is obviously broader than the noise band used for masking, the intensity ratio of tone and noise at the masked threshold should remain constant with overall intensity, and that is what we observed. There is physiological evidence for frequency tuning at a center frequency of 20 kHz (Hutchings and Lewis 1981). The initial tuning, however, is broader than at 4.5 kHz and the tuning curves widen very quickly with increasing intensity, but do not reach the exceptionally broad values measured in the present study (Table 2). Even if we look at the range of CR-bandwidths among individual animals almost all individual CR-bands at 20 and 70 kHz are extremely wide indicating a lack of tuning. This suggests that the untuned neurons responding in the high frequency range, which were also found by Hutchings and Lewis (1981), play an important role in initiating the behavioral response.

Mean "effective" bandwidths and CR-bands at 40 kHz center frequency indicate frequency tuning and resolution (Table 2). The range of values of CR-bands (38–60 dB) shows rather sharp tuning for some individuals and no frequency resolution for others. This is a puzzling result. Direct measurements of filter bandwidths in the critical band tests show very much less interindividual variability with frequency tuning – although very broad – present in all animals. Physiological correlates for these results do not exist yet, but we may predict units in the auditory periphery of *T. oceanicus* being broadly tuned to 40 kHz.

We found that critical bands expressed in Hz are somewhat (1.3–1.4 times) wider than CR-bands (Table 2); in vertebrates values between 1 and 2.5 have been reported (e.g. Scharf 1970; Sea-ton and Trahiotis 1975; Margolis and Small 1975; Ehret 1976; Saunders et al. 1978). Bilger (1976) discussed the problem of differences in widths between CR-bands and critical bands and argued that the critical ratio experiment is "to discriminate an intensive difference between a critical bandwidth of noise alone and a critical bandwidth of noise plus [tone] signal." Following this reasoning the assumption that at the masked threshold tone and noise energies in the critical band are equal has to be modified. Equality occurs only if the intensity difference limen (Weber fraction $\Delta I/I$) is equal to 1. In general the critical band, the critical ratio band and the intensity difference limens are related to each other by the following function (Bilger 1976; Dooling and Searcy 1979):

$$\text{CR-band (Hz)} = \text{critical band} \cdot \Delta I/I. \quad (5)$$

If Eq. 5, derived from vertebrate psychophysics, also holds for *T. oceanicus* it can be used to predict the intensity difference limens expressed as Weber fractions at 4.5 and 40 kHz. The values for $\Delta I/I$ calculated from averaged CR-bands and mean critical bands derived from individual critical bands are 0.76 at 4.5 kHz and 0.7 at 40 kHz.

Critical bands and CR-bands at 4.5 kHz indicate sharp frequency tuning or good frequency resolution in the auditory system at this frequency. Some frequency resolution at 40 kHz seems to be present. There is much discussion about the actual shape of critical band filters in vertebrates (see e.g. Patterson 1974, 1976; Margolis and Small 1975). While we also do not know the shape in *T. oceanicus* we can eliminate a rectangular filter since the absolute values of the slopes of the regression lines in Fig. 3 (4.25 and 4.68 dB/octave) are larger than the 3 dB/octave required by a rectangular filter.

In conclusion, we have shown that auditory

masking can be investigated behaviorally in the cricket *Teleogryllus oceanicus* and useful measures for estimating peripheral frequency tuning and resolution are obtained. In principle, the critical band concept can be extended to invertebrates.

Acknowledgements. We wish to thank Dr. R. Hustert for providing the crickets and Dr. H. Markl for comments on the manuscript. Supported by the Deutsche Forschungsgemeinschaft, Eh 53/5/7.

References

- Ball EE, Hill KG (1978) Functional development of the auditory system of the cricket, *Teleogryllus commodus*. *J Comp Physiol* 127:131–138
- Bentley DR, Hoy RR (1972) Genetic control of the neuronal network generating cricket (*Teleogryllus*, *Gryllus*) song patterns. *Anim Behav* 20:478–492
- Bilger RC (1976) A revised critical band hypothesis. In: Hirsh SK, Eldredge IJ, Hirsh IJ, Silverman SR (eds) *Hearing and Davis: Essays honoring Hallowell Davis*. Washington University Press, Saint Louis, pp 191–198
- Boyan GS (1979) Directional responses to sound in the central nervous system of the cricket *Teleogryllus commodus* (Orthoptera: Gryllidae) II. A descending interneuron. *J Comp Physiol* 130:151–159
- Casaday GB, Hoy RR (1977) Auditory interneurons in the cricket *Teleogryllus oceanicus*: Physiological and anatomical properties. *J Comp Physiol* 121:1–13
- Dooling RJ, Saunders JC (1975) Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations. *J Comp Physiol Psychol* 88:1–20
- Dooling RJ, Searcy MH (1979) The relation among critical ratios, critical bands, and intensity difference limens in the parakeet (*Melopsittacus undulatus*). *Bull Psychon Soc* 13:300–302
- 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 (1976) Critical bands and filter characteristics in the ear of the house mouse (*Mus musculus*). *Biol Cybern* 24:35–42
- Ehret G, Capranica RR (1980) Masking patterns and filter characteristics of auditory nerve fibers in the green treefrog (*Hyla cinerea*). *J Comp Physiol* 141:1–12
- Esch H, Huber F, Wohlers DW (1980) Primary auditory neurons in crickets: Physiology and central projections. *J Comp Physiol* 137:27–38
- Evans EF (1975) Cochlear nerve and cochlear nucleus. In: Keidel WD, Neff WD (eds) *Auditory system*. Springer, Berlin Heidelberg New York (Handbook of sensory physiology, vol V/2, pp 1–108)
- Fay RR (1974) Masking of tones by noise for the goldfish (*Carassius auratus*). *J Comp Physiol Psychol* 87:708–716
- Fletcher H (1940) Auditory patterns. *Rev Mod Phys* 12:47–65
- Greenwood DD (1961) Auditory masking and the critical band. *J Acoust Soc Am* 33:484–502
- Hill KG (1974) Carrier frequency as a factor in phonotactic behaviour of female crickets (*Teleogryllus commodus*). *J Comp Physiol* 93:7–18
- Hill KG, Boyan GS (1977) Sensitivity to frequency and direction of sound in the auditory system of crickets (Gryllidae). *J Comp Physiol* 121:79–97
- Hill KG, Loftus-Hills JJ, Gartside DF (1972) Pre-mating isolation between the Australian field crickets *Teleogryllus commodus* and *T. oceanicus* (Orthoptera: Gryllidae). *Aust J Zool* 20:153–163
- Hutchings M, Lewis B (1981) Response properties of primary auditory fibers in the cricket *Teleogryllus oceanicus* (Le Guillon). *J Comp Physiol* 143:129–134
- Loftus-Hills JJ, Littlejohn MJ, Hill KG (1971) Auditory sensitivity of the crickets *Teleogryllus commodus* and *T. oceanicus*. *Nature* 233:184–185
- Machmerth H, Theiss D, Schnitzler HU (1975) Konstruktion eines Luftschallgebers mit konstantem Frequenzgang im Bereich von 15 kHz–130 kHz. *Acustica* 34:81–85
- Margolis RH, Small AM (1975) The measurement of critical masking bands. *J Speech Hear Res* 18:571–587
- Moiseff A, Pollack GS, Hoy RR (1978) Steering response of crickets to sound and ultrasound: Mate attraction and predator avoidance. *Proc Natl Acad Sci USA* 75:4052–4056
- Oldfield BP (1980) Accuracy of orientation of female crickets *Teleogryllus oceanicus* (Gryllidae): Dependence on song spectrum. *J Comp Physiol* 141:93–99
- Paton JA, Capranica RR, Dragsten PR, Webb WW (1977) Physical basis for auditory frequency analysis in field crickets (Gryllidae). *J Comp Physiol* 119:221–240
- Patterson RD (1974) Auditory filter shape. *J Acoust Soc Am* 55:802–809
- Patterson RD (1976) Auditory filter shapes derived with noise stimuli. *J Acoust Soc Am* 59:640–654
- Pickels JO (1975) Normal critical bands in the cat. *Acta Otolaryngol* 80:245–254
- Pollack GS, Hoy RR (1979) Temporal patterns as a cue for species-specific calling song recognition in crickets. *Science* 204:429–432
- Pollack GS, Hoy RR (1981) Phonotaxis in flying crickets: Neural correlates. *J Insect Physiol* 27:41–45
- Pollack GS, Plourde N (1982) Directionality of acoustic orientation in flying crickets. *J Comp Physiol* 146:207–215
- Saunders JC, Denny RM, Bock GR (1978) Critical bands in the parakeet (*Melopsittacus undulatus*). *J Comp Physiol Psychol* 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 159–208
- Seaton WH, Trahiotis C (1975) Comparison of critical ratios and critical bands in the monaural chinchilla. *J Acoust Soc Am* 57:193–199
- Weber DL (1977) Growth of masking and the auditory filter. *J Acoust Soc Am* 62:424–429
- Zwicker E, Feldtkeller R (1967) *Das Ohr als Nachrichtenempfänger*. Hirzel, Stuttgart