

Physiological Aspects of Sound Communication in Crickets (*Gryllus campestris* L.)

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Summary. The ability of the cricket ear to code different sound stimulus parameters has been investigated and compared with the song parameters of the natural cricket songs.

1. The threshold curve of the whole tympanal nerve shows an optimum near 4 and 14 kHz (Fig. 2) for male and female crickets.

2. Near 2 kHz sound as well as vibration stimuli are answered by the same type of unit (Figs. 3, 4). In this range a strict division between the function of the sound and vibration reception organs is not possible.

3. Sound stimuli near 4 kHz are answered by numerous spikes of mostly small amplitudes (Figs. 2A, 5B). On the other hand, 14-kHz stimuli are answered most frequently by only one unit (Figs. 5B, 6A and B), though a maximum of 3 units has been recorded. The coding features of this 14-kHz (HF) unit have been analysed (Figs. 6, 7, 8, 9).

4. The anatomical facts, the simultaneous sound stimulus experiments and the ablations of the tympanal membranes indicate that the cricket ear is able to discriminate pitched sounds near 4 and 14 kHz.

5. Both, the spectrograms of the calling and rivalry songs have a main peak near 4 kHz and a secondary peak near 14 kHz (Fig. 10). The dominant components of the courtship song show a maximum only near 14 kHz (Fig. 11) and ultrasonic components up to 100 kHz.

6. The absolute sound level has been measured for the three cricket songs. From this, the theoretical range of the cricket songs has been calculated.

7. The 4-kHz optimum of the threshold curve matches the main peak of the sound frequency spectrogram for the calling and rivalry songs (Fig. 12). The 14-kHz optimum of the threshold curve matches the main peak of the courtship song spectrogram as well as the secondary peak of the calling and rivalry songs (Fig. 12).

Zusammenfassung. Die Befähigung des Grillenohres zur Kodierung verschiedener Schallreizparameter wird untersucht und mit den Gesangsparametern der natürlichen Grillenlaute verglichen.

1. Die Hörschwellenkurve des Gesamthörnervs zeigt bei männlichen und weiblichen Tieren je ein Optimum um 4 und um 14 kHz (Abb. 2).

2. Im Bereich von 2 kHz werden sowohl Schall- als auch Vibrationsreize durch die gleiche Einheit beantwortet (Abb. 3, 4). In diesem Bereich ist daher keine strenge Unterteilung zwischen der Funktion von schall- und vibrationsaufnehmenden Organen möglich.

3. Schallreize um 4 kHz werden durch zahlreiche Einheiten mit Spikes kleiner Amplitude beantwortet (Abb. 2A, 5B). 14-kHz Reize hingegen, werden meist durch

eine Einheit (maximal durch 3 Einheiten) mit Spikes größerer Amplitude beantwortet (Abb. 5B, 6A und B). Die Kodierungseigenschaften dieser 14-kHz (HF) Einheit werden untersucht (Abb. 6—9).

4. Die anatomischen Verhältnisse, die Simultanbeschallungen und die Ausschaltexperimente geben wichtige Hinweise für die Fähigkeit des Grillenohres, Frequenzen von 4 und 14 kHz zu unterscheiden.

5. Die Spektrogramme des Lock- und Rivalengesanges besitzen je ein Hauptmaximum um 4 kHz und ein Nebenmaximum um 14 kHz (Abb. 10). Bei den Hauptkomponenten des Werbegesanges treten nur ein Maximum bei 14 kHz (Abb. 11) und Ultraschallanteile bis mindestens 100 kHz auf.

6. Der absolute Schallpegel der drei Grillengesänge wird gemessen. Hieraus errechnet sich ihre theoretische Reichweite.

7. Zwischen dem 4-kHz Optimum der Hörschwellenkurve und dem Hauptmaximum des Tonfrequenzspektrogrammes von Lock- und Rivalengesang wird eine gute Übereinstimmung festgestellt (Abb. 12). Das 14-kHz Optimum der Hörschwellenkurve stimmt mit dem Maximum des Werbegesang-Spektrogrammes, und mit den Nebenmaxima von Lock- und Rivalengesang überein (Abb. 12).

A. Introduction

Since Pumphrey and Rawdon-Smith (1939) had established their "new theory" of hearing in insects it had been widely accepted that the auditory system of insects only processes changes of the sound amplitude. Recently, though, the question has been raised whether the insect auditory system can process sound frequency (pitch). With the studies of Katsuki and Suga (1958, 1960), of Horridge (1960, 1961), of Popov (1965) and of Michelsen (1966), the existence of a pitch discrimination in the ear of some insects has been demonstrated. Recently Michelsen (1971), especially, showed that the ability of the tympanal organ of the locust *Schistocerca gregaria* to discriminate sound frequencies is based upon the physical properties of the ear.

Though, no direct evidence has been presented for the existence of pitch discrimination in the hearing organ of crickets, indirect evidence has come from studies of central neurons with different frequency sensitivities (Popov, 1969, 1971). According to Nocke (1970; see also Worden and Galambos, 1972), Popov (1971) and Zaretsky (1972c), the hearing threshold curves of *Gryllus campestris* L., *Acheta domesticus* and *Scapsipedus marginatus* have two optima, one each near 4 and 14 kHz respectively. In *Teleogryllus commodus* and *Teleogryllus oceanicus*, the threshold curves also have optima near 4 kHz (Loftus-Hills, *et al.*, 1971); however, the thresholds have only been measured up to 10 kHz. It is therefore not known if a second optimum near 14 kHz also exists in these crickets.

It is the purpose of this paper to analyse the possibility of pitch discrimination in the cricket ear by comparing the response of the cricket ear to sounds of different pitch with the sound frequency components of the cricket songs, and to discuss their possible biological significance.

B. Material and Methods

Test Animals and Operations. The experimental animals were adult male and female field crickets *Gryllus campestris* L. of age not less than 10 days beyond the final moult.

For the recordings from the tympanal nerve the trunk with the forelegs was glued to a cork holder. The femur of the foreleg was glued to the holder, and the tibia was connected to the holder by a steel needle in order to exclude a vibration excitation by the sound stimulus and to avoid active movements of the preparation. The large tympanum was at about a 40° angle relative to the direction of the sound wave.

The front side of the middle-to-distal part of the femur was opened, and the main leg nerve was cut distal to *n10* (Fig. 1). The tympanal nerve was then exposed by partially removing the muscles. The tympanal nerve was freed from the main leg trachea with a glass needle and then cut immediately distal to the tracheal branch *t7* (Fig. 1). Thus, efferent commands were eliminated. Also, no pull on the receptors of the hearing organ was exerted when the tympanal nerve was lifted out of the haemolymph with the hook electrode. The side branch *n14* of the tympanal nerve (Fig. 1) was always cut. During all operations on the femur the main leg trachea remained undamaged.

To remove both tympani, I detached them from the cuticle on the periphery of the tympanum. With the small tympanum (Tym in Fig. 1) this operation can easily be performed. On the large tympanum, however, damage cannot be avoided to the posterior trachea which rests directly upon the tympanum (Schwabe, 1906).

Stimulation by Vibration and Sound. Sine waves from an audio oscillator (General Radio 1310A) were fed to the loudspeakers (Lansing 075, Le 20 and a peerless bass loudspeaker) through a modulator, an attenuator (Hatfield) and a 30-Watt-power amplifier. Another sound generator with a built-in amplifier (Philips GM 2308) and a loudspeaker (Lansing 075) were used for the simultaneous sound stimulation of the ear.

The loudspeakers were installed in the closed end of a wooden box lined with rockwool. The preparation was mounted on a stand in the opposite open end of the box, 1.3 m away from the loudspeakers. During the recordings, only the recording electrode projected into the sound field. The experiments were performed in a sound-isolated room, where the background noise level in the frequency range from 0.1 to 20 kHz is below 20 dB, and where the ambient temperature amounts to $24 \pm 2^\circ \text{C}$. In this set-up a good approximation to a free sound field is obtained in the frequency range 1–40 kHz (see Michelsen, 1971). It should be emphasized, however, that the sound field is somewhat disturbed below 1 kHz so the sound levels indicated for low frequencies are only approximate values.

All sound measurements were carried out with a 1/3-octave analyser (Brüel & Kjaer 2112) and the Brüel & Kjaer condenser microphones 4131 and 4135. In the following study, the sound pressure level is normally given in dB root mean square relative to $2 \cdot 10^{-5} \text{ N/m}^2$.

The tympanal nerve also picks up fibres of the subgenual organ (Schwabe, 1906). In order to exclude a stimulation of this organ, vibrations on the preparation stand and the electrode holder were measured with an accelerometer (Brüel & Kjaer 4312 and 4344). The amount of vibration was also tested during sound stimulation. In all cases, it was far below the vibration threshold of the subgenual organ (Dambach, 1972).

The vibrations used as stimuli in the experiments were produced by a shaker (Brüel & Kjaer minishaker 4810). With the acceleration values employed very little sound was emitted by the vibration platform.

Recording Technique. The recordings from the tympanal nerve were partly carried out with PVC-suction electrodes with a tip opening diameter near $35\ \mu\text{m}$. The exposed nerve was covered with saline. I also used a hook electrode ($80\ \mu\text{m}$ silver wire) for the determination of the hearing threshold and especially for analysing single units in the tympanal nerve, since this gives a better signal to noise ratio. In this type of recording, the tympanal nerve was surrounded by Vaseline, the viscosity of which was reduced with a few drops of paraffin oil.

The signals were preamplified in the usual way, displayed on an oscilloscope and filmed or photographed (for additional specifications on material and methods see also Nocke, 1971).

The threshold was determined with sound pulses of 60 ms duration; the rise and decay times of the sound pulses were 5 ms.

A constant sensitivity of the preparation was assured by repeated threshold determination for several test frequencies. For the majority of the threshold determinations the "semistatistical method" first described by Michelsen (1971) was used. Comparable results were obtained with the "headphone method" (Autrum, 1941).

Determination of the Sound Frequency Spectrograms. The cricket songs were picked up by a $1/4''$ -microphone (Brüel & Kjaer 4135) which was attached at a 30° angle to a vertical stand. After amplification (Brüel & Kjaer 2606) the songs were recorded on a multichannel tape recorder (Consolidated Electro Dynamics VR 3300) at $60''$ per second. For the analysis these recordings were played back at half-speed and fed through a wave analyser (Rhode & Schwartz FTA-BN 48302) to an oscilloscope and filmed.

For the Fourier analysis the cricket songs were amplified and sent directly to an oscilloscope and registered by a 35-mm camera. The oscillations of the cricket sounds were then digitized ("Animat" by Wandel & Goldermann) and subsequently processed by the computing center of the Technische Hochschule, Aachen (Control Data 6400-scope 3.3).

The absolute sound pressure level of the cricket songs was determined by measuring the amplified microphone voltages with an oscilloscope. A pistonphone (Brüel & Kjaer 4220) was used for the calibration of the recording apparatus.

C. Results

1. Anatomical Position of the Tympanal Nerve

To avoid influencing the biophysics of the tympanal organ the recordings from the tympanal nerve had to be made at some distance from the cricket ear. The selection of a suitable recording region was therefore preceded by an analysis of the anatomical position of the tympanal nerve between the hearing organ and the prothoracic ganglion (Fig. 1). In the tibia the tympanal nerve is, according to Schwabe (1906), not only connected to the hearing organ but also to parts of the subgenual organ complex, consisting of the subgenual organ and the tracheal organ. The tympanal nerve runs along the front side of the main leg trachea in the femur and joins the main leg nerve in the trochanter. After passing the coxa the tympanal nerve enters the prothoracic ganglion. Here the main leg nerve can easily be reached; the recorded auditory potentials are, however, very small. This may be due to the thickness of the nerve

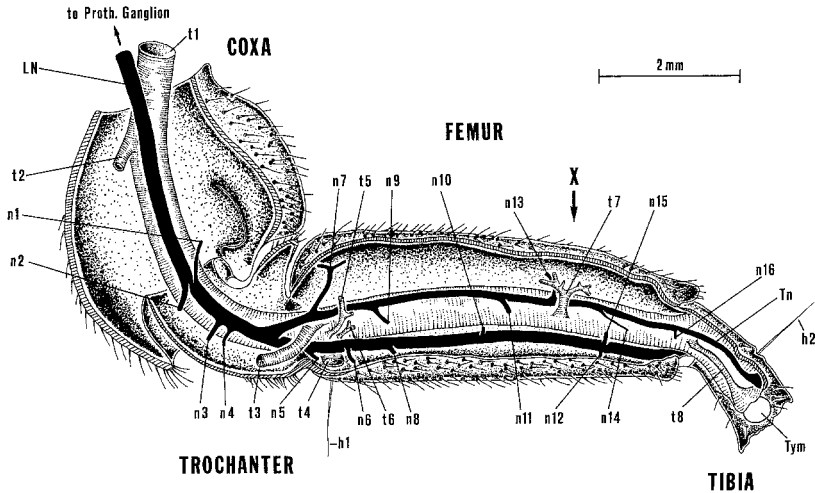


Fig. 1. *Gryllus campestris*. Innervation of the foreleg (drawn from methylene blue stained preparations). The recording region (X) is marked by an arrow. The muscles have not been drawn. *h1*, *h2* large hairs; *LN* main leg nerve; *n1*–*n16* side branches of the main leg nerve; *t1* main leg trachea; *t2*–*t7* side branches of the main leg trachea; *t8* anterior trachea; *Tn* tympanal nerve; *Tym* small tympanum

(about 130 μm) and/or to an unfavourable location of the hearing axons. The recording region finally chosen is shown in Fig. 1. It is situated near the middle region of the femur (arrow near X) where the tympanal nerve has picked up only the side branches *n14* and *n16*. As shown by electron-microscopical studies the tympanal nerve already contains more than 200 axons distal to the branch *n14* (Nocke, 1970). They partly originate from proprioceptors of the leg and their electrical activity jams many recordings with intense background activity (see for instance Fig. 6).

2. The Threshold Curve of Hearing

The threshold curve of the whole tympanal nerve, shown in Fig. 2 A, has a distinct optimum near 4 and 15 kHz. Between these two best frequencies the threshold is considerably higher. The responses to sound pulses at 4 and 15 kHz at 10 dB above threshold are also shown for the same cricket in Fig. 2A. Apparently, the 4-kHz pulse is answered by a great number of different units whereas the 15-kHz pulse is answered by only two units in this record.

Between threshold curves of male and female crickets there is no significant difference. The average data for the two best frequencies \bar{v} of 15 male and female crickets are summarized in Table 1.

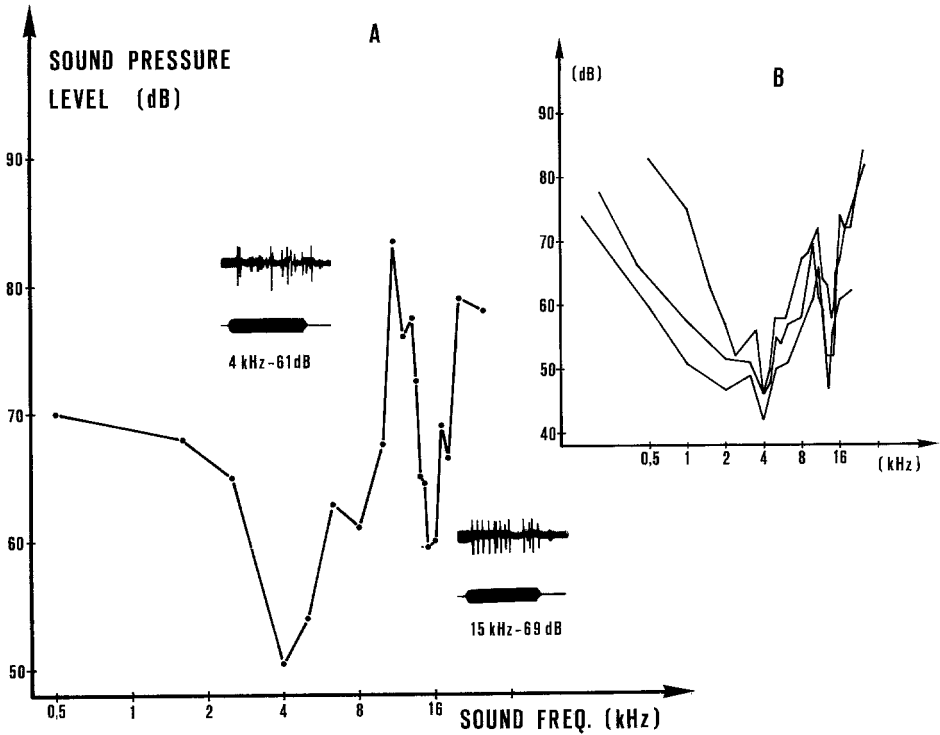


Fig. 2A and B. *Gryllus campestris*. A Threshold curve of the tympanal nerve. For the same cricket are inserted two records showing the response to 4 and 15 kHz frequencies both at a sound level 10 dB above threshold. The amplification is the same for both recordings. B Hearing threshold curve for three more crickets

Table 1

	Location		Hearing threshold	
	$\bar{\nu}$	extremes	SPL	extremes
1. optimum	3.85 kHz	2.5 and 5 kHz	44 dB	27 and 61 dB
2. optimum	13.9 kHz	12.5 and 16 kHz	59 dB	45 and 73 dB

Besides the two optimal frequencies, the slow rise of the hearing threshold curve below 4 kHz should be mentioned. In some crickets a third, not very distinct optimum can be seen near 2 kHz (see Fig. 2B).

In *Gryllus campestris* a response to airborne sound cannot only be recorded from the tympanal nerve but also from the homologous nerve of the middle leg. This had already been shown by Autrum (1941) for locusts and by Wever and Vernon (1959) for *Gryllus abbreviatus* and *Conocephalus strictus* (Tettigoniidae). However, the sound intensities necessary to trigger an acoustically correlated response from the middle leg nerve of *Gryllus campestris* are far above those needed for the tympanal organ of the foreleg. The same units (with spike amplitudes around 400 μV) respond within the range from 0.1–15 kHz not only to sound but also to vibration stimuli.

3. Frequency Dependent Responses of the Tympanal Organ

In the following section, the response of the tympanal organ to sound pulses of different pitch will be described. For clarity, the operating range of the tympanal organ will be subdivided as follows: responses below 4 kHz, near 4 kHz, and near 14 kHz; these responses will be described separately. It should, however, be kept in mind that the responses overlap, especially near 4 kHz.

a) Responses below 4 kHz. Only one or very few units of the tympanal nerve respond below 4 kHz irrespective of whether the foreleg is stimulated by substrate vibration or airborne sound. These units have the same relatively large spike amplitude (mostly around 300 μV) and they will be called low frequency (LF) units. Fig. 3 shows the response of these LF units in three different crickets (see also Fig. 5B).

The LF units are slowly adapting irrespective if a vibration or sound stimulus is used. They also have the same latency if the timelag caused by the travelling of sound is taken into account. These observations lead to the conclusion that the same units are being stimulated by sound as well as by vibration. The threshold curve of the LF units has a (not very distinct) optimum near 1 and 2 kHz if the units are stimulated by vibrations or sound. The 1-kHz optimum in many cases is missing if the LF units are stimulated by sound. Fig. 4 shows the threshold curves of a LF unit stimulated by sound and by vibration.

b) Responses near 4 kHz. At 4 kHz a stimulus just above threshold is answered by numerous spikes of different amplitudes (Figs. 2A and 5B). Discrimination of individual units is therefore very difficult, even near the threshold. The action potentials in the 4-kHz region are smaller than those of the LF units (Fig. 5B). No marked adaptation of the 4-kHz unit could be observed when the ear was stimulated by continuous tones. However, precise examination of adaptation is very difficult in this frequency region.

c) Responses near 14 kHz. The relationship between the sound levels and the responses to sound at 4 and 14 kHz is plotted for 5 crickets in Fig. 5A. The linear relationship in Fig. 5A may indicate that the intensity characteristic of the corresponding hearing neurons obeys a logarithmic function, but, if there are many active units, this relationship

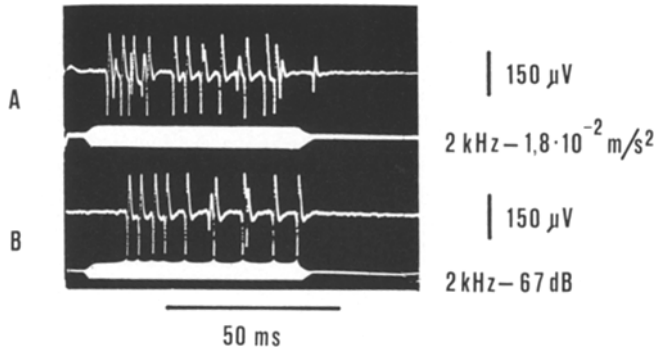


Fig. 3. *Gryllus campestris*. The response of the LF unit to a substrate vibration (A) and an airborne sound stimulus (B)

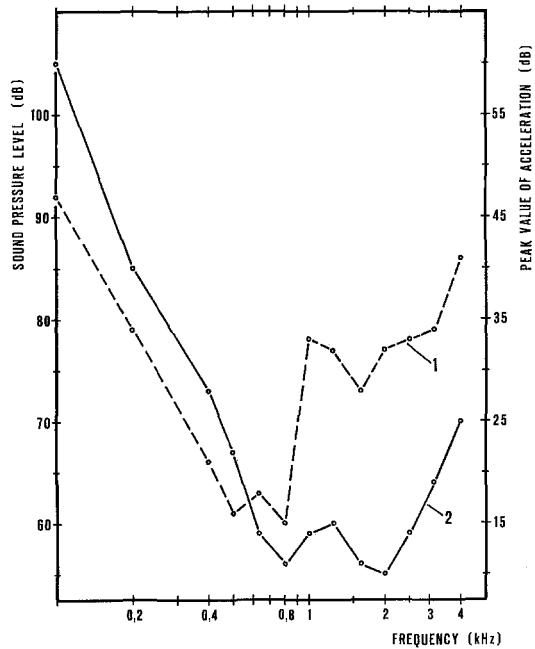


Fig. 4. *Gryllus campestris*. Comparison of the substrate vibration threshold (1) and the hearing threshold curve (2) for the same LF unit. The cricket was mounted on the preparation holder so that the sound wave front impinged on the surface of the large tympanum at a 90° angle. For the vibration stimulus the accelerating force acts in direction of the longitudinal axis of the tibia. A peak value acceleration of 45 dB is equivalent to 15 cm/s^2

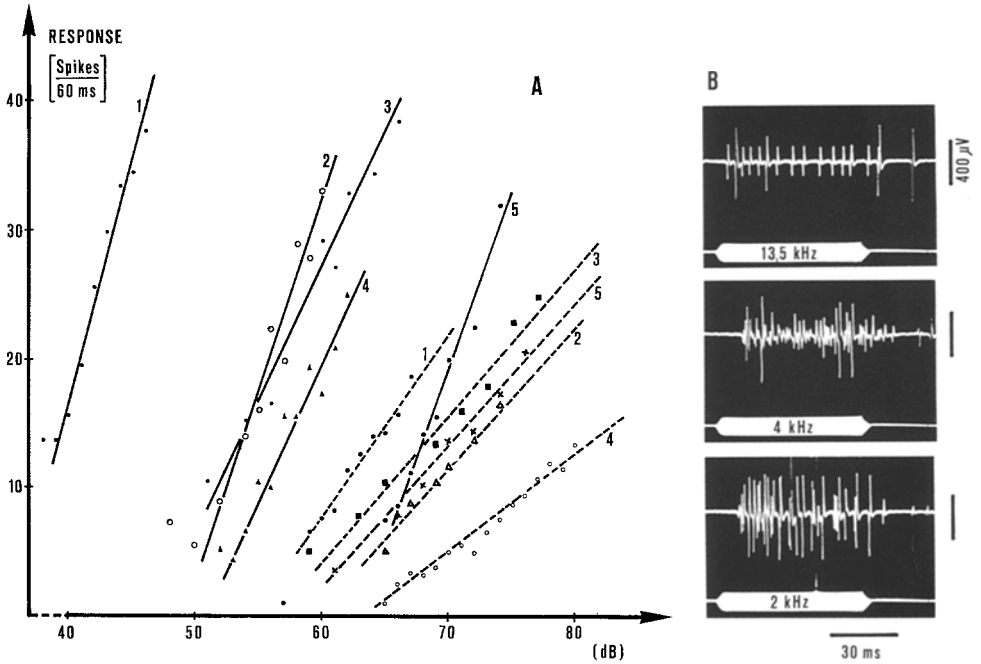


Fig. 5 A and B. *Gryllus campestris*. A Hearing nerve response to 4 (solid lines) and 14 kHz (dashed lines) sound stimuli of different sound level shown for 5 crickets (1–5). B Response to sound stimuli of 2 kHz, 4 and 13.5 kHz, each 10 dB above threshold. The large spikes seen in the 13.5-kHz response are not correlated to the sound stimulus

does not always mirror that of single units (see Michelsen, 1971). The slope for the 4-kHz receptors is, of course, steeper than that of the 14-kHz range, since there are more active units at 4 kHz. In the majority of cases only one high frequency (HF) unit was picked up (Fig. 6 A–C), but often two HF units (Fig. 6 D), and in a few cases three HF units, of differing amplitudes can be observed near 14 kHz. Both, intensity and duration are coded by the HF unit (Figs. 6 A and B). Furthermore, at sound levels 5 to 10 dB above threshold the HF unit responds initially with a burst, which is followed by a pause of 20–30 ms duration; the HF unit then starts to respond again (Fig. 7). The pause in the response of the HF unit is gradually bridged at higher sound levels.

The latency as a function of the sound level, corrected for the timelag caused by the travelling of sound is shown in Fig. 8. The latency changes very much for sound levels near the hearing threshold. The relationship between the latency and the sound level follows an exponential function

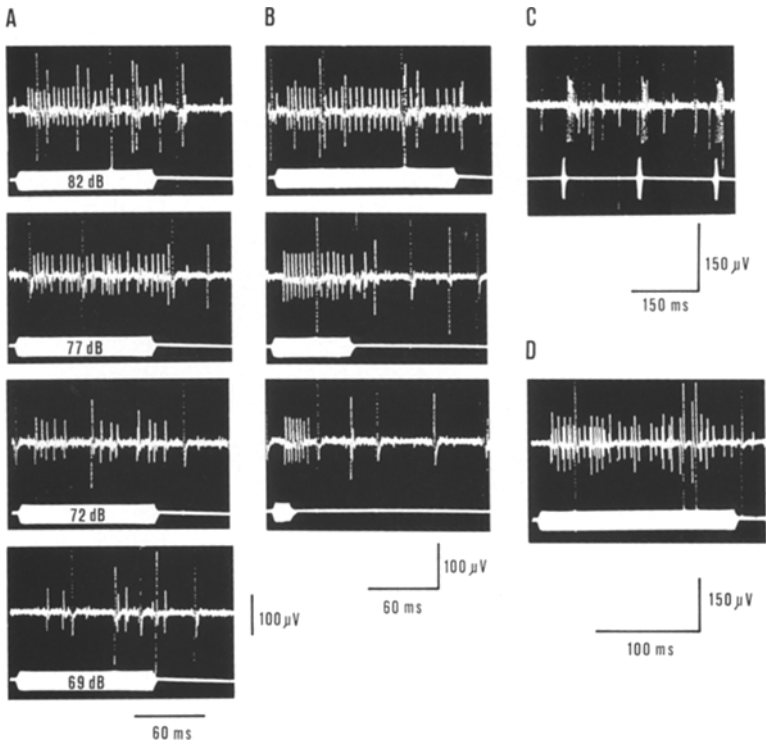


Fig. 6 A—D. *Gryllus campestris*. The coding qualities of the HF unit in different crickets. A Response to a 13.5-kHz stimulus of different intensity, and, B of different duration. C Each 14-kHz/75 dB stimulus of 15 ms duration is answered by 3–4 spikes. D 13.5-kHz/70 dB stimulus is answered by 2 HF units. In all recordings an acoustically noncorrelated background activity (large spikes) can be seen (further explanations see text)

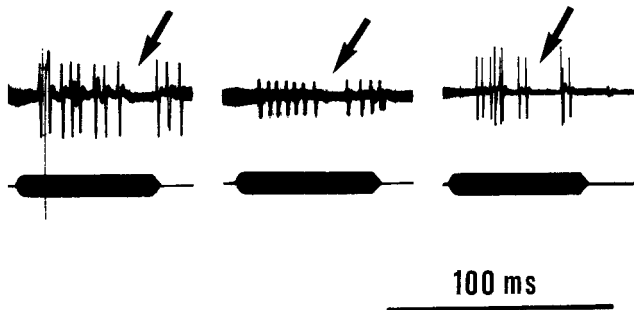


Fig. 7. *Gryllus campestris*. Response of the HF units of 3 crickets to sound stimuli of medium intensity (relative to the respective threshold), in the vicinity of 14 kHz (further explanations see text)

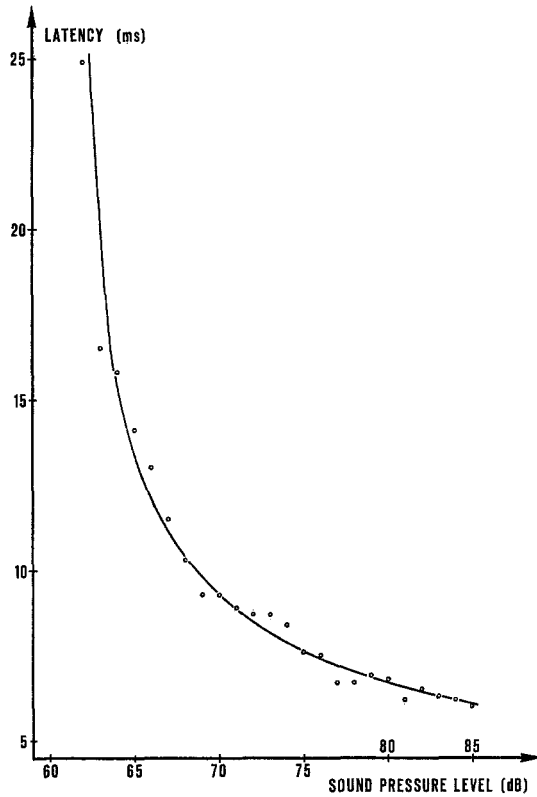


Fig. 8. *Gryllus campestris*. Sound level dependence of the latency for a HF unit (further explanations see text)

of the form $y = a^x + b$. It should be noted, however, that the latency determination is slightly inaccurate because slopes of the sound pulses change with the sound level.

The HF unit adapts only slightly over a period of 60 ms (Figs. 6 A and B). However, a distinct adaptation of the HF unit can be observed if sound pulses with a duration of several seconds are used. In the example of Fig. 9 the HF unit adapts almost entirely within three seconds at both employed sound levels. It is remarkable that the general tendency of decrease is repeatedly interrupted by short increases in the response (arrows in Fig. 9).

d) Origin of the 14-kHz Response. Although it is physically very unlikely that the HF unit is stimulated by hairs on the leg surface, this possibility had to be ruled out experimentally. The total exposed surface

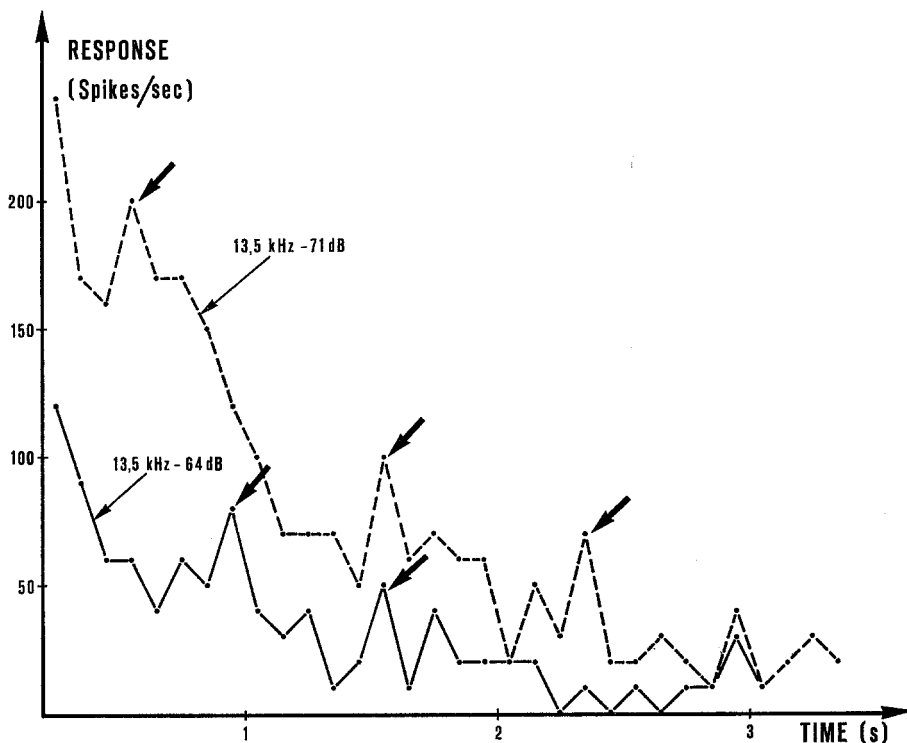


Fig. 9. *Gryllus campestris*. Adaptation of the HF unit for two sound levels (further explanations see text)

of the foreleg was covered by vaseline, but the fixation of the hairs had no influence on the response of the HF unit.

If the small typanum is detached at its periphery from the sclerotized ring encircling the typanum, the HF unit ceases to respond. The response of the 4-kHz units, on the contrary, seems unchanged by this operation. If the large typanum is detached from the sclerotized ring encircling the typanum, it still remains connected to the main leg trachea (Schwabe, 1906). This probably explains why the cricket ear still responds after the operation to 4-kHz sound stimuli. The sensitivity is about 30 dB less. After this operation the background activity mostly increased so much that it was very difficult to decide whether the HF unit was still responding. In two experiments, however, it could be seen that the response of the HF unit remained unchanged after this operation.

It is also of special interest whether the HF unit response is restricted to sound stimuli near 14 kHz, or, if it will also respond near 4 kHz. To

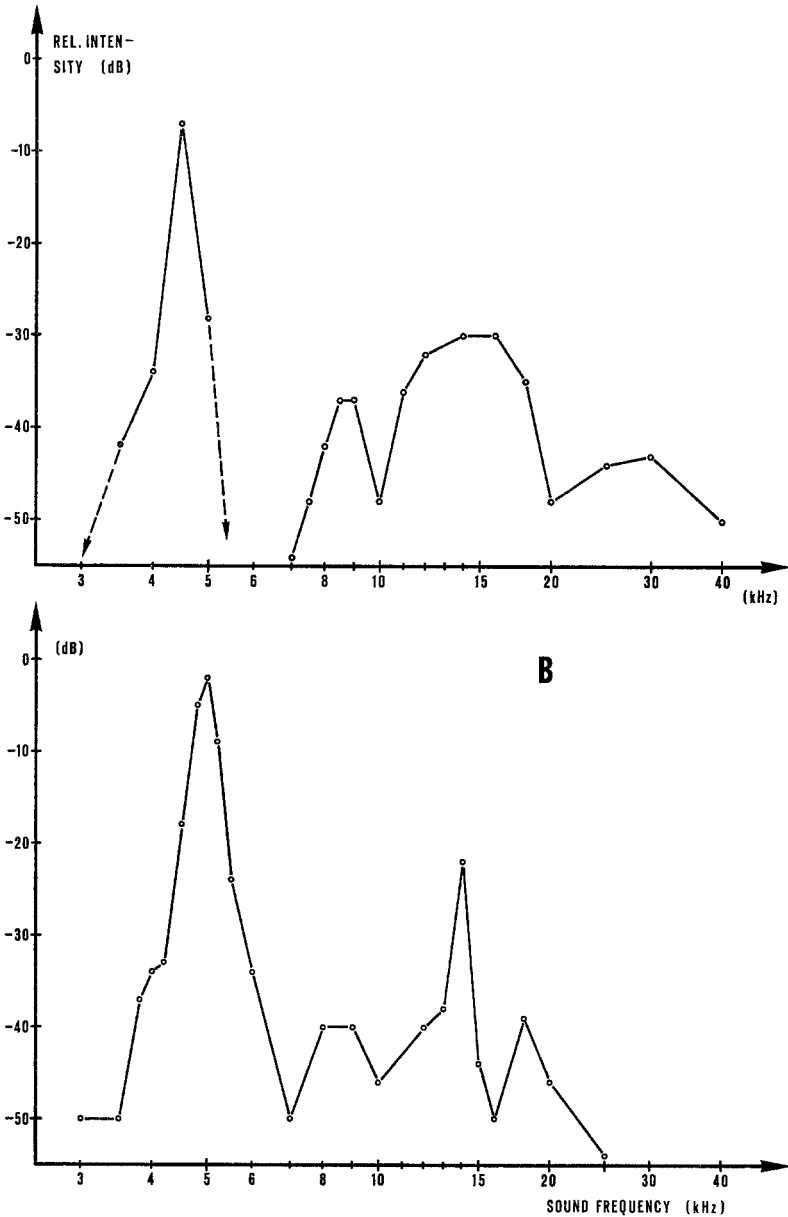


Fig. 10 A and B. *Gryllus campestris*. Wave analyser measurement of the calling (A), and rivalry song spectrograms (B). The relative intensity of the calling song below 3.5 kHz and at 5.5 kHz, 6 and 6.5 kHz is far below 50 dB and has not been plotted. Dashed lines point to values of relative intensity below the measuring capability of the analysing apparatus (further explanations see text)

answer this question, two stimuli were simultaneously presented to the cricket ear: a 14-kHz pulse (on the average 6 dB above threshold) and a 4-kHz continuous tone. The 14-kHz sound pulse was answered by the HF unit with a burst of spikes which were heard in the headphone. Starting from zero dB the sound level of the continuous tone was gradually increased until the burst response of the HF unit was just masked by the response to the 4-kHz tone. On the average 32 dB were needed to mask the HF unit. From the hearing threshold curve (Fig. 2) one can expect, that an even higher 4 kHz sound pressure level is needed to stimulate the HF unit. It therefore seems very likely that pitched sounds near 4 kHz and 14 kHz can be discriminated by the cricket ear.

4. Frequency Components of the Cricket Songs

The spectral components of the cricket songs were determined in order to look for a correlation between the sound spectrograms and the hearing threshold and its biological significance.

a) Calling and Rivalry Songs. The spectrograms of the calling and rivalry songs, with characteristic main peaks near 4 kHz, minima near 8 kHz and secondary peaks around 14 kHz, are shown in Fig. 10. The main peak has been described by Lottermoser (1952), Huber (1960) and Dumortier (1963).

The average sound level of ten crickets, measured at a distance of 50 mm in an undisturbed sound field, was 106 dB for the rivalry song and 102 dB for the calling song.

b) Courtship Song. High frequency components up to 100 kHz in the courtship song had already been found by Lottermoser (1952).

The existence of a high frequency optimum in the hearing threshold curve made an exact analysis of the frequency components in the courtship song necessary. The next two paragraphs will deal only with the tick sounds (ticks), which are the dominant syllables of the courtship song.

Fig. 11A shows the result of a Fourier analysis of a single tick (Fig. 11A inset shows analysed segment of the tick), computed for the frequency range from zero to 49,9 kHz with steps of 100 Hz. The spectrogram shows a maximum near 15 kHz. Spectrograms of the courtship song measured with the wave analyser are plotted for five more crickets, upon one another, in Fig. 11 B. These spectrograms show a sound level difference of at least 40 dB between the main peak around 14 kHz and the 4-kHz region. The spectrum up to 40 kHz varies very little from tick to tick and constitutes a "finger-print" of the individual cricket. If one compares the tick series analysis of several crickets it is striking that the main peak of the spectrogram is always very close to 14 kHz. On the

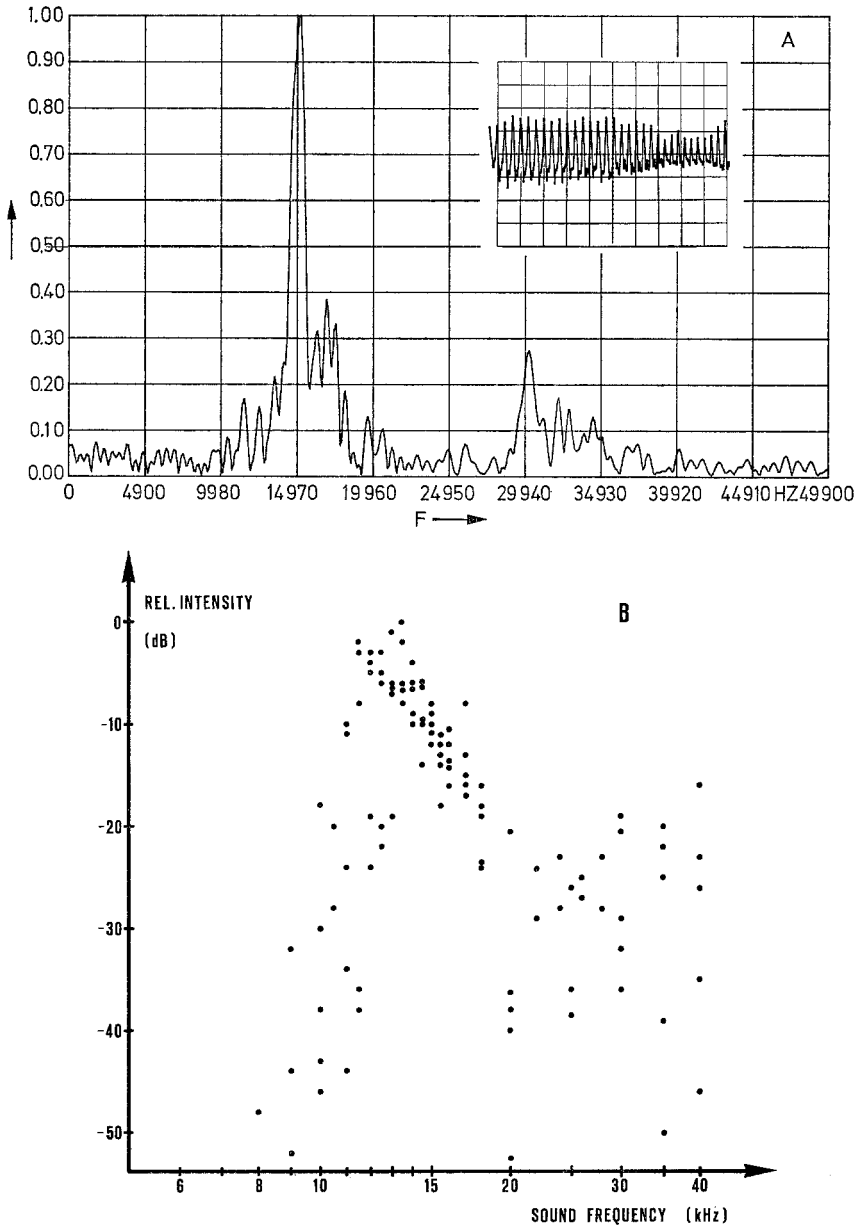


Fig. 11 A and B. *Gryllus campestris*. A Computed Fourier analysis of a single tick (inserted picture shows the analysed segment of the tick). B Tick spectrogram for 5 crickets (wave analyser measurement). For all 5 crickets the components in the 5-kHz region are below the measuring capability of the analysing apparatus (further explanations see text)

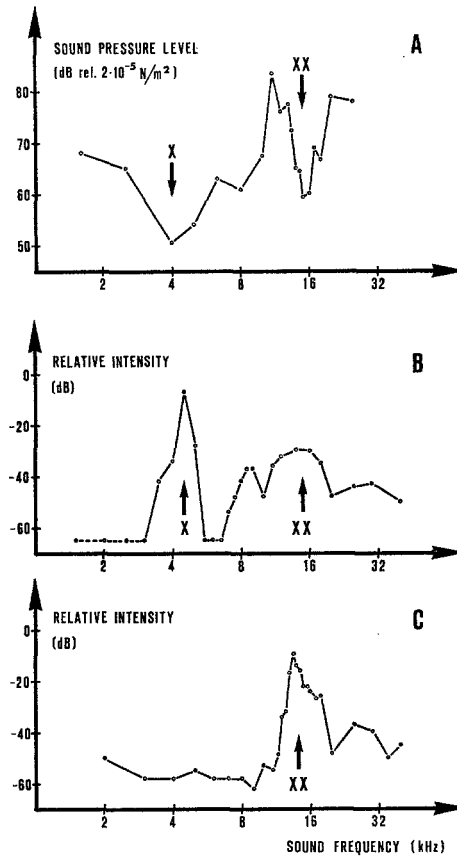


Fig. 12. *Gryllus campestris*. Comparison of the hearing threshold curve (A) with the spectrograms of the calling (B) and the courtship song (C). The agreement of both hearing threshold optima with the corresponding maxima of the song spectrograms is marked by (X) and (XX)

other hand, the relative intensity of the ultrasonic components (20–100 kHz) vary greatly from cricket to cricket.

The ticks have a mean sound level of 103 dB when measured in an undisturbed sound field at a distance of 50 mm from the animal.

The "Zwischensilbenlaute" of the courtship song are located in the interval between two ticks. According to Huber (1970) these sounds have their main frequency components around 4 kHz, and this was confirmed in the own experiments. The number of "Zwischensilben" in different cricket individuals varies between 6 and 26, and their duration also varies significantly. In addition, the amplitude of the "Zwischensilben"

shows a strong and irregular modulation. The highest amplitudes of these sounds are at least 30 dB below the main peak of the tick sound spectrogram. The significance of the "Zwischensilben" for the acoustical behaviour of crickets remains obscure.

In Fig. 12 the threshold curve of the tympanal nerve (A) is compared with the spectrograms of the calling song (B) and the courtship song (C). (The spectral components of the rivalry song are very similar to those of the calling song, see Fig. 10). The low frequency threshold optimum near 4 kHz corresponds to the main peak of the calling song spectrogram. The ticks of the courtship song, on the contrary, lack these frequency components. The high frequency hearing threshold optimum near 14 kHz coincides with the main peak of the courtship song and the secondary peak of the calling song spectrograms.

Furthermore, the HF unit can respond to very short (15 ms) 14-kHz sound pulses similar to the ticks of the courtship song, as shown in Fig. 6C. It is interesting to note that the interval between these artificial ticks can be lowered to a few milliseconds *without* causing a visible adaptation of the HF unit.

D. Discussion

1. Responses to Sound and Vibration

Below 4 kHz the threshold curve of the whole tympanal nerve rises markedly slow. In some crickets it passes through an indistinct third optimum which may be due to the LF units responding with the lowest threshold near 2 kHz. The songs of the male *Gryllus campestris*, however, do not contain a 2-kHz component. Therefore, the functional significance of the LF units is not clear.

Since these units can also be stimulated by vibration of the leg it seems more sensible to assign their function to the subgenual organ complex. The sensory axons from the subgenual organ in the foreleg join not only the main leg nerve, but also the tympanal nerve through the subgenual branch (Schwabe, 1906). Furthermore, Dambach (1972) determined the vibration threshold curve for the subgenual organ complex of the foreleg by recording from the main leg nerve close to its entry into the prothoracic ganglion. Because of the great similarity between the threshold curves, that Dambach determined with that of the LF units in this paper (Fig. 4) it may be assumed that the recordings of Dambach contain the LF units as a component.

But the question still remains, how the subgenual organ complex is stimulated by sound. These organs are mechanically coupled to the tympanal organ by a bridge of nervous tissue (Schwabe, 1906), and, as such, may be stimulated via the ear drum(s). It is interesting that one of the resonances of the large tympanum in the cricket *Teleogryllus*

commodus occurs near 2 kHz (Johnstone *et al.*, 1970). At around 2 kHz, a strict distinction between the functions of the sound and vibration reception organs is apparently *not* possible to make.

2. Mechanism of the Pitch Discrimination

Michelsen (1971), showed that the ear of *Schistocerca gregaria* is able to discriminate sounds of different pitch on the basis of the resonance properties of the tympanal membrane and the distribution of the auditory sense cells on the tympanum.

Considering the anatomical facts of the cricket ear (Schwabe, 1906) from a physical point of view, it should be assumed that the small anterior tympanum, together with the small trachea, has a higher resonance frequency than the large posterior tympanum with the associated main leg trachea. However, Johnstone, *et al.* (1970) showed for the cricket *Teleogryllus commodus* that both the small and the large tympanum have similar resonance frequencies: the small near 6 and 12 kHz; the large near 5 and 12 kHz. Part of this difference between the expected and the measured oscillation properties of the tympana could, however, be caused by the mass of the Mössbauer source fixed to the surface of the tympana analysed in their experiments.

Important to the study of pitch discrimination is the question whether the function of the HF unit responding to sound stimuli near 14 kHz is related to one of the tympana. In the ablation experiments it was shown that the HF unit fails to respond if the small tympanum is removed. But the response of units to a 4-kHz stimulus remained unchanged. If the large tympanum is removed the HF units still respond, whereas the sensitivity of the 4-kHz units dropped by about 30 dB. These experiments demonstrate that the HF unit is part of the tympanal organ and that it is functionally connected to the small tympanum.

In the ear of *Schistocerca* all sense cells attach to one membrane and owe their selectivity to the different positions of the vibrational modes of the ear drum. In the cricket ear, however, different sound frequencies may affect the two tympana in different ways. Thus, the "place principle" (Whitfield, 1967) would be realized.

The extent of pitch discrimination also depends upon the amount of overlap between the groups of auditory sense cells. Some evidence for the magnitude of this overlap has been provided by the experiments where the ear was simultaneously stimulated by two different sounds. Apparently the HF unit responds to a 14-kHz stimulus independent of a simultaneously presented 4-kHz stimulus. The 14-kHz response of the hearing nerve is only masked when the 4-kHz stimulus is more than 30 dB above the 4-kHz threshold.

The experiments described show that the cricket ear discriminates pitch and sends this information to the CNS. From central auditory neurons of crickets we already know (Popov, 1969, 1971) that a certain amount of frequency discrimination may be present.

3. Possible Biological Significance of Pitch Discrimination in Crickets

a) *Recognition of Songs.* *Gryllus campestris* uses three different songs which could perhaps be distinguished by means of certain song parameters: the *song pattern* (pulse interval, chirp interval and number of pulses per chirp; see Alexander, 1967), the *transients*, *amplitude* and *duration* and *carrier frequency* of the song syllables. However, for *Scapsipedus marginatus* (Gryllidae) Zaretsky (1972a) was able to show that sharp *transients* are not important (see however, Busnel *et al.*, 1956, for acridids).

The *duration* of syllables in a given song varies considerably among different individuals and even in the same individual within one chirp. In addition the duration of the syllables transmitted by one and heard by another individual will differ because of the reverberations in the natural environment. Furthermore, a comparison of the syllable duration in all three types of songs shows too little difference to consider this parameter to be important for intraspecific song identification. The *intensity* (amplitude) of the syllables received by the ear depends not only upon the distance of the sound source but also upon the acoustical conditions (reflective and absorptive properties) of the natural environment. It therefore is very doubtful whether this parameter can be used for the identification of the songs. Consequently, we are left with two song parameters with which to distinguish the three songs: *song pattern* and the *carrier frequency*.

Behavioural studies of Walker (1957) on tree crickets (Oecanthidae) and of Zaretsky (1972a) on *Scapsipedus marginatus* (Gryllidae) demonstrate the importance of the song pattern. With artificial chirps based on the natural pattern and a carrier frequency of 5 and 18 kHz, Zaretsky was able to initiate a phonotactic response in *Scapsipedus marginatus*. The significance of the song pattern for the process of song recognition in *Gryllus campestris* has not yet been analysed, but there seems little doubt that it is important. Because the calling and courtship songs differ not only in their pattern but also in their carrier frequencies, they both are recognizable song parameters for *Gryllus campestris*.

However, the role of pitch information in the process of song recognition has yet to be tested by behavioural experiments.

b) *The Sound Level of the Songs.* The calling song of the male is used to communicate with the female over relatively large distances. The

courtship song, on the other hand, precipitates the willingness of the female cricket to copulate and must be transmitted and heard over a distance of only a few centimeters. From the average sound level emitted by the cricket and from the mean hearing threshold near 4 and 14 kHz, the theoretical range is calculated to be 41.6 m for the calling song and 9.6 m for the courtship song. Aylor (1972) showed by noise reduction measurements on different forms of vegetation that the sound attenuation will increase very much with the frequency. Therefore, the attenuation by such surrounding vegetation as grass will be much higher for the 14-kHz ticks of the courtship song than for the 4-kHz component of the calling song. So, it is physically sensible that the cricket uses the low frequency calling song for "long range communication".

The sound level of the emitted songs is so much above the hearing threshold that communication between two specimens is possible even if the tuning of the sound transmitter (male) differs from the receiver (female), within the individual variation.

The calling song not only has a main peak near 4 kHz but also a secondary peak near 14 kHz. The 14-kHz component of the calling song has a lower intensity than the 4-kHz component and it is muffled considerably more by the surrounding vegetation. This fact could be used by the female cricket for her orientation in the sound field of the male. A female following the calling song would inevitably pass through the following regions of the sound field. At a very great distance from the male only the 4-kHz component of the calling song is heard, which will increase as the female approaches its mate. Then, in addition, the 14-kHz component will be heard and its intensity will also increase as the male is further approached. Lastly, at close range below 100 mm, the male emits directed sound (Nocke, 1971). If the female now follows the highest sound pressure, she will eventually reach the male and can trigger by tactile stimuli the courtship song.

In *Gryllus campestris* the small tympana point in a forward direction. In case they have a distinct directional sensitivity, it could well be that the HF units associated with these tympana provide additional clues to the position of the courting male. This information could be used to guide the female onto the back of the male after which, copulation is initiated.

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