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# SOUND RECEPTION IN THE BUSH CRICKET *METRIOPTERA BRACHYPTERA* (L.) (ORTHOPTERA, TETTIGONIOIDEA)

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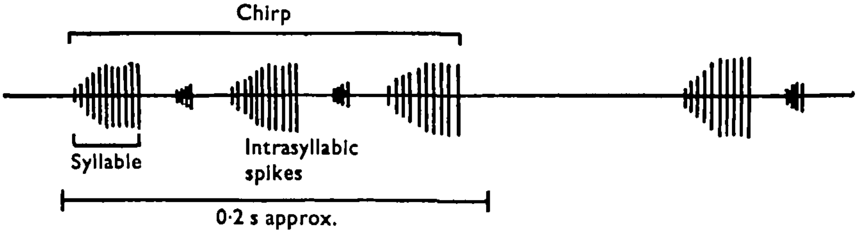
## INTRODUCTION

The phenomenon of acoustic communication in insects has been tackled broadly on two fronts; the mechanism of sound production with its associated behaviour; and the neurophysiological, anatomical and behavioural features of sound reception.

The production of sound with a wide frequency band by bush crickets (Tettigonidae) and grasshoppers (Acrididae) is well known, and the mechanisms for its production have been documented by Haskell (1964) and Alexander (1967). The songs produced have been shown to be always species-specific, often with considerable ultrasonic components. The mechanisms by which these high-frequency sounds are produced are considered by Pierce (1948); Broughton (1963*a*, 1964); Suga (1966); Morris & Pipher (1967); Bailey (1967, 1970); and Bailey & Broughton (1970). These workers established for bush crickets that the frame surrounding the tegminal 'mirror' (the area of thin membrane surrounded by the cubital complex) is set vibrating by the impacts of the plectrum (the anal margin of the same tegmen) as it passes over the teeth of the file on the cubital vein of the other tegmen. In this way a 'syllable' of sound (Text-fig. 1) will be produced with each closing, or opening, or both movements of the wings. It was originally thought (Pierce, 1948) that the mirror membrane resonated at the tooth impact rate but this hypothesis has now been questioned by Bailey (1967, 1970) who maintains that if and when resonance occurs it is set up in the mirror frame. Sound is produced in the grasshoppers, on the other hand, by the rubbing of the teeth on the inner surface of the femur of the metathoracic legs, as a result of movements of the legs, against the margin of the tegmen.



Text-fig. 1. A diagrammatic representation of the song of *M. brachyptera* to illustrate the terms used in the text.

The response characteristics of the tettigonioid auditory system have been inves gated by a number of authors: Wever & Bray (1933); Pumphrey & Rawdon-Smith (1936); Haskell (1956, 1957); Suga & Katsuki (1961); Usherwood, Runion & Campbell (1968); Rowell & McKay (1969); and McKay (1969, 1970), though little work has been done on the movements and tuning of the tympanum itself (Johnstone, Saunders & Johnstone, 1970 measured these in a gryllid). Some workers, (Suga & Katsuki, 1961; Rowell & McKay, 1969; McKay, 1970), have been concerned primarily with the analysis of the central mechanisms of hearing, while others (Wever & Bray, 1933; Pumphrey & Rawdon-Smith, 1936; McKay, 1969), have considered the responses in the tympanal nerve to artificial sound with only passing reference to the species song. Where the species song has been used as stimulus, this has been reproduced from tape, often without adequate provision for, or without sufficient emphasis on, the reproduction of the full frequency range contained in the live song. Hence it is probable that only a percentage of the total sound spectrum was transmitted, and confusion regarding the important features of the sound stimulus inevitably resulted. In consequence the adequate stimulus to excite the insect tympanal organ has variously been considered to be 'amplitude modulation' in the sense of variation in spike height (Pumphrey, 1940), 'rise time' of song pulses (Busnel and Burkhardt, 1962), and the 'starting and terminal transients' of song pulses (Howse, 1968). Pumphrey & Rawdon-Smith (1939) and Pumphrey (1940) maintained that the discharge of the action potentials in the tympanal nerve reflected any periodicity in the stimulating sound that was below the limit for synchronization (of the order of 100 Hz in their experiments); this could be a pure tone or an amplitude modulation superposed on it, or both. Haskell's treatment is made more difficult to interpret for two reasons; first, the published oscillograms of the songs of his insects are so condensed as to show little of their intrasyllabic structure, and, secondly, he uses the term 'pulse' in a sense limited to his particular paper. He concluded, however (1956), that in his insects the different syllable rates held the key to the species recognition of the song, since the only common factor in two forms of stimulation, recorded song and artificial stimulation, was that the volleys of action potentials were synchronous with the syllables of the stimulus which induced them.

Another feature of insect song which has been considered to be of importance is its frequency content. There is little evidence at present that the tympanal organ analyses sounds in terms of their frequency, although Katsuki & Suga (1960), Horridge (1961) and Michelsen (1966) have proposed at least two frequency-sensitive receptors.

The only point of agreement in this matter is that, whatever the important characteristics of the song might be to the animal, the pattern of action potentials in the tympanal nerve must in some way reflect this information if the song is to be of any specific behavioural significance. This paper attempts an analysis of the impulse pattern in the tympanal nerve in response to a variety of insect song stimuli in order to determine the relationship of the syllable rate and/or any intrasyllabic features with the action-potential sequence; and also whether any form of filtering occurs at the tympanal organ of the song of an insect of a related species or family, as a result of the characteristics of the receiving organ.

## MATERIALS AND METHODS

### 1. *Terminology*

*Natural song* is used to refer only to the song of the live insect; all other stimuli are termed *recorded songs*. The *syllable* corresponds to the sound produced by a single one-way movement of the tegmina or leg; the short amplitude peaks within each syllable (Text-fig. 1) will be called *intrasyllabic spikes*. A group of syllables within the continuing song will be called a *chirp*, following the nomenclature of Broughton (1963*b*).

### 2. *Insects*

The insect used for each preparation was the female *Metrioptera brachyptera* (L.), collected from a single site in the New Forest. The stimuli used were the natural proclamation songs of this species, the audio-frequency and high-frequency recordings of this song, and the natural song, audio-frequency and high-frequency recordings of the song of *Chorthippus parallelus* (Zetterstedt).

### 3. *Recording and analysis of the Natural song*

The songs were recorded at 15 i.p.s. (38 cm/s) on a good audio-frequency tape-recorder (Akai X-300) modified in circuitry to respond within ± 2 db over the frequency range 200–28 kHz; and an Akai X-300 microphone with a response flat to 10 kHz. This recording was played back through an ordinary 4 inch (10 cm) moving-coil loudspeaker placed 70 cm away from the preparation. The intensity of the audio-frequency of the song was monitored on the 'A' scale of a Brüel and Kjaer sound-level meter flat to 20 kHz. Decibels are quoted relative to a sound pressure level of $2 \times 10^{-4} \mu$ bar r.m.s.

The song was also recorded at 37½ i.p.s. (95 cm/s) on a Precision Instruments P.I. 6100 tape-recorder through a solid dielectric capacitance microphone (Pye & Flinn, 1964; Pye, 1968) and played back through the same microphone. In this way, recording and reproduction of song elements with frequencies up to at least 150 kHz was achieved. The wide-band recording was at other times played back through a band-pass filter, set to give a narrow frequency band with slopes of 24 db/octave either side of selected frequencies.

The high-frequency components of the song were identified by monitoring with a tuned ultrasound detector operating over a variable 5 kHz band.

Subsequent analysis of the songs was carried out using an oscilloscope and camera for examination of the waveforms and a Kay sonograph for frequency analysis.

### 4. *Preparation*

The female *M. brachyptera* was held ventral side uppermost on a base of Plasticine, and the sternites were removed to expose the mesothoracic and prothoracic ganglia. These ganglia were cleared, disturbing the tracheal system as little as possible. The pro-mesotheracic connectives were cut, as were all the branches of the prothoracic ganglia except the third mixed nerve on each side. The motor branch of this nerve was cut and the tympanal nerve was hooked up on a modified Labgear–Harding micro-dissector, the 20 μ tungsten needle of which was used as the recording electrode. The indifferent electrode was a pin pushed through the abdomen. The preparati[illegible] remained active for up to 8 h, although the amplitude of the action potentials began to fall after about 6 h. The preparation was enclosed in a screened cage, and all stimuli were directed at the preparation from in front.

The responses in the tympanal nerve were fed through a Tektronix 122 low-level pre-amplifier to a Tektronix 502 A dual beam oscilloscope. The recorded stimuli were passed directly to the lower beam of the oscilloscope from the line outputs of the tape-recorders. The natural song was monitored by the ultrasound detector set at a convenient frequency and the output was passed to the lower beam. Direct print-out of both stimulus and response was obtained by taking the vertical amplifier outputs of the oscilloscope to a Mingograph 34 multichannel recorder.

## RESULTS

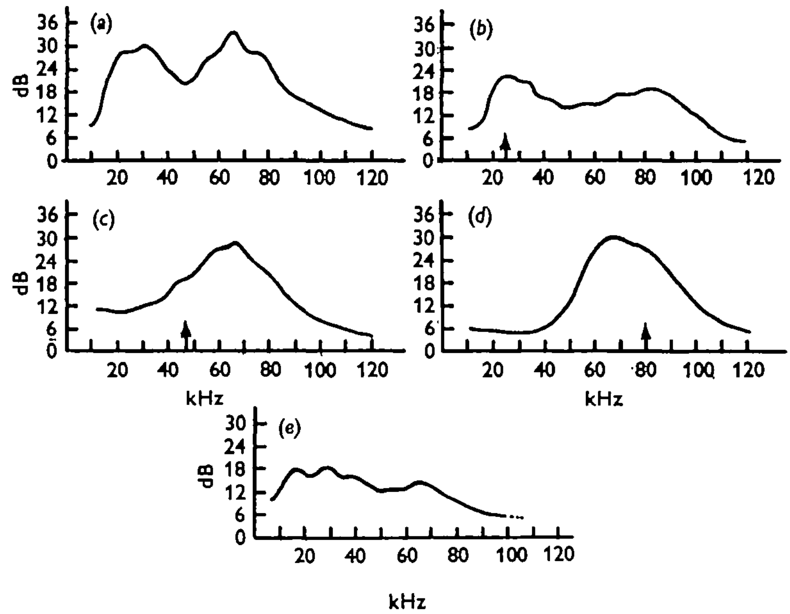
### 1. *Analyses of songs*

The songs recorded from *M. brachyptera* consist of chirps persistently repeated at about three chirps/s (Ragge, 1965, quotes two to six chirps/s depending on temperature). Each lasts for about 120 ms and is formed of five syllables, three long (25–40 ms) and loud, alternating with two short (about 5 ms) and soft (Plate 1*a*). These presumably correspond to the alternating 'closing' and 'opening' strokes of the tegmina. The remaining opening stroke can be detected some time before the chirp but appears to be almost silent. Each loud, closing syllable consists of from 25 to 40 intrasyllabic spikes corresponding to individual tooth strikes. The last syllable of each chirp has the longest duration and the largest number of spikes. The soft, opening syllables appear to be formed of a similar number of spikes but they are so compressed that counting is difficult.

Each spike consists of a sound pulse of very short duration. Closing spikes (Plate 1*b*) show a rapid onset within one cycle, followed by a highly damped decay with a half-life of about 0·1 ms. The opening spikes (Plate 1*c*) are more rounded in shape, building up and decaying with a similar pattern. Between the spikes the base line shows an irregular, less damped oscillation of lower amplitude and frequencies.

Sonagraph analyses of the recordings support these descriptions. Due to the steep amplitude modulation the spectrum is broad, without any well-defined limits. The main energy in the closing syllables is judged to lie between 15 kHz and 85 kHz in two main bands roughly centred on 25 and 67 kHz. These bands appear to be harmonically unrelated (Pierce, 1948, found similarly unrelated components in *Conocephalus* species) and, indeed, some displays suggest that both bands are double, with four 'carriers' in all, at about 22, 30, 65 and 77 kHz. The 65 kHz component is the strongest and 77 kHz the weakest. The weaker opening syllables mainly cover a band from 35 to 75 kHz, again with a suggestion of two bands centred roughly on 45 and 65 kHz. A temporally integrated spectrum of the song is given in Text-fig. 2*a*. Morris (1970) has found a main peak at 33 kHz with smaller peaks at 15 and 63 kHz in the spectrum of *M. sphagnorum*.

The song recorded from *C. parallelus* consists of single chirps with irregular intervals of several seconds, again with loud 'downstroke' syllables and soft 'upstroke' syllables. The sound intensity increases over the first six to seven pairs of syllables and syllable rates are about 8 pairs/s with 5·5 pairs/s in one animal (Ragge, 1965, quotes a range around 7/5). The details are somewhat ill-defined and variable between individuals. The upstroke syllables last about 15–25 ms, while the downstroke syllables last about 25–60 ms. Spikes in both syllables (Plate 1 *d–f*) show a rapid onset within one cycle or so, followed by a damped decay within about 0·2 ms. The envelope of each spike is, however, irregular due to the presence of multiple components and no firm figure can be given to its dimensions.



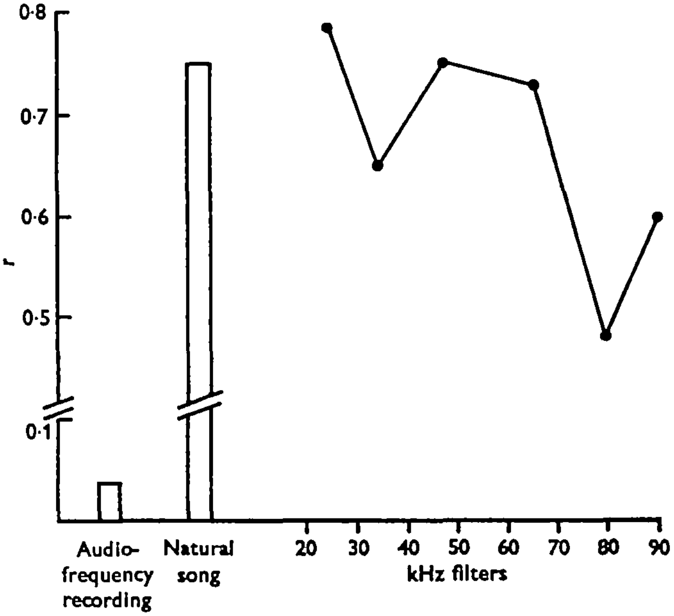
Text-fig. 2. Integrated ultrasonic spectra (time constant 15 ms) of the two recorded songs. (*a*) The original recording of *M. brachyptera*. (*b–d*) The song of *M. brachyptera* as replayed through a capacitance transducer at three different filter settings. (*e*) The original recording of *C. parallelus*.

The sonagraph analysis shows that the main sound energy lies between about 7 kHz and about 80 kHz although again the limits are diffuse due to rapid, spiky amplitude modulation. Within this range four bands appear at about 10–15 kHz, 22–25 kHz, 37–40 kHz and 60–70 kHz, the lower three varying in intensity but usually being stronger than the top band. A further band is sometimes found at 45–48 kHz but most individual displays suggest that the bands do not form a single harmonic family. An integrated spectrum of the song is given in Text-fig. 2(*e*).

### 2. *Responses to the conspecific songs*

Before the stimulus was presented there was a low level of activity in the tympanal nerve. This activity was presumably a response to the low-intensity sound in the environment such as the acoustic hum of the recording equipment, to which the preparation was particularly sensitive.

Plate 2(*a*) shows the response recorded from the tympanal nerve to the audio-frequency recorded song played through the moving-coil loudspeaker placed 70 cm from the preparation. A synchronous response was barely detectable even though t average intensity was 85 db at the preparation, compared with 45 db for the natura song. On the other hand, the response to the song of the live conspecific 50 cm away (Plate 2*b*) showed clearly correlated activity for the duration of each chirp. The high-frequency recording of the species song was then played to the preparation, varying only the band-pass filter settings. The responses obtained are shown in Plate 3. Although action potentials were recorded with filter settings at 90–200 kHz, it was not possible to correlate these accurately with the stimulus because of the limitations of the recording apparatus.



Text-fig. 3. A graph of the correlation coefficients obtained for the action potentials and intrasyllabic spikes, against the appropriate frequency-filter settings.

Table 1. *Correlation coefficients of the number of action potentials in the tympanal nerve of* M. brachyptera *with the number of intrasyllabic spikes in the the species song*

| Stimulus | Correl. coeff. | No. of syllables for calc. | Av. no. of a.p.s. /syllable | Av. no. of spikes /syllable | '*t*' | '*p*' |
|---|---|---|---|---|---|---|
| Audio-frequency tape-recording | 0·0328 | 14 | 35·6 | 30·6 | 0·1142 | < 0·9 |
| Natural song | 0·7502 | 27 | 92·6 | 84·9 | 5·654 | < 0·01 |
| High frequency tape recordings (kHz filter) | | | | | | |
| 25 | 0·7855 | 11 | 64·3 | 61·7 | 3·823 | < 0·01 |
| 35 | 0·6463 | 7 | 65·0 | 96·5 | 2·044 | < 0·1 |
| 47 | 0·7464 | 14 | 74·3 | 99·4 | 3·897 | < 0·01 |
| 65 | 0·7334 | 18 | 59·0 | 61·5 | 4·280 | < 0·01 |
| 80 | 0·4814 | 11 | 93·0 | 47·8 | 1·591 | < 0·2 |
| 90 | 0·5932 | 9 | 59·4 | 99·7 | 1·839 | < 0·2 |

Correlation coefficients for the two traces of each pair were calculated by counting the number of intrasyllabic spikes in the song and the number of action potentials in the nerve, which were greater than an arbitrary amplitude consistent for each song. The values are given in Table 1. The correlation coefficients were then plotted against the frequency-filter settings to produce the graph shown in Text-fig. 3.

### 3. *Responses to the songs of* C. parallelus

The tympanal nerve response of *M. brachyptera* to the audio-frequency recorded song of *C. parallelus* is shown in Plate 4*a*, and may be compared with that obtained to the natural song (Plate 4*b*).

The correlations obtained for these results are given in Table 2.

Table 2. *Correlation coefficients of the number of action potentials in the tympanal nerve of* M. brachyptera *with the number of intrasyllabic spikes in the song of* C. parallelus

| Stimulus | Correl. coeff. | No. of syllables for calc. | Av. no. of a.p.s. /syllable | Av. no. of spikes /syllable | '*t*' | "*p*' |
|---|---|---|---|---|---|---|
| Audio-frequency tape recording | 0·7491 | 24 | 27·8 | 21·1 | 5·297 | < 0·01 |
| Natural song | 0·9697 | 15 | 55·1 | 49·6 | 14·28 | < 0·01 |
| High-frequency tape-recording: 25 kHz filter | 0·9765 | 7 | 54·0 | 90·9 | 10·91 | < 0·01 |

## DISCUSSION

Although the songs of both *M. brachyptera* and *C. parallelus* have considerable ultrasonic components, this is not the only feature common to both. By analysing the response obtained in the tympanal nerve it should be possible to determine the precise features of the natural sound which are of potential behavioural significance. Further, by using recorded song as stimulus, and reproducing this through different frequency filters, it may be possible to determine whether the responses to recorded song differ significantly from those obtained to the natural song, and whether any important features have been lost.

If any filtering of the auditory stimulus occurs at the tympanal organ as a result of its structural characteristics, thus providing a degree of species specificity at the receptor level, then maximal responses should be obtained to the natural conspecific song, and these responses should decrease in relation to the degree of distortion of the song.

The responses obtained in the tympanal nerve of *M. brachyptera* to the electrodynamic playing of the natural song, with a probable top frequency limit of 15 kHz, shows a low signal-to-noise ratio, though there is some suggestion of temporal correspondence of the action potentials to song syllables (Plate 2*a*). Inspection of the sonagram of the song of *M. branchyptera* suggests two reasons for this: firstly, the frequency band of this song extends from 15 to 95 kHz, so that much of the signal is lost in the audio-frequency recording and reproduction (especially the latter). Secondly, any background noise below 15 kHz in the recording chamber will be effectively amplified out of all proportion to the original signal due to the high replay levels used. This type of recording and reproduction therefore results in a maximal distortion of the natural song, such that only about 15% of the frequency spectrum is record and then amplified out of context. Consequently it is not surprising that the correlation coefficient between this song pattern and the action-potential sequence is as low as 0·0328, even though the intensity of the song at the preparation was measured as 85 db compared with 45 db for the natural song. It can be concluded therefore that a much greater proportion of the natural song must be reproduced before any valid statement can be made about the tympanal nerve responses.

Comparison of the responses to the audio-frequency recording with those obtained to the natural song (Plate 2*a*, *b*), emphasizes this point. It can be seen that there is a close temporal correspondence between the duration of the syllable and the duration of the group of action potentials. Text-fig. 2 shows that there are intrasyllabic features which correspond very closely to the action potentials. This correspondence produces a correlation coefficient of 0·7502. The action potentials corresponding to each syllable show no constant repeating pattern (Pumphrey, 1940; Haskell, 1956), but neither does the intrasyllabic spike sequence. There is, however, a constant relationship between the action potential sequence and the intrasyllabic spike sequence of the syllable which produced it.

The responses to each of the high-frequency stimuli show a consistently high correlation (Table 1). We would now suggest, from the visual inspection of the traces obtained, the correlation coefficients and the characteristics of the incident stimuli, that the intrasyllabic spikes are steep-fronted pulses or pulse complexes which (by virtue of their steep fronts) introduce a high proportion of energy in higher and lower sidebands, and that the sequence of these 'transients' is the important feature of the species song. If so, then the song is encoded in a pattern of impulses in the tympanal nerve which corresponds with the pattern of intrasyllabic spikes.

Comparison of the oscillogram of *M. brachyptera* (Plate 1*a–c*) with that of *C. parallelus* (Plate 1*d–f*) shows that the latter has a much more pronounced steep-fronted structure. If the important features of the song are the intrasyllabic, steep-fronted pulse complexes, then the natural song of *C. parallelus* should produce a closer correspondence between the response potentials and the intrasyllabic spikes and hence a higher correlation coefficient. If, on the other hand, some degree of selectivity occurs at the tympanum, then a decrease in correlation may be due to the fact that either the pulse complexes are not important or that the tympanal organ is tuned in some other way to the species song.

Visual inspection of the responses obtained to the natural song of *C. parallelus* shows that extremely close matching of potentials and spikes (Plate 4*b*), and it is not surprising that the correlation coefficient is as high as 0·9697, while that of the high-frequency recorded song is 0·9765. Thus, both are greater than the correlation obtained for the species song. Even the responses to the audio-frequency recording (Plate 4*a*) gave a correlation coefficient of 0·7491, which is as high as that obtained to the natural song of the species. This high value is probably due to two factors: (1) the presence of a lower frequency in the song spectrum of *C. parallelus*, and (2) the fact that the important features of the insect song are the intrasyllabic elements considered above. The second criterion is probably of greater importance since elimination of the low-frequency signal by passing the high-frequency recording through a 25 kHz filter produces a higher correlation value.

The higher correlation values given by the song of *C. parallelus* would strongly suggest that no species-specific filtering mechanism is involved in the transduction of the incident stimulus by the tympanal organ of this species.

It is now clearly essential that in experiments on insect hearing, the high-frequency, steep-fronted structure of the species song must be adequately reproduced by employing an instrument of adequate frequency response, otherwise the results may have little behavioural significance. Further, the theory that the nervous response follows only the time course of Pumphrey's 'amplitude modulation' envelope of the syllables, with no correlated intrasyllabic structure, must now be considered as an incomplete explanation.

## SUMMARY

1. This paper presents an analysis of the impulse patterns in the tympanal nerve of *Metrioptera branchyptera* (L) in response to a variety of insect song stimuli in order to determine the relationship of the syllable rate and of intrasyllabic features to the action-potential sequence.

2. Recordings of the proclamation songs of *M. brachyptera* and *Chorthippus parallelus* (Zetterstedt) made with a conventional audio-frequency tape-recorder and with a high-frequency tape-recorder have been analysed. The song of *M. brachyptera* is composed of five syllables/chirp, corresponding to the opening and closing strokes of the tegmina; each syllable consists of twenty-five to forty intrasyllabic spikes which correspond to individual tooth strikes. The main sound energy lies between 15 and 85 kHz centred roughly on 25 and 67 kHz in the closing syllables and on 45 and 65 kHz in the weaker opening syllables.

3. The song of *C. parallelus* consists of single chirps with loud downstroke syllables and softer upstroke syllables. The main sound energy lies between 7 kHz and 80 kHz, centred on four bands at about 10–15 kHz, 22–25 kHz, 37–40 kHz and 60–70 kHz.

4. Live song, audio-frequency recordings and high-frequency recordings of *M. brachyptera* song were used as stimuli for the tympanal nerve preparation. The action potentials produced in response to the live or to the high-frequency recording of the song show a high correlation with the intrasyllabic spikes, though not in response to the audio-frequency recording. Inadequate reproduction may therefore be an important potential source of error.

5. By presenting the high-frequency recording through a band-pass filter various degrees of distortion of the song are achieved, and in this way it is shown that the important features of the proclamation song of the species are the intrasyllabic spikes.

6. The action potentials recorded from the tympanal nerve of *M. brachyptera* in response to the live song, audio-frequency recordings and high-frequency recordings of *C. parallelus* confirm the importance of the intrasyllabic spikes, and show that no 'tuning' of the tympanal organ to the species song occurs.

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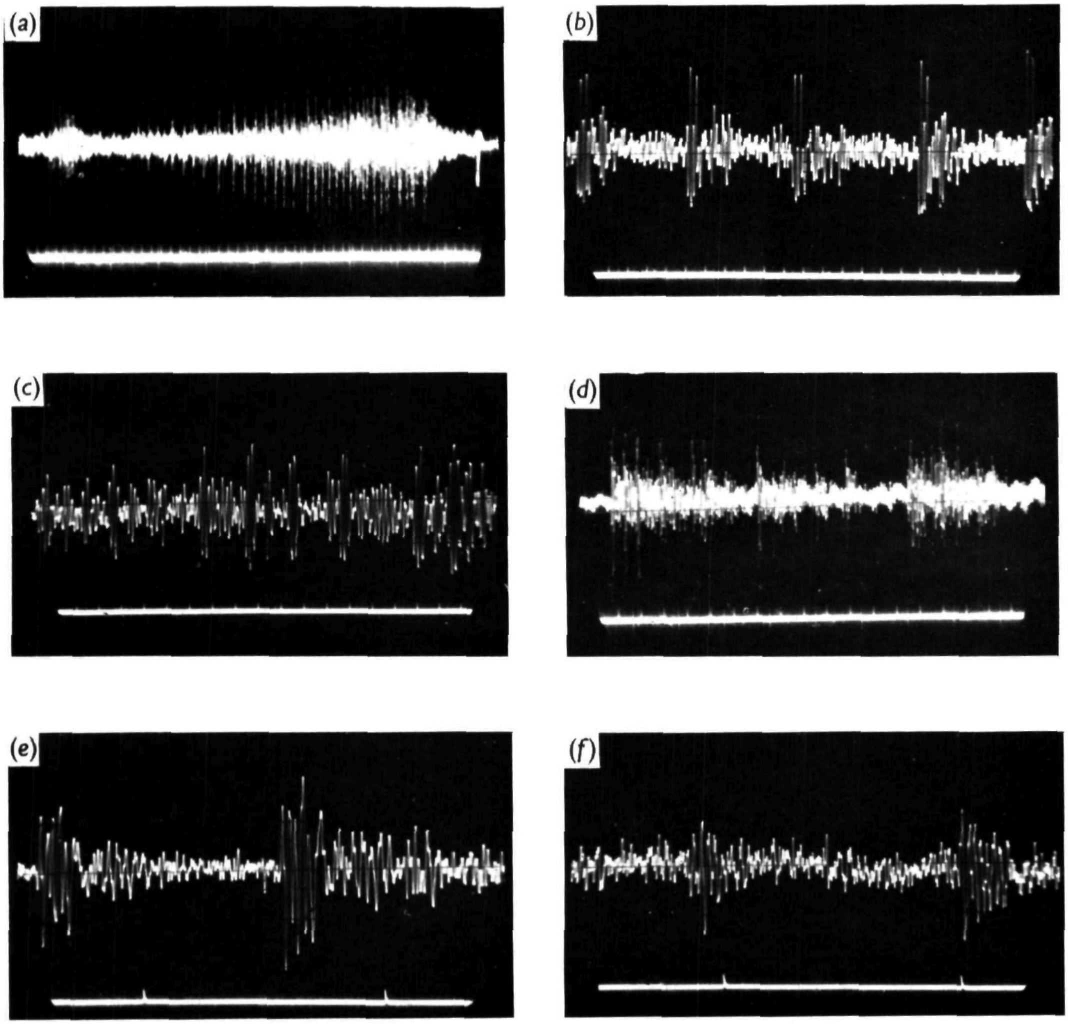
## EXPLANATION OF PLATES

### PLATE 1

The waveforms of the songs. (*a*) Opening and closing syllables of *M. brachyptera*. Time trace 1 ms. (*b*) Spikes from a closing syllable of *M. brachyptera.* Time trace 0·1 ms. (*c*) Spikes from an opening syllable of *M. brachyptera.* Time trace 0·1 ms. (*d*) Most of a downstroke syllable of *Chorthippus parallelus.* Time trace 1 ms. (*e*) Spikes from a downstroke syllable of *C. parallelus.* Time trace 1 ms. (*f*) Spikes from an upstroke syllable of *C. parallelus.* Time trace 1 ms.

### PLATE 2

(*a*) The responses obtained in the tympanal nerve of *M. brachyptera* (upper trace) to the audio-frequency recording of the species song (lower trace). Time marker 0·1 sec. (*b*) The responses obtained in the tympanal nerve of *M. brachyptera* (upper trace) go the natural song of the species (lower trace). Time marker 0·1 sec.



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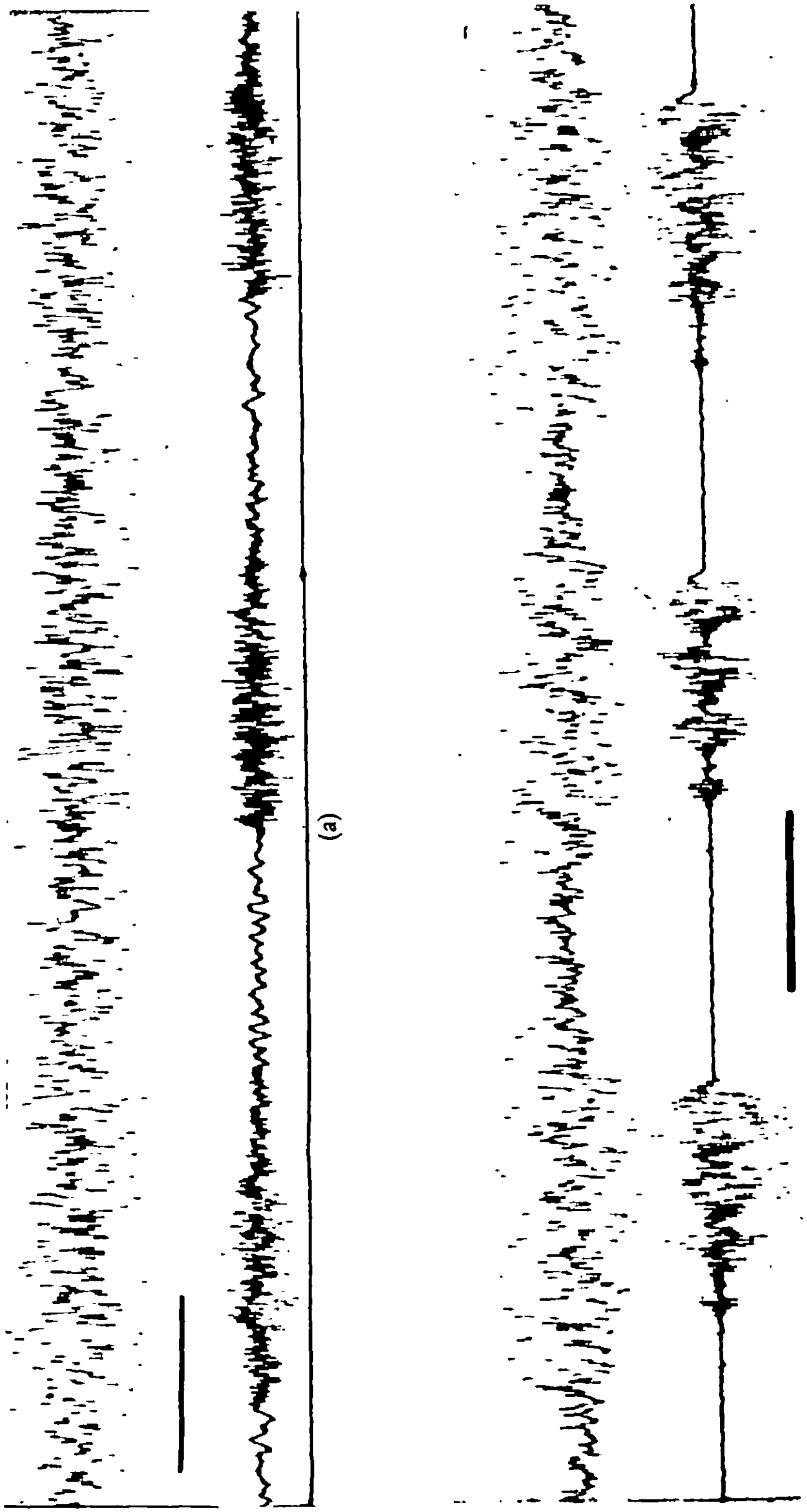

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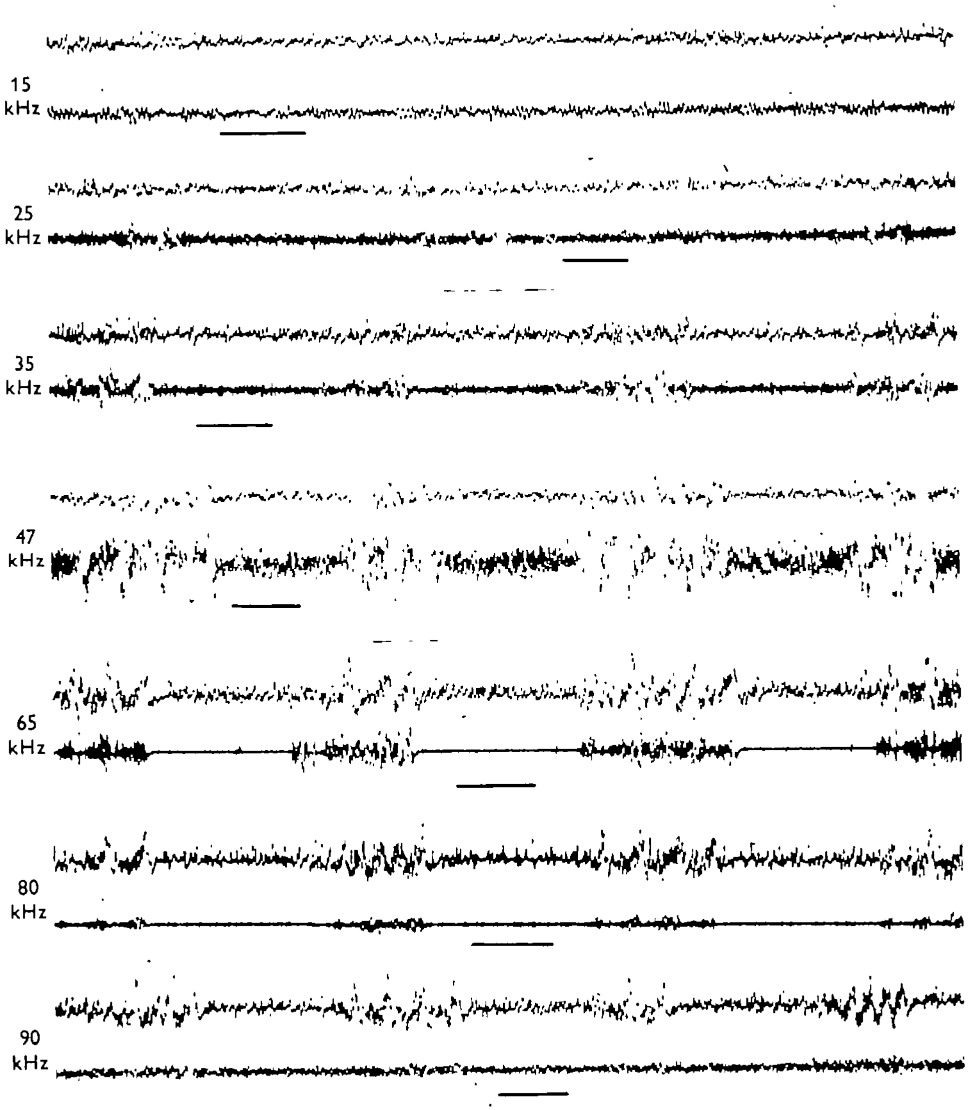

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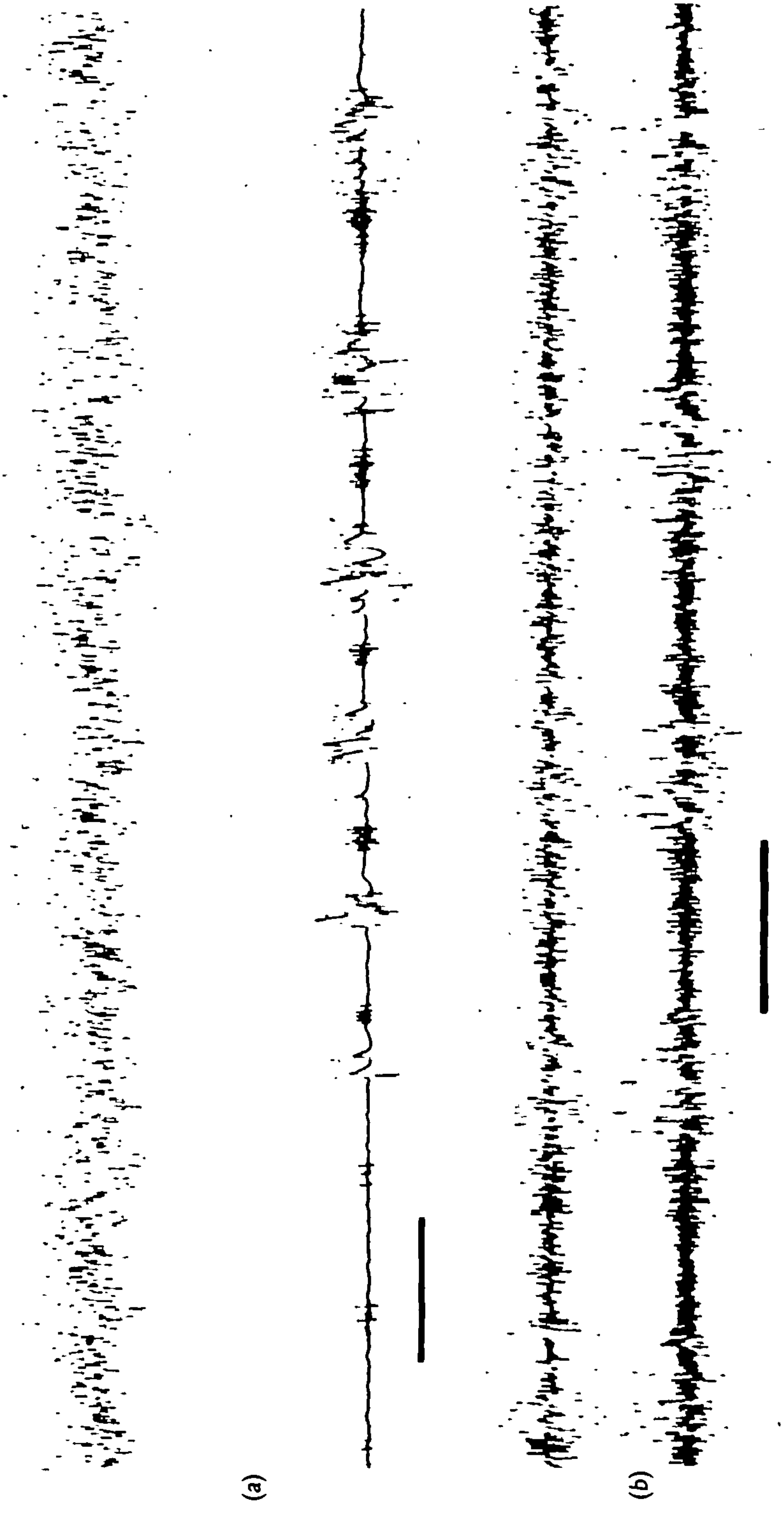

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PLATE 3

The responses obtained in the tympanal nerve of *M. brachyptera* (upper trace) to the high-frequency recording of the species song (lower trace). The figures given are the filter settings used during the high-frequency playback. Time marker 0·1 sec.

PLATE 4

The responses obtained in the tympanal nerve of *M. brachyptera* (upper trace) to the song of *C. parallelus* (lower trace). (*a*) Responses to the audio-frequency recordings. (*b*) Responses to the natural song. Time marker in each case 0·1 sec.