THE TRANSMISSION OF BUSH-CRICKET CALLS IN NATURAL ENVIRONMENTS

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Summary

This study discusses the structure of the calls of bush crickets *Steropleurus nobrei* and examines the way the structure of records of a bush-cricket call, comprising pure tone bursts and bursts of white noise, changes as these sounds propagate through different environments. Measurements of the coherence and spectral composition at different distances from the sound source are made in open and thickly vegetated environments. The results show that coherent frequency components in reproductions of the records of the natural call propagate over greater distances than do other components. The results are discussed in relation to the possible sources of information contained in insect calls and how the environment degrades these information sources as the call propagates away from the source. The consequences of the structure of the calls on the properties of the auditory organs of bush crickets is also discussed.

Introduction

The phonotaxis of female bush crickets towards singing conspecific males is a well-known phenomenon. Before this behaviour can commence the listening female must 'recognise' the call. Interposed between the calling and receiving individuals is a noisy communication channel, the biotope in which the species live. Noise within the channel arises from several sources. First, and possibly, most important is the effect of the wind on vegetation which generates considerable broad-band noise similar to white noise. Second, noise is generated by other animals living in the same biotope, competing for space in the same communication channel. Third, there is the effect of the biotope on the communication channel. Reflection of the sound by the ground and surrounding vegetation (reverberation) produces severe distortion of the call as it passes through the channel (Michelsen, 1985).

Problems similar to those outlined above are encountered in human verbal communication. Speech intelligibility is an important factor to be considered in the

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design of working environments where face to face verbal communication is the principal means of information transfer. This problem has been studied by French and Steinberg (1947) and later by Webster (1965). The assessment of speech interference by noise is based on the measured noise power in three octave bands centred on 500 Hz, 1 kHz and 2 kHz and on the ability of noise in these bands to mask speech. The resulting measure is called the preferred speech interference level (Hassall and Zaveri, 1979).

Similar measurements are not possible at present for bush-cricket calls since not all the components of the call which convey the information required to initiate phonotaxis are known.

The acoustic properties of bush-cricket calls

The calls of the bush cricket are generated by the action of a plectrum on the right forewing across a series of ridges (file) on the underside of the opposing wing, thus causing vibration of specialised resonant areas of either or both wings. One complete wing movement generates a syllable of the call. The syllable consists of a series of transient pulses of sound, each generated by the action of the plectrum on a single file tooth and described as the plectrum-tooth impulse. Figs 1–3 illustrate some high-resolution oscillogram traces of a short part of the calls and associated power spectra of three species of bush cricket. These oscillograms clearly indicate that the calls shown consist of a series of harmonic, transient pulses of sound produced by a single dominant, harmonic, highly damped, vibratory mode of the

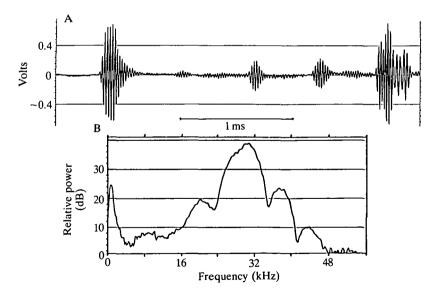


Fig. 1. (A) Oscillograms of the first two plectrum impulses of the call of a male *Poecilimon schmidti*. The small pulses are caused by reflection of the first impulse from nearby objects. (B) A Fourier power spectrum plotting relative power in decibels (dB) against frequency in kilohertz (kHz) of the first plectrum impulse of a series of calls as above.

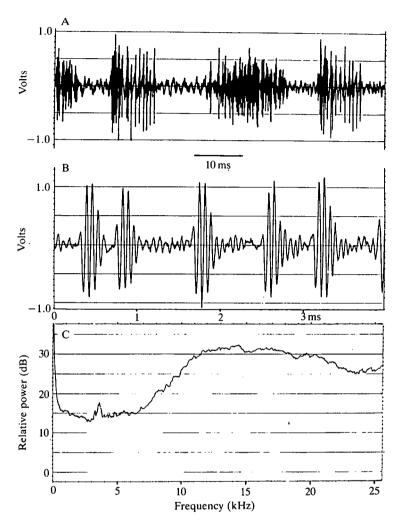


Fig. 2. (A) Part of the male call of *Polysarchus denticauda*. (B) Expanded section of part of the call in A. (C) Fourier power spectrum of a series of pulses, as in A.

wing resonator; the so-called carrier frequency. The sound level between the pulses does not drop to zero, as might be expected for highly damped transient pulses, but leaves a background which seems to be phasically related to the transient. The background may arise in part as reflections of the transient from the body of the insect or other close objects. With the exception of that derived from Fig. 2B, the power spectra derived from these calls (Figs 2C, 3D) do not apparently reflect the simple structure of the oscillograms. The reason for this is that these spectra are convolutions of at least three separate, though related, spectra (see Hartley and Stephen, 1989). First, there is the spectrum of the modal vibrations of the wing structures. A second spectrum is that due to the envelope of transient pulses, and third there is the spectrum associated with the intervals and

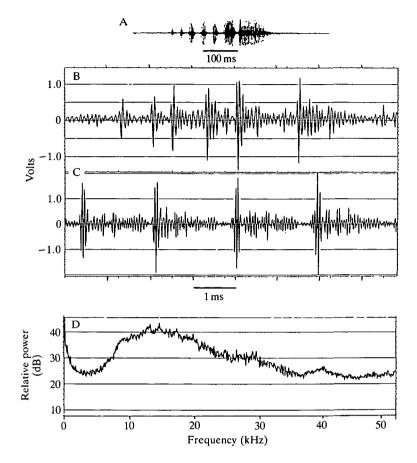


Fig. 3. (A) Complete male call of *Steropleurus nobrei*. (B) Expanded trace of the second syllable of the call in A. (C) Expanded section of the last semi-syllable of the call in A. (D) Fourier power spectrum of the complete call in A.

'noise' between the pulses. Referring again to the oscillogram traces of those calls consisting of several transient pulses, although the pulses are all very similar, the noise between the pulses and the pulse interval are obviously variable (see Figs 2, 3). Consequently, the power spectra of these components are not constant, i.e. the amplitude and phase of the frequency components which define the transient pulse shapes and the intervals between the pulses are only partially coherent (see equation 4). Only the modal vibration frequency of the wing resonator is coherent. In the resulting convoluted spectrum it is impossible to identify the contributions of the three basic spectral building blocks of the recorded power spectrum. An exception is for *Poecilimon schmidti* (Fig. 1B), where Fourier transformation was performed on the initial pulse of each call (Hartley and Stephen, 1989). Each of these basic spectra may have quanta of information associated with them. The question addressed in this paper is how the biotope transmission channel affects the information contained in each of these basic building blocks. In an attempt to

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examine this question we have measured the change in coherence of coherent, pure tone bursts of similar structure to the recorded plectrum file impulses as they pass through different environments. We have also measured the change in coherence of white noise tone bursts and, finally, we have measured the change in coherence over distance of parts of the call of a bush cricket.

Materials and methods

The bush-cricket call used in these experiments was that of the ephippigerine *Steropleurus nobrei* from a culture in the Zoology Department, University of Nottingham. Recordings of the call of *Steropleurus* were made on a Racal Store 4 reel-to-reel tape recorder using a QMC high-frequency microphone (model SM2) in a large open environment at $38.1 \,\mathrm{cm \, s^{-1}}$ (frequency response 50 Hz to >25 kHz).

Signal analysis

Extensive use has been made in the experiments described in this paper of a Bruel & Kjaer 2032 dual-channel signal analyser (referred to as the analyser in this paper). This machine is basically a real-time, two-channel, fast Fourier analyser. Having evaluated the Fourier spectra of the incoming signals on the two channels, the analyser offers routines which enable the operator to manipulate the individual basic spectra. It is also possible to compare the two spectra so as to reveal relationships, if any, between the two signals. Extensive use of these analysis routines has been made in this paper.

Coherence analysis

The coherence of two signals a(t) and b(t) is a linear measure of the similarity of the frequency structure, that is the amplitudes and relative phases of the components of the Fourier spectra, of the two signals. Mathematically, the coherence as a function of frequency, f, evaluated by the analyser, is defined as:

$$\gamma^2(f) = \frac{|G_{ab}(f)|^2}{G_{aa}(f) \cdot G_{bb}(f)},\tag{1}$$

where $G_{aa}(f)$ and $G_{bb}(f)$ are the autospectra of the signals a(t) and b(t) and $G_{ab}(f)$ is the cross-spectrum of the two signals a(t) and b(t). A full mathematical discussion of equation 1 is given by Randall (1987). The calculation of $\gamma^2(f)$ by the analyser is based on the evaluation of averaged spectral functions. If the signal a(t) is identical with the signal b(t):

$$a(t) \equiv b(t) \tag{2}$$

then

$$|G_{ab}(f)|^2 = G_{aa}(f) \cdot G_{bb}(f), \qquad (3)$$

and, from equation 1:

$$\gamma^2(f) = 1. \tag{4}$$

Any process which produces a change in a(t) with respect to b(t) leads to $\gamma^2(f)$

becoming less than unity. The coherence may fall below unity for any of the following reasons. (i) The presence of uncorrelated noise in a(t) and/or b(t). (ii) A non-linear relationship between a(t) and b(t). This occurs, for example, if b(t) is derived from the signal a(t) after propagation through a resonant environment. In this case (neglecting any attenuation of the signal) the signal b(t) is equal to the original signal a(t) plus a non-linear component due to the resonance. (iii) Any time delay between the two signals. Thus, propagation of the signal a(t) through a reverberant environment leads to b(t) containing coherent components derived from a(t) with different propagation (delay) times. The reduction in coherence is proportional to the square of the additional delay time Δt due to the reverberation.

In this paper extensive use has been made of what are referred to as coherent tone bursts. The technique for generating these tone bursts is described in Fig. 5. These tone bursts are such that all the bursts are identical, i.e. all bursts have the same phase and frequency structure. If a(t) and b(t) are successive tone bursts, then:

$$a(t) \equiv b(t) \,. \tag{5}$$

From equation 4,

$$\gamma^2(f) = 1.$$
 (6)

This is a sufficient condition to define the bursts as being coherent.

Coherent power

The coherent output power (COP) is a particularly useful measure derived from the coherence $\gamma^2(f)$. It is defined from it as follows:

coherent output power =
$$\gamma^2(f) \cdot G_{bb}(f)$$
. (7)

The COP gives a measure of that part of the measured output autospectrum of the signal b(t) that is coherent with the autospectrum $G_{aa}(f)$ of the original (input) signal a(t). The relevance of the COP to bush-cricket communication is discussed later in this paper.

Logarithmic filtering

The major closing syllable of the call of *Steropleurus nobrei* (see Fig. 3C) consists of a series of plectrum-tooth impulses. The Fourier spectrum derived from such a call consists of frequency components associated with the vibration of the wing resonator, components arising from the envelope of the plectrum-tooth impulse and, finally, components associated with the repetitive plectrum-tooth impulses. The frequency components of principal biological interest are those associated with the vibration of the wing resonator. These can be effectively filtered out from the total Fourier spectrum using logarithmic or cepstrum techniques. These techniques are fully discussed by Randall (1987).

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Experimental methods

The coherence measurements presented in this paper are a comparison of the frequency structure of the call or tone burst detected by a microphone placed close to the source of sound with the frequency structure of the same signal detected by another variably distant microphone. Two Bruel & Kjaer microphones, type 4133, were used, each directly linked to the analyser with 50 m screened cable. The experiments were carried out at two sites in the garden of the house of R. O. Stephen in Leicester. The garden consists of a large, flat lawn $24 \text{ m} \times 12 \text{ m}$ surrounded by flower beds 3 m in width. One half of the grass, left to grow to a height of 10 cm to approximate a flat open meadow, was used as experimental site one. One of the bordering flower beds, containing a mixture of shrubs and annual flowers growing to an average height of 1 m, was used as experimental site two. Both sites were initially marked out with markers placed at 1 m intervals along a straight line over a distance of 20 m.

The sound source used in the experiments was a small Audax speaker (model HD 100D25). The frequency response of the speaker was measured *in situ* with the analyser using a white noise signal derived from the analyser. The speaker was placed 2m above the ground in the centre of the lawn and a Bruel & Kjaer microphone was placed 0.5 m from the speaker at the same level as the speaker. The measured frequency response is shown in Fig. 4.

Before beginning experimental measurements, the propagation time of sound between a stationary microphone close to the sound source and the roving microphone at each 1 m mark was measured. The speaker was driven by the internal impulse generator of the analyser. The acoustic impulse detected by each microphone was displayed simultaneously on the screen of the analyser. Using the time cursor on the analyser, the propagation time between the two microphones

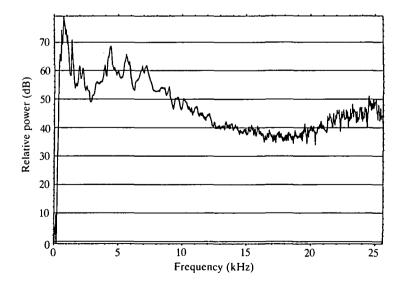


Fig. 4. Frequency response of the Audax speaker

could be measured with an accuracy of $1 \mu s$ for the maximum microphone spacing of 20 m in still air.

Once the transmission times had been established, the coherence of part of the major syllable of a male *Steropleurus nobrei* (Fig. 3C) replayed from a tape loop, a repetitive pure tone or a white noise burst was measured at 0 m, 1 m, 2 m, etc. microphone separation. The two microphones were always placed at the height of the sound source and pointed directly towards the source. The analyser was triggered either directly from the tone burst gating pulse or from the rising phase of the envelope of the tone burst or plectrum-file impulse detected by the fixed microphone. All the coherence measurements shown are the average of 50 consecutive sweeps of the analyser.

The pure tone bursts used were of constant frequency and phase structure. The electronic set-up used to generate these tone-bursts is shown in Fig. 5. The white noise signal was obtained from the internal signal generator of the analyser. The tone gate was constructed around a Motorola MC3340P audio attenuator chip.

The call of *Steropleurus nobrei* consists of two distinct parts: an initial series of about five short closing syllables of irregular plectrum-tooth impulses lasting about 5 ms each, followed by a long opening and closing syllable (Fig. 3A). The major closing syllable lasts about 60 ms and consists of about 30 equally spaced plectrum-tooth impulses. The two different syllable types of this call thus have different tooth-strike rates. It was possible to compare the effect on environmental transmission of the two different syllables. The modal wing vibration frequency is the same for both syllables. Tape loops of a single short, and part of the long, syllable were made for a Racal Store 4 tape recorder at $38.1 \,\mathrm{cm \, s^{-1}}$ (frequency response 50 Hz to >25 kHz). These tape loops were replayed at the same speed and then broadcast using the Audax tweeter. No-short term 'wow' could be discerned listening to the broadcast calls. The period of the modal wing vibration estimated from records of the broadcast tape loop calls was the same as that of the original recording. The frequency of this component of the call was thus unchanged within the accuracy of estimation of the period (See Fig. 3); it is therefore not unreasonable to assume that the remainder of the frequency structure was also unchanged. Certainly no obvious changes could be discerned from records of the tape loop calls (not shown).

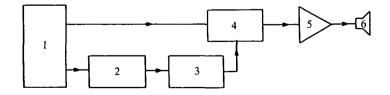


Fig. 5. Block diagram of the electronic set-up used to produce coherent acoustic tone bursts. (1) Exact model 337 digital phase generator, (2) pulse counter module, (3) pulse width module, (4) tone gate, (5) power amplifier, (6) speaker.

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Results

The experiments described below were carried out on days when the wind was low. Unfortunately, the air was never totally still and, as a result, the background noise level was never absolutely constant. The major component of the background noise was caused by movement of the surrounding vegetation by the wind. Mean background noise levels were approximately 35dB SPL and constant over the frequency band 1-25 kHz. The wind also had two other important effects. First, it caused the propagation time of the sound pulses between the two microphones to vary. Second, at the second experimental site, the wind blowing through the plants would have caused local areas of turbulence in the air leading to distortion of the propagating sound. Even the onset of the most gentle breeze caused the coherence to fluctuate from measurement to measurement. As a result, some of the changes in coherence observed are due to air movements. This effect was kept to a minimum by only recording late at night on days when air movements were at a minimum. Coherence measurements on the analyser involve an averaged comparison of a section of the call, repeated 50 times, detected by the near microphone with precisely the same section of the call picked up by the far microphone after it has passed through the biotope. Slight shifts in the propagation time caused by air movements will cause the average coherence to fall. Such effects are, of course, not relevant to the receiving insect as it is only interested in the overall frequency structure of the sound it hears.

Coherence measurements with coherent pure tone bursts

Fig. 6 illustrates the coherence of the pure tone bursts with a 15 kHz carrier

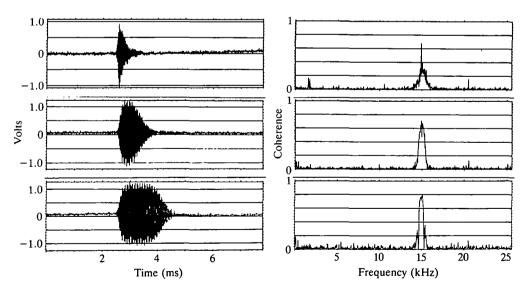


Fig. 6. The change in coherence of 15 kHz coherent tone bursts of different duration. The tone bursts are shown in the three left-hand traces. The corresponding coherence at 2 m microphone separation is shown in the three right-hand traces.

frequency, of durations 0.5, 1.0 and 2.0 ms, and an interburst interval of 100 ms. The maximum amplitude of the three bursts was made equal. The microphones were 0.5 m and 2.5 m, respectively, from the speaker, and the speaker and microphones were placed 50 cm above the grass level. The analyser was triggered by the rising phase of the tone burst picked up by the microphone 0.5 m from the speaker. These results show that pulses of increased duration propagate coherently better than pulses of short duration. Since the carrier frequency was the same for the three pulses, the only factor that had changed was the frequency structure of the envelope. Increasing the pulse duration increases the amplitude of lower-frequency components in the envelope spectrum. These lower-frequency components of shorter tone bursts (see Figs 9, 11).

Fig. 7 illustrates the change in coherence, with distance, of the 1 ms coherent tone burst under the conditions described for Fig. 6. The frequency distribution of the coherence reflects the frequency components in the power spectrum of the original tone burst, which are coherent at both microphones at the respective spacings. As the separation between the microphones increases, the original power spectrum is attenuated and overlaid by 'noise'. Consequently, the frequency distribution of the coherence shrinks until, at a 4m spacing, the only

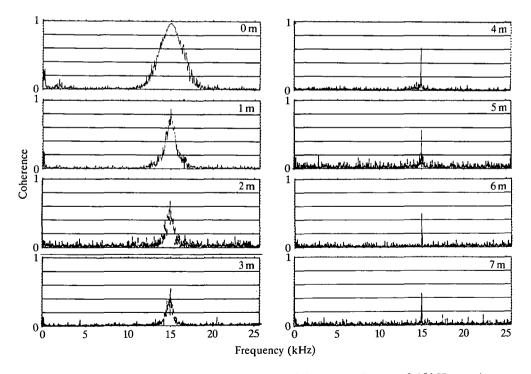


Fig. 7. The coherence of a coherent series of 1 ms tone bursts of 15 kHz carrier frequency. Tone burst was measured at a height of 50 cm over grass. The separation between microphones is 1 m increments. Numbers give separation distance between microphones in metres.

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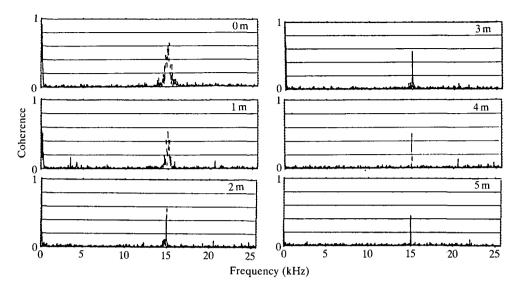


Fig. 8. Change in coherence (at 1 m intervals, as in Fig. 7) of a 1 ms 15 kHz tone burst (as in Fig. 7) measured at a height of 50 cm above the ground in thick vegetation.

component of the original tone burst to remain coherent, i.e. capable of transmitting useful information, is the 15kHz carrier. All other frequency components which characterised the tone burst are totally incoherent and any useful information associated with them has been lost. The measurement of the coherence at 2 m separation in Fig. 7 and that shown in Fig. 6 were carried out at different times. The change in coherence between these two measurements reflects the magnitude of the changes observed due to varying environmental conditions. Fig. 8 illustrates the effect on the coherence of changing from the open short-grass site to the dense vegetation site. The microphones and speaker were placed 50 cm above ground level. The vegetation reduces the distance over which any component of the tone burst can be coherently propagated by 2-3 m. As before, the carrier frequency propagates coherently for the greatest distance. Measurements were also carried out using tone bursts of different carrier frequencies in the range 0-25 kHz. The results (not shown) were similar to those shown in Figs 7 and 8: as expected, lowering the carrier frequency increased the maximum range of propagation of the signal. The 15 kHz results are illustrated as this frequency is very close to the modal vibration frequency of Steropleurus nobrei.

Coherence measurements with white noise tone bursts

Fig. 9 illustrates the coherence and autospectra measured at 2 m intervals for a 50 ms gated white noise pulse. The measuring microphones and speaker were at grass height (10 cm). The analyser was triggered from the gating pulse. The autospectra show the changes that have been observed many times before; that is, a frequency-dependent attenuation with increasing distance and the effect of

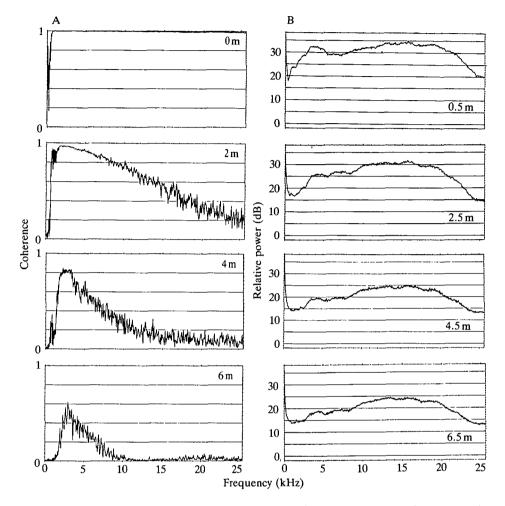


Fig. 9. (A). The change in coherence (with distance) of a white noise pulse measured at 2 m intervals 10 cm above the grass. The separation distance between the microphones is as indicated (in metres). (B) Autospectra of the white noise pulse measured by the distant microphone as above. This microphone is a further 50 cm from the speaker.

sound reflected from the ground interfering with sound waves along the line of sight from the speaker to the distant microphone. The fluctuations in the amplitude were not particularly large. If one looks at the coherence, the effects observed in the autospectra become magnified. We can see that the low-frequency components in the sound propagate coherently with increasing distance better than the high-frequency components. The effects of reverberations (reflections from the ground) generate fluctuations in the coherence which depend on the distance between the two speakers. As expected, the two signals are totally coherent with the microphones placed at the same distance close to the source.

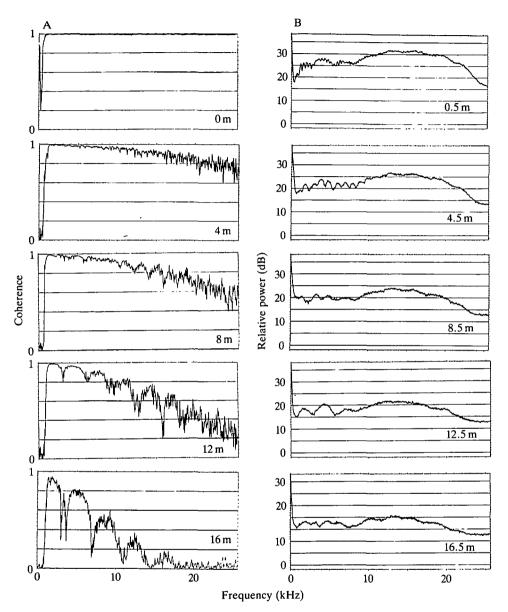


Fig. 10. (A). Coherence of a white noise pulse measured at 4 m increments over grass at a height of 1 m, from 0 to 16 m separation, as indicated. (B) Autospectra of the white noise pulse measured at 4 m increments by the distant microphone in A. Upper trace in A is 0.5 m from speaker, lower trace in B 16.5 m from speaker.

The 'roll-off' in coherence below 1 kHz is due to the loss of power of the speaker below 1 kHz.

Fig. 10 illustrates the effect of increasing the height of the sound source and microphones to 1 m above grass level. Reverberation, principally from the ground, is the major effect which generates distortion of the signal. This can be seen as

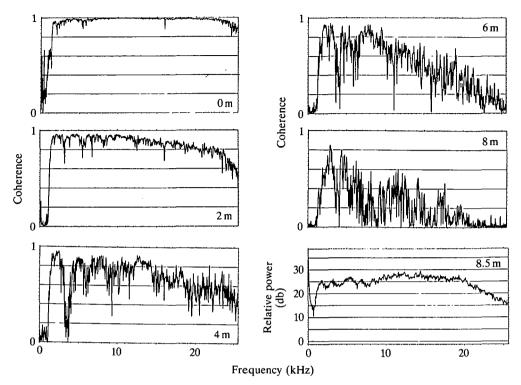


Fig. 11. Coherence of a white noise pulse measured at 2 m increments in thick vegetation at a height of 50 cm. Upper left trace 0 m separation. The lower right trace illustrates the autospectrum measured at 8.5 m.

fluctuations (approximately $5 \, dB$ in magnitude) in the autospectra with increasing separation between the microphones. These fluctuations in the autospectra are magnified in the coherence.

Fig. 11 illustrates the effect of moving to the dense vegetation site. The microphones were 50 cm above ground level. Reverberation from the surrounding plants and the ground is probably the most important factor producing the changes in coherence observed.

Coherence of insect calls

Fig. 12 illustrates the coherence, coherent power and logarithmically filtered spectra of the long pulse of the call of *Steropleurus nobrei* at microphone separations of 0, 2, 4 and 8 m measured at the dense vegetation site. The reduced

Fig. 12. Propagation of the call of *Steropleurus nobrei*. (A–D) The coherence of the final semi-syllable of the call measured at microphone separations of 0, 2, 4 and 8 m in dense vegetation. (E) The coherence of the second syllable measured at a microphone spacing of 8 m. (F,G,H) The coherent output power of the final semi-syllable at distances of 0, 2 and 8 m. (J,K) The logarithmically filtered power spectra of the final semi-syllable measured 0.50 and 8.50 m from the speaker. The arrows mark the modal vibration frequency of the wing resonator.

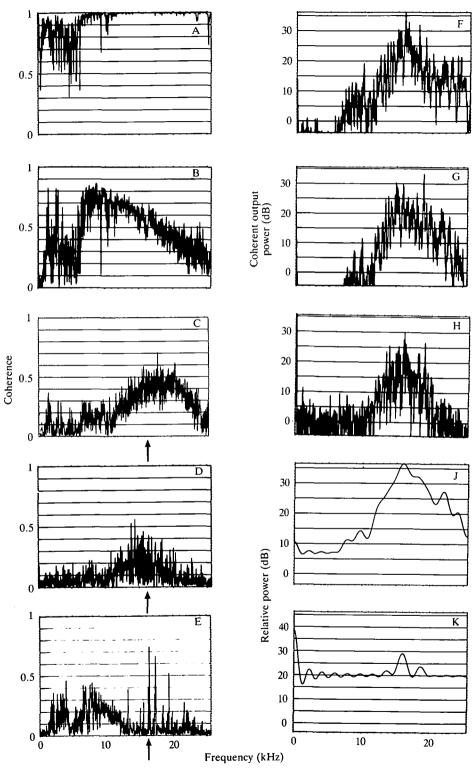


Fig. 12

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coherence observed below 6 kHz at 0 m microphone separation is due to the falloff in power in the call below this frequency observed in the autospectrum. With increasing separation between the two microphones, the coherence of the call falls off as the call detected by the distant microphone is overlaid by environmental noise. At a separation of 8 m, the only frequency components in the original call with any significant coherence are those centred about the modal vibration frequency of the wing resonator (indicated by the arrow). This frequency was estimated by measuring the period of the damped harmonic oscillation seen in the analogue signal of a single plectrum-tooth impulse. Similar results were observed for the coherence of the short syllable, the coherence at 8m separation only is shown in Fig. 12E. The observed coherence of this part is less than that of the major syllable, because the brevity of the syllable reduces the total acoustic power in the call. As a result, the same level of background noise has proportionately a much greater effect. Other than this, the short syllable appears to propagate in the same manner as does the major syllable. Both parts appear to propagate as a train of coherent (i.e. constant frequency and phase structure) tone bursts.

The coherent output power in the major syllable clearly remains centred about the modal frequency of the wing resonator. At 8 m separation the only significant coherent power in the syllable is at this frequency.

The logarithmically filtered spectra have been shown rather than the more familiar autospectra. This filtering procedure removes frequency components associated with the intervals between successive plectrum-tooth impacts and leaves only those associated with the modal wing vibration. At a microphone separation of 8 m the only significant component in the call is at the modal frequency.

Discussion

Over the last half century an extensive literature has built up on the acoustic behaviour of bush crickets and other Orthoptera. In spite of this, the specific components contained in the calls necessary for phonotaxis remain largely unknown. Whatever these components are, they need to be 'recognised' by the receiving animal as having been broadcast by the conspecific before phonotaxis can begin. Precisely what 'recognition' of the received signal entails is not known in the case of bush crickets.

Because of the inherently simple structure of many bush-cricket calls, the coherence of the call as measured in this paper can be used as a measure of the degradation of the call with distance. The results of this investigation have shown that the propagation of a recorded call of *Steropleurus* and a white noise pulse, both having roughly similar overall autospectral (see Figs 3C and 11 lower right-hand trace) properties and broadcast by the same speaker, are totally different when measured in terms of the coherence. For the white noise pulses the lowest frequencies maintain coherence over the greatest distances. In the case of the call, it is the frequency associated with the modal vibration of the wing resonator that

maintains the greatest degree of coherence with increasing distance. In addition, the coherent output power detected by the distant microphone is also centred about this frequency. Further, the observations on the propagation of coherent tone bursts in the environment indicate that the specific frequency structure of the plectrum-tooth impulses of the call of *Steropleurus* may be responsible for the way the call propagates through the environment.

As the distance from the source (either a calling cricket or a loudspeaker) increases, the only frequency component in the call to retain any degree of coherence is the frequency associated with the modal wing vibration frequency. Observations of the calls of many bush crickets we have recorded (e.g. Fig. 1) have shown that successive plectrum-tooth impulses look like highly damped, pure tone, coherent (in terms of equation 4) pulses of sound. It is thus not unreasonable to assume that the observations on the call of *Steropleurus* may apply to other bush-cricket calls.

The observations discussed above raise the interesting question of how the auditory system of a bush cricket receives and recognises the call. The function of the central nervous system is to extract species-specific information from the signals presented to it by the auditory system. It is on the basis of the information received that a decision is made to commence phonotaxis. The information content or entropy of a call is totally determined by its frequency structure. For Steropleurus the major closing syllable consists of about 30 equally spaced, nearly identical, plectrum-tooth impulses. The overall information in this syllable is made up of three components, one associated with the modal vibration, a second associated with the intervals between successive plectrum-tooth impulses, and a third associated with the remaining frequencies, components such as those associated with the plectrum-tooth impulse envelope. The latter two information sources both have a broad frequency structure. Fidelity of information transfer requires fidelity of frequency transmission. Our results suggest that, because of reverberation, attenuation and noise, these two components will have all but vanished in a dense biotope at distances greater than a couple of metres. The information associated with the wing vibration, because of its coherent nature, can propagate over relatively large distances before becoming degraded. Stephen and Bailey (1982) have shown, for the bush cricket Hemisaga and other West Australian bush crickets, that auditory reception and directionality are highly frequency selective. These observations, together with the results obtained in this investigation, suggest that phonotaxis at any distance from a source may be highly frequency selective.

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