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SHORT COMMUNICATION

A PARADOXICAL PROBLEM IN INSECT COMMUNICATION: CAN BUSH CRICKETS DISCRIMINATE FREQUENCY?

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Many bush crickets (Tettigoniidae) produce calls that consist of trains of transient high-frequency pulses (Fig. 1). Each pulse is generated by a file tooth on one wing being struck by a plectrum on the other, causing the wing resonator to produce harmonic transients each composed of only two or three cycles of oscillation. In animals, high-frequency sound can only be detected by means of some form of auditory filter, since the refractory period of the nervous system restricts direct measurement using periodicity to frequencies below 1 kHz. The necessity of using a filter produces a paradoxical situation with these brief transients. If the bandwidth of a tuned filter is such that frequency can be accurately discriminated, the response time may exceed the duration of the signal and then there would be no output. To respond to such a signal, the filter bandwidth must be increased but then frequency information is lost.

The stridulatory apparatus of bush crickets is an elaborately constructed device with design features peculiar to each species. When activated, the resonating area produces a characteristic modal vibration – the so-called carrier frequency of the call. This is inbuilt and cannot be altered by the insect. Other features of the call – tooth strike rate, amplitude modulation, syllable length and syllable sequence – could be altered, since they are theoretically controlled by the insect's nervous system. If the tooth strike rate is such that the wing resonator is synchronously excited then a long harmonic call can result, as in *Ruspolia differens* (Serville) (previously *Homorocoryphus*) (Bailey, 1970) and *Mecopoda elongata* (Linnaeus) (J. C. Hartley and R. O. Stephen, personal observation). Such calls present no problem in frequency determination. If, however, the tooth strike rate is low, each impulse may produce only a few oscillations which decay well before the next impulse, as shown by the examples in Fig. 1 and given for many other species (Table 5.1, Sales and Pye, 1974). The use of brief harmonic transients is therefore by no means a rare occurrence in the Tettigoniidae. If these brief transients are to have a communication value, is their frequency important or is it just the pulse

Key words: Tettigoniidae, sound reception, acoustic filter, transient sound, Helmholtz resonator, *Conocephalus dorsalis*, *Steropleurus ortegai*.

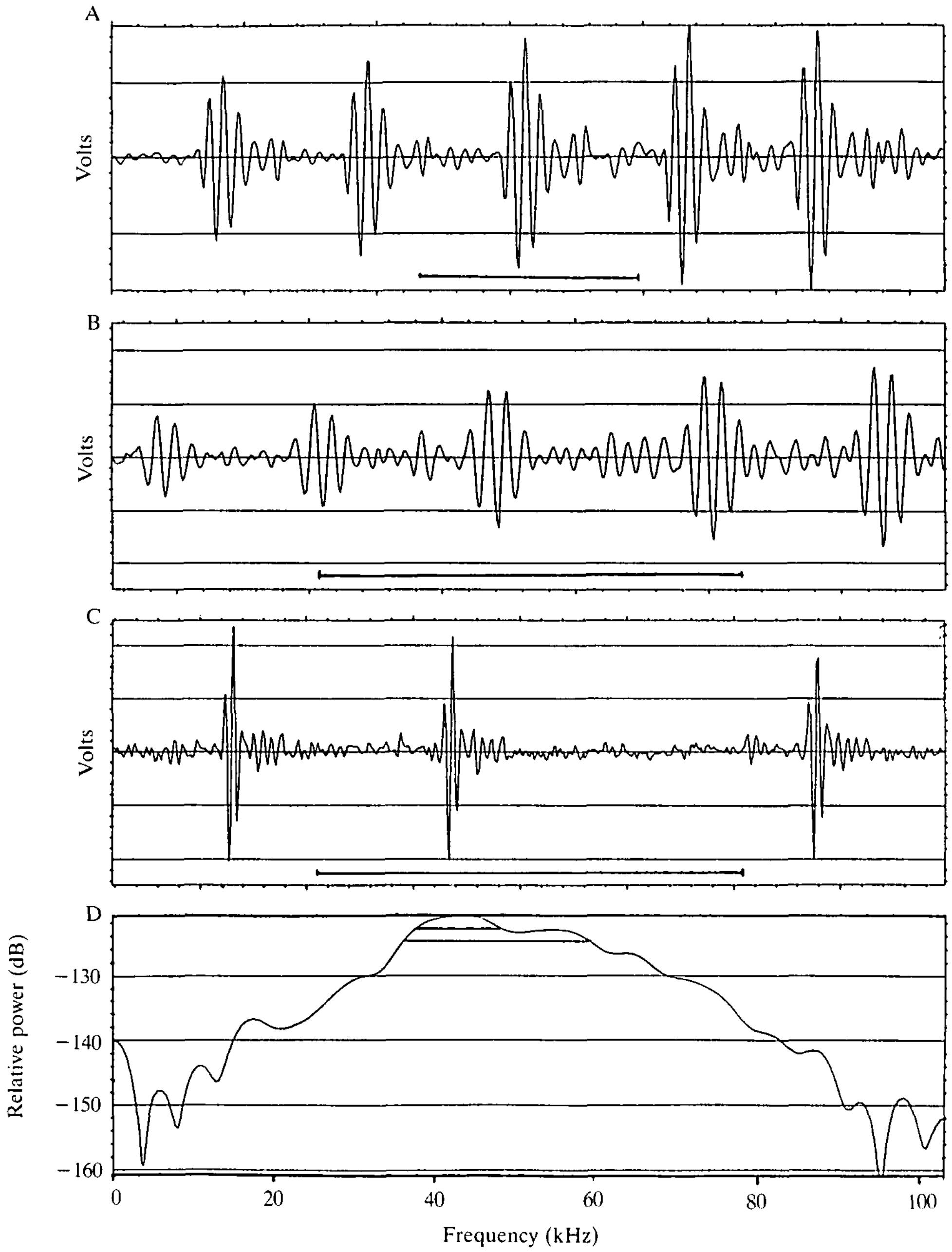

Fig. 1. (A–C) Analogue traces of part of the calls of bush crickets from three different subfamilies: (A) *Steropleurus ortegai* (Pantel) (Ephippigerinae); (B) *Metrioptera roeseli* (Hagenbach) (Tettigoniinae); (C) *Conocephalus dorsalis* (Latreille) (Conocephalinae). Times bars, 1 ms. (D) Power spectrum of oscillations arising from a single tooth strike in the call of *Conocephalus* produced by a Bruel & Kjaer 2032 FFT analyser. Upper line represents the 12 kHz uncertainty at −3 dB below maximum, lower line represents the 12 kHz uncertainty at −5 dB.

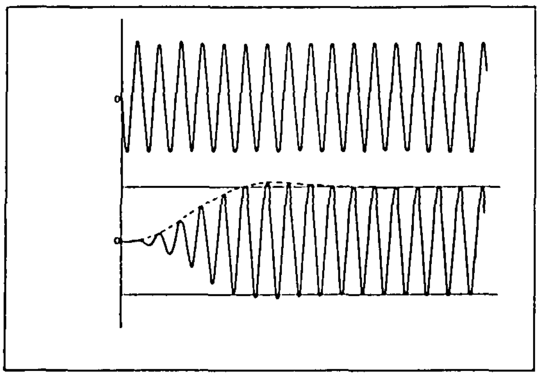

Fig. 2. Typical filter response (lower record) from one-third octave filter to a sudden sinusoidal input (upper record) (after Randall, 1977). It clearly shows that several oscillations are required to build up to a detectable response.

pattern that identifies the call? If the frequency is important, how can it be determined?

Detection and analysis of harmonic transients are governed by constraints imposed by the signal and the detector system. Thus, for brief harmonic transients:

$$\Delta f \Delta \mathrm{t} = 1\,, \tag{1}$$

where Δf is the frequency uncertainty of the transient and Δt its duration. For the tuned filter in the detector:

$$(B/f_0)n = 1\,, \tag{2}$$

where B is the bandwith, f_0 its centre frequency and n the number of cycles required for the filter response to reach its maximum value (Randall, 1977). A typical filter response is shown in Fig. 2. For any filter network, if the bandwidth B of the filter is less than the uncertainty Δf, then the bandwidth of the output signal is determined by the duration Δt of the input transient, rather than by the bandwidth of the filter. The only effect of a filter of bandwidth less than Δf will be to attenuate the input signal simply because the filter cannot respond rapidly enough. If the filter is not to attenuate the input signal, its bandwidth must be greater than Δf, but then the filter will not be able to discriminate the frequency.

Taking the call of *Conocephalus dorsalis* as an example (Fig. 1C), each tooth strike generates a transient with only two oscillations before decaying, leaving a long and variable gap before the next impulse. The frequency of these oscillations, estimated from the trace, is 44 kHz. The calculated frequency uncertainty is ±11 kHz (equation 1). The power spectrum of a single tooth strike (Fig. 1D) also shows frequency uncertainties of 12 kHz at the −3 dB level and 23 kHz at −5 dB (upper and lower bars, respectively, in Fig. 1D). Thus, precise determination of the frequency of the transient is impossible, illustrating the type of acoustic paradox confronting the insect.

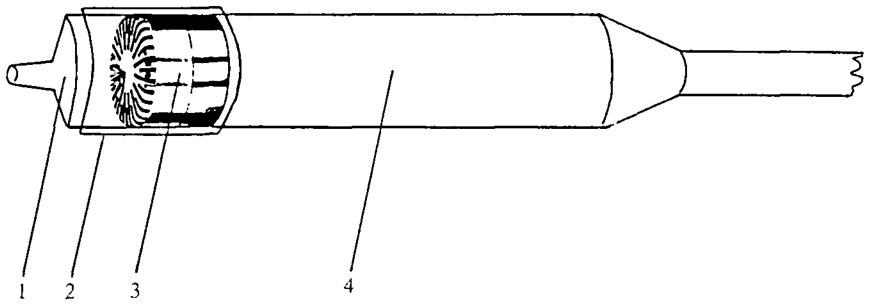

Fig. 3. Microphone with Helmholtz modification. (1) Front section of 10 ml disposable syringe, (2) silicone rubber seal, (3) Bruel & Kjaer microphone type 4133, (4) Bruel & Kjaer preamplifier type 2619.

Since the harmonic transient is generated by the vibration of the highly specialised wing resonator, which is peculiar to each individual species, it must be assumed that the insect has a way of receiving the information contained within the transient. This information could become available if the ear contained an additional high Q resonator. Stephen and Bailey (1982) suggested that the air pockets contained by the external tympanal chambers (slit cavities) of the ears of *Hemisaga* could act as as pair of coupled Helmholtz resonators. A feature of Helmholtz resonators is their high value of Q. The effect of including such resonators into the ear would be to extend the overall duration of each pulse, thereby effectively increasing the number of cycles in each transient. This should significantly improve the frequency discrimination.

To test this, we constructed a Helmholtz resonator which could be attached to the front of a 0.5 in (12.5 mm) Bruel & Kjaer microphone (Fig. 3). The frequency response of the modified microphone (Fig. 4A) is now highly tuned with a centre frequency of 2.6 kHz. An Audax tweeter was then driven to produce a transient pulse at this frequency. The transient signal was initially recorded through the microphone without the resonator (Fig. 4B). The resonator was re-attached and the transient recorded again (Fig. 4C). The addition of the resonator has clearly enhanced both amplitude and duration of the transient. Changing just the

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Fig. 4. Experimental results. (A) Frequency response of the microphone, with Helmholtz resonator attached, to a white noise signal. (B–E) Analogue traces of experimental pulses. The relative positions of the microphone and speaker were kept constant. (B) Transient pulse at 2.64 kHz broadcast by the Audax HF speaker as received by the unmodified microphone. (C) The same transient as perceived by the microphone fitted with the tuned Helmholtz resonator. (D) The response of the microphone/Helmholtz resonator tuned as above (B) to a 3.64 kHz transient pulse of the same number of oscillations as in A. (E) The response of the microphone/ Helmholtz resonator tuned as above (B) to a 1.64 kHz transient pulse of the same number of oscillations as in A.

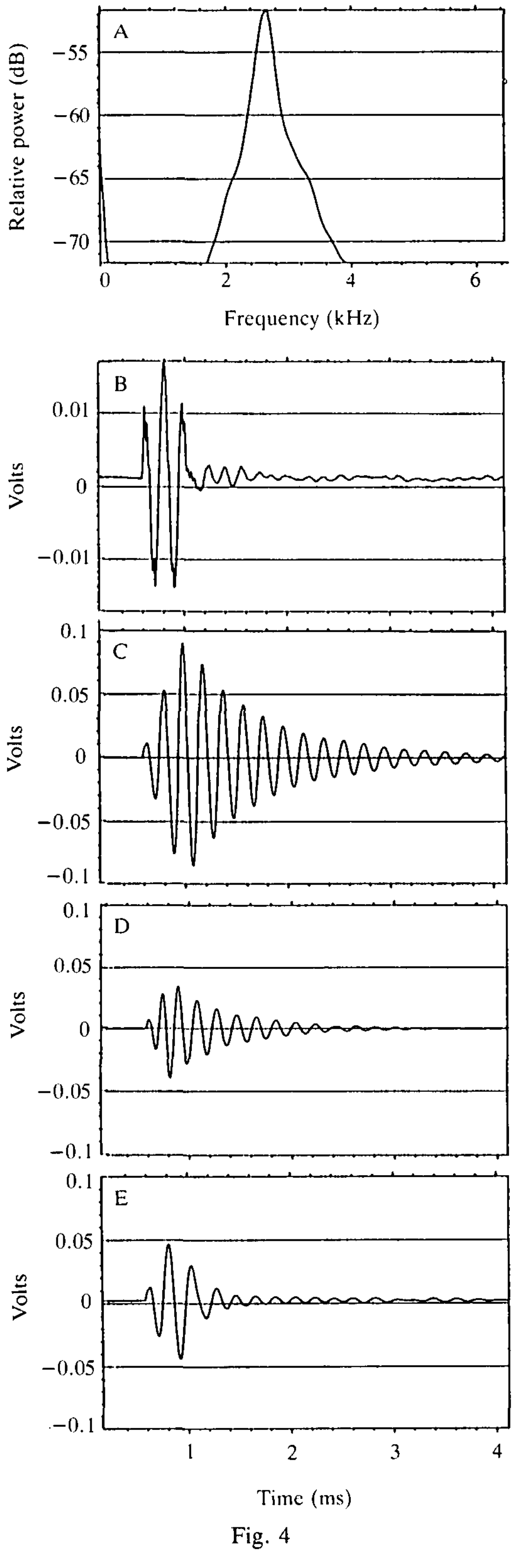
A
Relative power (dB)
-55
-60
-65
-70
0
2
4
6
Frequency (kHz)
B
Volts
0.01
0
-0.01
C
Volts
0.1
0.05
0
-0.05
-0.1
D
Volts
0.1
0.05
0
-0.05
-0.1
E
Volts
0.1
0.05
0
-0.05
-0.1
1
2
3
4
Time (ms)

Fig. 4

frequency of the transient, but keeping the number of oscillations, amplitude and relative positions the same, produced results shown in Fig. 4D,E. At both higher and lower frequencies, not only is the perceived pulse shorter but it is also of much lower intensity. One problem resulting from these very brief transients is that rise time and envelope shape will both contribute substantially to the convoluted sound (the overall combined sound, see Randall, 1977) to which our system was tuned. Our relatively crudely constructed Helmholz resonator is unlikely to perform as well as those with several million years' refinement behind them.

Many Tettigoniidae have developed slit chambers over their ears. There seems to be no generally accepted explanation for the function of these structures, although it has been suggested that in *Hemisaga* they could improve location of the species call and hence aid phonotaxis (Stephen and Bailey, 1982). We now suggest that they may also enable frequency determination of harmonic transients that would otherwise be too brief to resolve. This argument is particularly applicable to ephippigerines, which all appear to use extremely brief transients lasting no more than three or four oscillations, as exemplified by *Steropleurus ortegai* (Fig. 1A). That the rise time of the perceived transient will be slightly delayed matters not, as the relative time intervals will stay the same. Auditory sensitivity may also benefit from an improvement in the signal to noise ratio which will inevitably follow from an enhanced frequency sensitivity.

The Mecopodinae and many Phaneropterinae have exposed tympana with no development of slit chambers. *Mecopoda elongata* with its long harmonic call, as previously mentioned, needs no enhancement system. The phaneropterines *Ancistrura nigrovittata* (Heller, 1988), *Poecilimon schmidti* (Hartley and Stephen, 1989), *Leptophyes punctatissima* and *L. laticauda* (J. C. Hartley and R. O. Stephen, personal observations) produce calls in which each tooth impulse produces a brief tone burst consisting of at least six oscillations. Such pulses will not present the extreme frequency resolution problems that appear with the Ephippigerinae.

It might be argued that it is the tooth-strike frequency and not the resonant frequency of the wing that is important in species such as *Conocephalus*. However, as shown in Fig. 1C, this is clearly not regular enough to generate a distinctive frequency. In behavioural experiments on *Requena*, Bailey and Yeoh (1988) found that females were able to differentiate between 16 and 28 kHz, but were unable to discriminate between 28 and 36 kHz. This is rather better than the signal frequency uncertainty apparent in *Conocephalus*. Kalmring *et al.* (1990) report that transient pulses at the right frequency are most important components in many bush cricket communication systems. The tettigoniid ear is known to have a spatial arrangement of receptors associated with particular frequencies (reviewed by Rheinlaender and Römer, 1990).

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References

BAILEY, W. J. (1970). The mechanics of stridulation in bush crickets (Tettigonoidea, Orthoptera). I. The tegminal generator. *J. exp. Biol.* **52**, 505–517.

BAILEY, W. J. AND YEOH, P. B. (1988). Female phonotaxis and frequency discrimination in the bushcricket *Requena verticalis*. *Physiol. Ent.* **13**, 363–372.

HARTLEY, J. C. AND STEPHEN, R. O. (1989). Temporal changes in the quality of the song of a bush cricket. *J. exp. Biol.* **147**, 189–202.

HELLER, K.-G. (1989). Bioakustik der europaischen Laubheuschreken. Weikersheim, Germany: Verlag Joseph Margraf.

KALMRING, K., ROESSLER, W., SCHROEDER, J., STIEDL, O., BICKMEYER, U. AND BAILEY, W. J. (1990). Importance of tooth impact rate in acoustic communication in bushcrickets. In *Sensory Systems and Communication in Arthropods* (ed. F. G. Gribakin, K. Wiese and A. V. Popov), pp. 248–253. Basel: Birkhauser Verlag.

RANDALL, R. B. (1977). *Application of B&K Equipment to Frequency Analysis.* Naerum, Denmark: Bruel & Kjaer.

RHEINLAENDER, J. AND RÖMER, H. (1990). Acoustic cues for sound localization and spacing. In *The Tettigoniidae: Biology, Systematics and Evolution* (ed. W. J. Bailey and D. C. F. Rentz), chapter 13, pp. 248–264. Bathhurst, NSW, Australia: Crawford House Press.

SALES, G. D. AND PYE, J. D. (1974). *Ultrasonic Communication by Animals.* London: Chapman & Hall.

STEPHEN, R. O. AND BAILEY, W. J. (1982). Bioacoustics of the ear of the bushcricket *Hemisaga* (Saginae). *J. acoust. Soc. Am.* **72**, 13–25.