

Stridulation and Tegminal Resonance in the Tree Cricket *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae)

Enrico Sismondo

10 Robin Hill Road, Scarsdale, New York 10583, USA

Accepted October 10, 1978

Summary. Study of the stridulatory mechanism of the tree cricket *Oecanthus nigricornis* F. Walker has yielded the following principal results:

1. The normal carrier frequency of the song is equal to the tooth-impact frequency throughout the range 3,000 Hz (at 15 °C) to 4,600 Hz (at 32 °C).

2. Under conditions of thermal equilibrium, pulse frequency and tooth-impact frequency are strongly correlated: however, the two frequencies are not controlled by the same underlying mechanism, as shown by marked differences in their reaction to step changes in temperature.

3. Tegminal free resonances have been identified in the range 1,000–6,900 Hz; between 3,800 and 4,600 Hz the resonances form a virtually continuous series, corresponding to modes of vibration in which the three major distal cells of the tegmen plus a variable portion of the harp oscillate as a single membrane, whose amplitude maximum is near the center of the tegmen distal to the harp (Fig. 8A, B); these free resonances are excited by corresponding tooth-impact frequencies and are responsible for the normal carrier of the song at temperatures above 22 °C. Below 3,800 Hz free resonances have also been found and their modes of vibration identified: typically in this range a stationary node bisects each tegmen transversely, with maximum amplitude of oscillation at the distal margin of the tegmen, and a secondary maximum in the basal region near the file vein (Fig. 9B, E). A continuous series of prominent tegminal resonances exists in the range from 5,100 to 5,850 Hz (i.e. outside the tooth-impact frequency band): these higher modes correspond to a characteristic vibration pattern in which the principal tegminal surface is trisected by two stationary nodes (Fig. 8D, E, F). The free resonance of the harp membrane is at 6,000–6,200 Hz, well outside the range of carrier frequencies of the song; other major tegminal cells are tuned to similar frequencies. The resonance of

individual tegminal cells may be excited as a secondary, low-amplitude component of the song, which is particularly evident during the early stages of each sound pulse when amplitude of the carrier is low.

4. Exceptional individuals stridulate with carrier frequencies in the range 5,200–5,750 Hz, i.e. in the range of the higher tegminal resonances: in this case the carrier does not equal tooth-impact frequency. This phenomenon has been reproduced experimentally by constraining the tegmina to vibrate in the modes identified for these resonances. In both normal and experimentally modified specimens, when the carrier frequency equals a higher tegminal resonance, the carrier is excited as an ultra-subharmonic resonance of the tooth-impact rate. This phenomenon indicates the presence of nonlinearities in the tegminal resonator.

5. A comparison of these results on *Oecanthus* with published data on *Gryllus* reveals significant differences, which are correlated with differences in structure between the two genera. Stridulation in *Oecanthus* is discussed in the light of published theories concerning the mechanism of tegminal resonance, and the concept of a resonator with continuously variable tuning is supported.

Introduction

Tree crickets of the genus *Oecanthus* stridulate with carrier frequencies that are strongly temperature-dependent (Walker, 1962a, b, 1963). This study explores the mechanism whereby the tegmina are capable of amplifying sound over a broad range of tooth-impact frequencies, although the principal individual tegminal membranes are sharply tuned to narrow frequency bands. The problem was recognized by Lutz and Hicks (1930) and explicitly formulated by Dumortier

(1963), in connection with the song of field crickets (*Gryllus*): in that genus the principal tegminal membrane is tuned to a frequency within the range of tooth-impact frequencies (Nocke, 1971), whereas in *Oecanthus* the tuning of single tegminal membranes is outside that range (Walker, 1962b). Pierce (1948) reported the simultaneous presence of anharmonically related frequencies in the song of *Oecanthus*, but left the identification of tooth-impact frequencies and tegminal resonances uncertain. The present work identifies resonances and modes of vibration of the tegmina of *Oecanthus*, and explains the presence of anharmonic components in terms of nonlinearities in the tegminal oscillator.

Materials and Methods

Stridulation, both under natural and artificial conditions, was recorded on magnetic tape at 19 cm/s (Grundig TK-340, GDM-310 microphone). Crickets were unrestrained, and sang in a small mesh cage (6 × 6 × 2 cm) open on all sides and mounted on a thin support away from sound-reflecting surfaces. The intensity of the song is a maximum in front and behind the stridulating insect, on an axis roughly perpendicular to the plane of the elevated tegmina, and is lowest at all azimuths in that plane: whenever possible the microphone was located either in front or behind the insect, at distances from 25 to 40 cm; in some cases, such as when most of the tegminal membranes had been removed experimentally, it was necessary to bring the microphone within 5 cm of the cricket to maintain adequate signal-to-noise ratio. In the low-temperature experiments, crickets were transferred in their mesh cage into an open container immersed in an ice bath. The inner walls and floor of the container were lined with 1 cm of insulating foam to minimize temperature gradients and to reduce acoustic reflections. Temperature was measured with a thermistor probe mounted within the mesh cage, in close proximity to the stridulating insect.

Under experimental conditions, and particularly at low temperatures, males were reluctant to stridulate; they were induced to do so by confining a female of the species with them: under these conditions, males tend to produce short trills of a few seconds' duration. Most of the work reported here was based on such courtship trills rather than on the long calling trills made by isolated undisturbed males.

In the experiments in which the tegmina were made to resonate artificially, live crickets were held by a fine clip, which clasped the tegmen under study as close to the thorax as possible (within 1 mm) and held the other tegmen so that it did not overlap the first: by this method the tegmina were held horizontally at right angles to be body, with the inner surface upwards permitting access to the file. The tegmen under study was dusted with talcum powder, and the file was stroked by hand with an artificial scraper (Fig. 1), consisting of a thin strip of acetate plastic, bent at right angles and beveled at the end so that it would fit between consecutive teeth of the file, which are typically spaced between 20 and 40 μm apart (Fig. 7). Both left and right tegmina were tested in the same fashion: the file of the left tegmen is well developed, and although not functional in stridulation, it is adequate to permit mechanical excitation of the tegmen. The scraper was manipulated with only sufficient force to excite audible sound, but carefully avoiding gross deflections of the tegmen as a whole: the teeth were struck at rates between 10 and 100 per s, so that free damped oscillations following each tooth strike had time to decay completely before

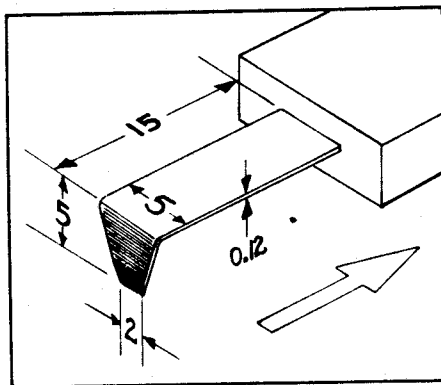


Fig. 1. Sketch of artificial scraper with dimensions in mm

the next tooth impact (Fig. 3G). As the file was stroked, agitation of the powder was seen over the vibrating areas of the tegmen: the powder migrated to well-defined linear positions representing stationary nodes. With a little practice, a consistent nodal pattern could be sustained over several consecutive traverses of the file: sound was continuously recorded, and after several traverses the nodal pattern was photographed. The microphone was mounted directly beneath the tegmen being studied: in the acoustic coupling experiments the microphone was replaced by a small loudspeaker mounted in the same position. The frequency of the test tones was determined by the same method described below to determine carrier frequency of stridulation; the volume of the test tone was raised until a stable nodal pattern appeared on the dusted tegmen: the volume setting was noted, but sound intensity was not measured.

Frequency determinations were made from traces such as those shown in Fig. 3: these represent the upper half-cycles of the waveform, and are enlargements of records made as follows. A strip of high-speed film, 6 by 26.5 cm, is mounted on a revolving drum driven by a synchronous motor. A moving assembly, mounted on a track and driven by a second motor, contains two light-emitting diodes behind adjacent slits, whose images are focused on the film by a lens. As the optical assembly travels parallel to the axis of the drum, the images of the slits generate a continuous helical record on the film. One light-emitting diode is driven at the AC line frequency (60 ± 0.2 Hz), producing a series of short dashes on the film to serve as a time base. The second light-emitting diode is driven by an amplifier receiving input from the tape recorder: when the original recordings (made at 19 cm/s) are played back at 4.75 cm/s, one strip of film contains 7 s of real-time sound with an effective time-scale of 4.26 m/s: frequency resolution is limited to about 18 kHz. With this apparatus several hundred consecutive pulses are readily recorded for detailed analysis: average frequency for each pulse is obtained by counting cycles over its duration, with a standard error in frequency determinations of single pulses of less than 0.5%: frequencies reported in Table are averages of several determinations on different pulses, and are reported to the nearest 1 Hz, while frequencies reported in the text of the paper are rounded appropriately. Instantaneous frequency (reciprocal period of successive cycles) was calculated by i) overlaying 6 to 10 pulses cycle by cycle to match consistent irregularities in frequency and amplitude; ii) measuring each period microscopically; and iii) averaging the periods of corresponding cycles from each pulse. The maximum error in instantaneous frequency is estimated to be less than 2.0% at 4,000 Hz.

Results

Characteristics of Natural Stridulation

A total of 45 males of *Oecanthus nigricornis* was used in this study: they were all collected in Westchester County, New York. *O. nigricornis* sings in continuous trills consisting of rapidly delivered uniform pulses: typical relationships between pulse frequency, carrier frequency, and temperature for this population are shown in Fig. 2; they match closely those reported by Walker (1963) for the "slow-trilling" form of *O. nigricornis*. Pulse rate rises nearly linearly with temperature, while carrier frequency increases approximately as the 0.6 power of temperature. Considerable variation exists between individuals; the actual best fit exponent for pulse rate is somewhat greater than unity for most specimens, but the difference from 1.0 is not significant: this result is consistent with published findings for other stridulating Orthoptera (Walker, 1975). The calibration curves of Fig. 2 only apply to crickets which are in thermal equilibrium with their surroundings, which means in practice that they have been exposed to the test temperature for considerable time, not less than one hour; the response to rapid temperature changes will be discussed in a later paragraph.

A normal sound pulse (Fig. 3A) consists of an initial smooth rise in amplitude, a long middle section during which amplitude remains nearly constant, and a final section during which amplitude decays smoothly; in some individuals amplitude may rise abruptly at the beginning, or may drop off irregularly at the end. Instantaneous frequency (i.e. reciprocal period of consecutive cycles) is quite irregular, with individual cycles spanning a range of 100–200 Hz about the local average, but mean frequency remains relatively constant over a pulse (Fig. 4A). Each individual has a characteristic pattern of frequency variation within each pulse; while the variations shown in Fig. 4A are not much greater than the experimental error in single instantaneous frequency determinations, the variations are real, in that they are consistent from pulse to pulse. In some specimens the first 5 or 10 cycles of each pulse are considerably higher in frequency than the rest, and in others each pulse ends irregularly, with wider than normal amplitude and frequency excursions over the last few cycles.

In many individuals the primary sound pulse is followed by a secondary pulse of similar or somewhat lower amplitude, whose frequency is near to that of the primary pulse (Fig. 3B). Secondary pulses are variable in length, from very short trains of 2 or 3 cycles to trains nearly as long as the primary pulse: at certain favorable temperatures the two pulses be-

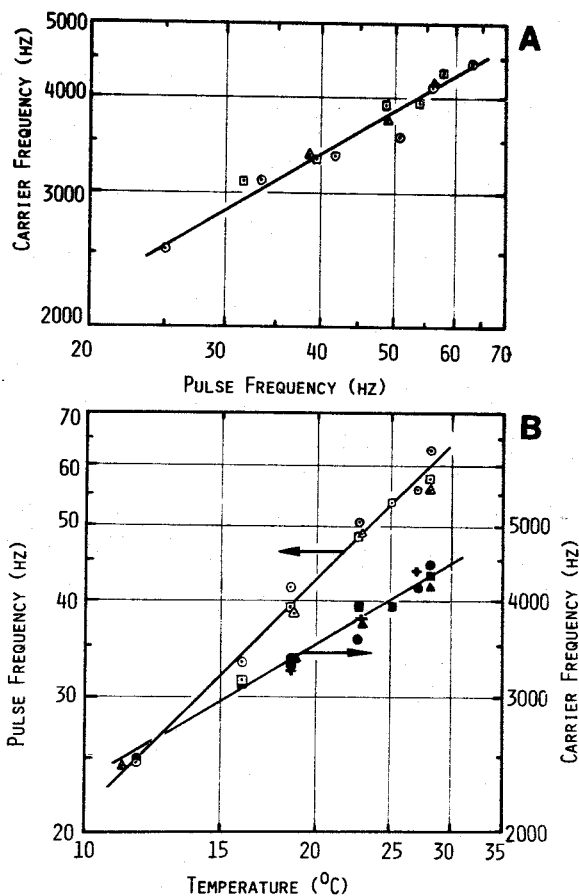


Fig. 2A and B. Average equilibrium relationships between pulse frequency, carrier frequency, and temperature for the population of *O. nigricornis* used in this study. Data for several individuals are superimposed on the plots. A Relationship between pulse frequency and carrier frequency. B Temperature dependence of pulse frequency (scale at left) and carrier frequency (scale at right). The lines represent the equations: Pulse frequency (Hz) = $2.13 T$; Carrier frequency (Hz) = $581 (T)^{0.6}$, where T is temperature in °C

come continuous, as in Fig. 3C, yielding a long train of 75 to 80 cycles, occupying over 90% of each pulse period. Very short secondary pulses with dominant frequencies in the range 5,500–6,300 Hz are also rarely found.

In some specimens, during the initial section of the primary pulse, the waveform has a fine structure in which each positive half-cycle is bimodal: as amplitude rises, the waveform becomes more nearly sinusoidal (Fig. 3D); this suggests excitation of a high free resonance, estimated for various individuals to lie between 6,000 and 9,000 Hz, most commonly below 7,000 Hz.

A few rare individuals (3 among 45 studied) are capable of producing pulses at several alternative carrier frequencies. Typically a pulse begins with a carrier in the range 5,200–5,750 Hz, and switches abruptly in mid pulse to the normal, lower carrier frequency

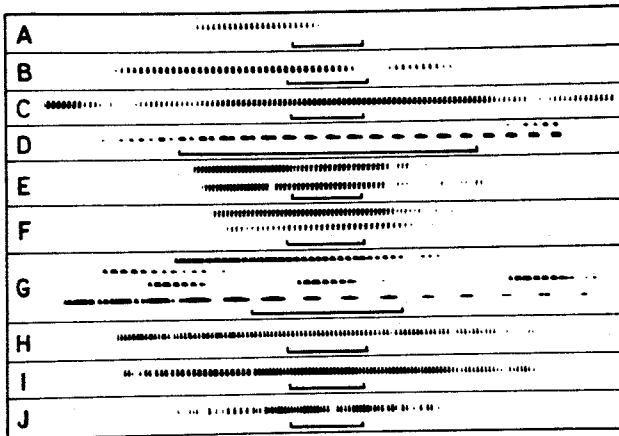


Fig. 3A-J. Individual pulses of *O. nigricornis* (scale on each trace represents 3.5 ms). **A** Normal sound pulse; see Fig. 4A. **B** Normal sound pulse followed by secondary pulse made during opening stroke of the tegmina. **C** Abnormally long pulse: fusion of normal primary and secondary pulse. **D** Complex waveform during early portion of a pulse; note enlarged time scale. **E** Pulses showing sudden change from anomalous high carrier frequency to normal tooth-impact frequency; see Fig. 4B. **F** A pulse entirely at the anomalous carrier frequency, and (below) a normal pulse from the same trill. **G** Representative free-vibration trains resulting from artificial excitation of single file teeth; see Fig. 4C, D, E. **H** Pulse at anomalous high carrier frequency, produced by specimen modified as in Fig. 9F. **I** Pulse showing change from tooth-impact frequency to anomalous high carrier, produced by specimen modified as in Fig. 9G; see Fig. 4F. **J** Pulse showing carrier frequency equal to harp resonance: specimen modified as in Fig. 9H

(Figs. 3E, 4B): in the same trill, some pulses may be entirely at the anomalous frequency and others entirely at the normal carrier frequency (Fig. 3F). Both normal and anomalous carriers have approximately the same amplitude.

The anomalous carrier frequencies described above must not be confused with abnormally high carriers produced by crickets that have not fully adjusted to the prevailing temperature. The calibration curves shown in Fig. 2 apply to specimens in thermal equilibrium with their surroundings: it is not unusual, however, to hear *O. nigricornis* on a cold evening singing at the "correct" pulse frequency for that temperature, but with a carrier frequency 500 to 800 Hz above normal. In specimens transferred quickly from high (25–28 °C) to low ambient temperature (11–13 °C), pulse rate approaches equilibrium exponentially, with an average time constant of 160 s; at the end of 10 min the pulse rate is normally within 2 Hz of the equilibrium value (Fig. 5A). Carrier frequency, on the other hand, approaches equilibrium in steps of 100–300 Hz lasting 200–400 s each; the

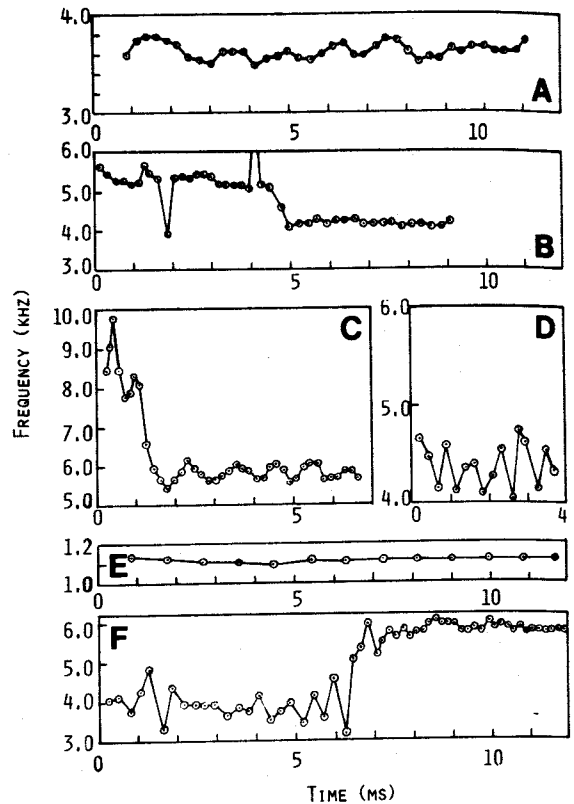


Fig. 4A-F. Instantaneous frequency plots for selected pulses. **A** Normal pulse; see Fig. 3A. **B** Pulse showing change from anomalous carrier to tooth-impact frequency; see Fig. 3E. **C-E** Free-vibration trains produced by artificial single tooth impacts; see Fig. 3G. **F** Pulse at tooth-impact frequency switching to high carrier frequency, produced by individual modified as in Fig. 9G; see Fig. 3I

time constant of an exponential function fitted to the average trend of several specimens is 1,575 s (about 26 min), but the mechanism is clearly more complex than simple exponential decay. Figure 5B shows the course of deviation from steady-state relationships during rapid temperature fluctuation.

Identification of Tooth-Impact Frequency

The first step in the study of tegminal resonance is the correct identification of the excitation frequency, i.e., the frequency of impacts of the scraper of the left tegmen on the file teeth of the right tegmen.

I carried out a series of experiments on numerous individuals and at different temperatures: they were all variations on the following procedure in which I excised a small number of teeth from the file of a specimen, recorded his stridulation, then removed another group of teeth and again recorded the sound (see Fig. 6). The effect of these operations on the

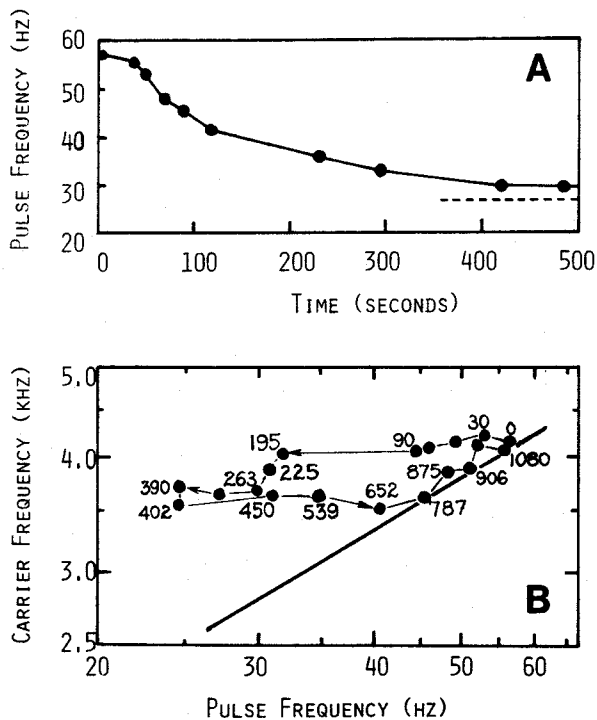


Fig. 5. **A** Response of pulse frequency to a step change in temperature. At time zero, the cricket was transferred from an environment 28 °C to one at 12.4 °C. Dashed line shows final equilibrium value. **B** Abnormal carrier frequencies of crickets subjected to temperature changes: time in s indicated at various points on the plot; solid line shows average equilibrium relationship. From $t=0$ to $t=402$ s adjustment to a step change from 27 °C to 11 °C; from $t=402$ to $t=1080$ adjustment to gradual temperature rise at 1 °C/min: throughout this latter period pulse rate tracked its steady-state curve within 3 Hz or better

waveform of each pulse, and detailed correlations of file structure with pulse structure in both normal and modified individuals, clearly confirmed that in the range 3,000–4,600 Hz the carrier frequency of the song is identical with tooth-impact frequency. Other observations are summarized below:

1. During the principal sound pulse the file is stroked from the inner margin of the tegmen towards the costal margin, i.e. against the “set” of the file teeth (Fig. 7): this means that the principal sound pulse is made during the closing stroke of the tegmina.

2. Not all of the file is stroked by the scraper, the initial impact occurring usually between teeth 8 and 20 (numbered beginning at the posterior end of the file near the inner margin of the tegmen).

3. Secondary pulses are produced by tooth impacts during the opening stroke of the tegmina.

4. When the file has marked natural irregularities in tooth spacing, or when it has been altered artificially by removal of selected teeth, these irregularities can be reliably identified in almost every pulse as

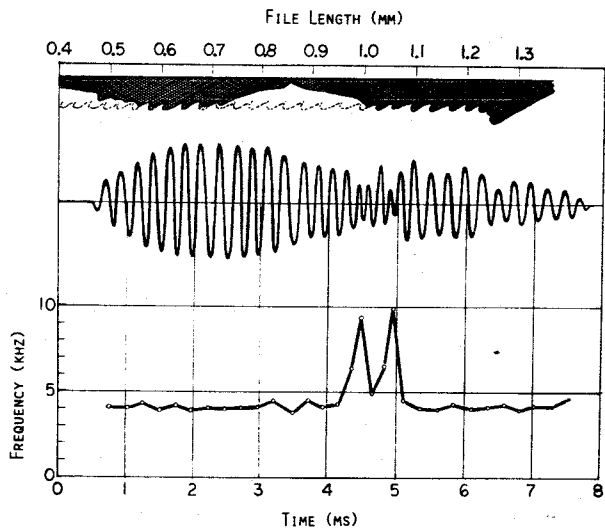


Fig. 6. Effect of file modification on the waveform of the latter part of a pulse. (Top): the file after removal of two sections. (Middle): the waveform, positioned to correspond with the file above. (Bottom): instantaneous frequency on the same time scale as waveform

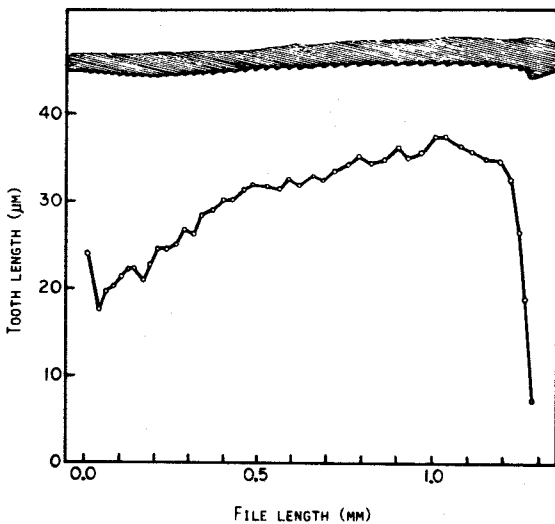


Fig. 7. Structure of the file of the right tegmen of *O. nigricornis*. Number of teeth and other details vary between individuals

local anomalies in amplitude and/or instantaneous frequency: this permits the correlation of file structure with pulse waveform needed to identify tooth-impact frequency. When pulses end irregularly, this arises in most cases from scraper impact on the last, much larger tooth of the file (Fig. 7).

5. When the pulse waveform is reliably identified with tooth impacts over a particular section of the file, the local and average velocity of the scraper over the file can be calculated from the time between tooth impacts and the distance between the corresponding file teeth. The velocity of the scraper relative to the

file increases throughout most of each closing stroke: in a typical example, the scraper accelerated smoothly from 70 mm/s at the start of a pulse to 140 mm/s after 7 ms, and decelerated to zero in the next 2.5 ms. This velocity profile largely compensates for the gradual increase in tooth length along the file (Fig. 7) to yield nearly constant tooth-impact frequency throughout each pulse, although, as mentioned above, local irregularities in tooth spacing are still evident in the pulse waveform.

6. The average carrier frequency during free vibration (i.e., where file teeth are artificially absent or following the last normal tooth impact) does not change appreciably from the frequency during the preceding time period (Fig. 6). The persistence of oscillations at the average tooth-impact frequency in the absence of excitation by tooth strikes suggests the existence of tegminal resonances in the same range as typical tooth-impact frequencies.

Artificial Excitation of Tegminal Resonance

In order to determine the modes and frequencies of free vibration of the tegmina, I performed the following experiments on live restrained specimens, in which vibration of the tegmina was induced by artificial stimulation of the file. The nodal patterns, revealed by the position of stationary bands of powder on the tegmina, varied depending on how much pressure was applied by the scraper, and in which direction the file was stroked. Typical nodal patterns are shown in Fig. 8: the light areas represent stationary nodes, and the dark areas, antinodes; during the course of the experiment, regions of maximum amplitude could be identified visually by the degree of agitation of the powder. The tegminal margins appeared to be nodes, but the powder tended to fall off the edge rather than accumulating there.

Analysis of the average dominant frequency of numerous free decay pulses (such as Figs. 3G and 4C, D, E) revealed that to each principal nodal pattern corresponds a fairly narrow range of frequencies (about 500 Hz), as is shown in Fig. 8. The lower frequencies, in the range from 3,800 to 4,600 Hz (Fig. 8A, -B) were only excited when the file was stroked forward towards the costal margin of the wing; the higher frequencies (5,100–5,850 Hz: Fig. 8D, E, F) were produced when the file was stroked backwards. Trains of very low frequency (1,040–2,800 Hz) were produced when, during a forward stroke, the last, much enlarged tooth of the file was traversed: I was unable to duplicate such vibrations consistently enough to obtain a pure nodal pattern for the lower frequencies; however, from vi-

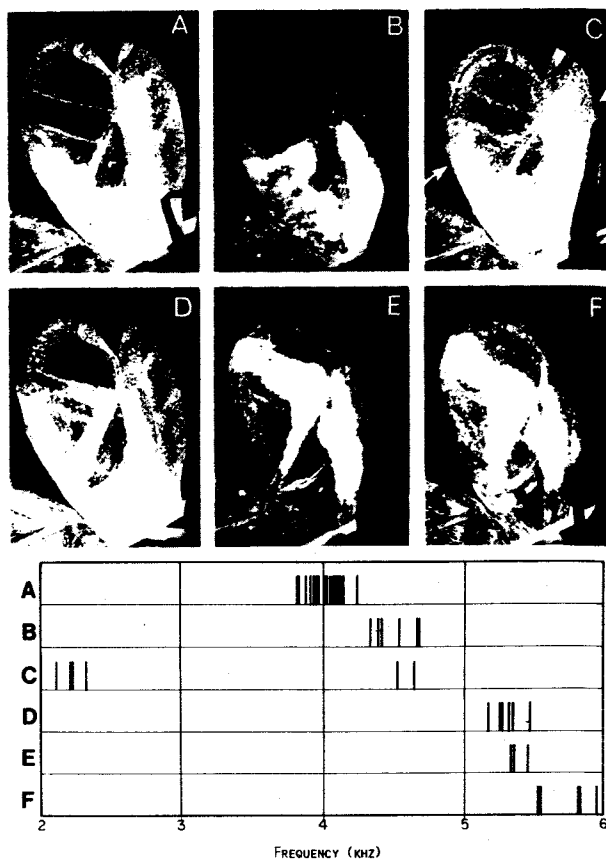


Fig. 8A–F. Modes of vibration (above) and corresponding tegminal resonances (below) for the right tegmen of *O. nigricornis*, obtained by artificial stimulation of the file. Light areas represent stationary nodes, while dark areas are regions of vibratory activity. Representative mean frequencies in free vibration are (in Hz): A 4,010; B 4,460; C 2,230 and 4,590; arrows indicate a weak node possibly associated with vibration at the lower frequency; D, 5,310; E, 5,380; F 5,840

sual observation while the experiment was in progress, there seems to be a single transverse node across the tegmen, somewhat like the pattern shown in Fig. 9E, with the distal portion of the tegmen vibrating in cantilever fashion. One run, in which resonances were excited both at 4,590 and 2,230 Hz, yielded the nodal pattern of Fig. 8C: the weak transverse node marked by arrows in the photograph presumably represents the contribution of the lower resonance.

Nodal patterns are similar between different specimens and between the two tegmina of any one individual, but the corresponding frequency bands may differ by as much as 200 to 300 Hz in average value. All the work reported here was carried out on live crickets: dry tegmina of pinned specimens give higher frequencies than those of live insects.

There are important physical differences between the excitation of tegminal resonance by isolated tooth impacts and the case in

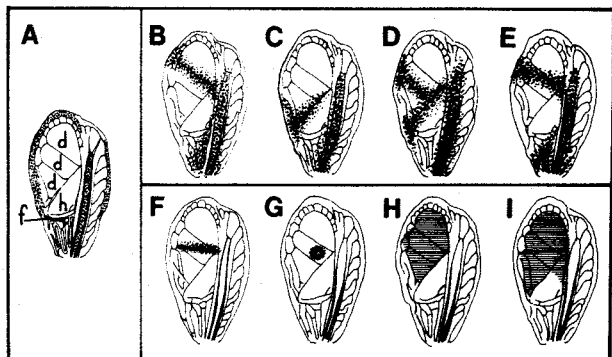


Fig. 9. A Right tegmen of *O. nigricornis* in ventral view. (*h*): harp; (*d, d, d*): distal cells of resonator; (*f*): file vein. B-E Modes of vibration obtained by acoustic coupling. Stippling: stationary nodes; clear areas: regions of vibratory activity. Excitation frequencies (in Hz): B 3,300; C 4,050–4,150; D 4,800; E 575 and similarly, 287 (possibly a higher harmonic, e.g. 3,450 Hz). F-I Artificial modification of tegminal resonance. F A fine wire forming an artificial node in the indicated position. G A small weight glued to the tegmina in indicated position. H Hatched areas coated with varnish to isolate harp resonance. I Hatched areas varnished: reduction of effective harp area to raise its natural frequency

natural stridulation. The frequency spectrum associated with single isolated tooth impacts is broad-band, and does not favor excitation of any particular resonant frequency over another: thus the frequencies observed in free vibration following impact depend only on the natural characteristics of the tegmen, and on the force, direction and point of impact on the file. The presence and position of the clamp at the base of the tegmen seems to have no influence on the results, as long as it is not farther than 2 mm from the thorax: the base of the tegmen is quite stiff, crowded with closely spaced strong veins, and probably has little if any acoustic function. Excitation of isolated file teeth identifies natural tegminal resonances and their corresponding modes of vibration, but does not prove that they are the same as those that prevail in natural stridulation, where the excitation frequency spectrum has its strongest component at the tooth-impact frequency.

Tegmina of live specimens were also made to vibrate by acoustic coupling, using test tones of known frequency. By dusting the tegmina with talcum, nodal lines could be seen and photographed as before. The nodal patterns were frequency-dependent, and in general resembled those obtained by mechanical excitation of the file. Maximal response was observed in the range 4,050–4,150 Hz, with the pattern shown in Fig. 9C: a similar pattern obtained by mechanical excitation (Fig. 8B) had a corresponding frequency averaging 4,460 Hz (on a different individual). As frequency of the test tone was raised, new nodes formed in the distal region of the tegmen, while a node remained over the distal vein of the harp, much as in Fig. 8E and F: Fig. 9D shows the nodal pattern for 4,800 Hz, a frequency near the maximum observed in natural stridulation: this mode is intermediate both in geometry and in frequency between those of

Fig. 8B (average frequency 4,460 Hz) and 8D (5,310 Hz) obtained by mechanical excitation. At excitation frequencies below 4,000 Hz, the main transverse node was seen to migrate towards the distal margin of the tegmen (Fig. 9B, 3,300 Hz); at around 2,900 Hz, little motion was visible in the basal two-thirds of the tegmen, activity being a maximum at the distal end. With test tones below 1,000 Hz, response was only obtained at very high volume, which resulted in peak clipping by the loudspeaker and thus the production of a sound rich in higher harmonics; the pattern of vibration was then virtually the same as that for frequencies many times higher (Fig. 9E, 575 Hz), suggesting that the vibration was excited by a higher harmonic of the test tone: the pattern at 287 Hz was virtually identical to that at 575 Hz (but with broader nodal lines), further supporting the hypothesis. Stationary nodes may form on prominent veins, may cross them at various angles, or may lie entirely on membranes away from the veins; small changes in frequency correspond to slight rotations or translations of the nodes.

The results obtained by acoustic coupling generally confirm those found by mechanical excitation of the file: they indicate that the modes of vibration corresponding to frequencies in the higher range of carriers of the song (4,000–4,800 Hz) are similar regardless of whether vibration is excited mechanically by single tooth impacts or acoustically by frequencies in the tooth-impact range of natural stridulation. They also support the previous tentative conclusion that at frequencies below 3,800 Hz the principal mode of vibration involves a single transverse node across the tegminal surface.

At first glance it would appear that vibration with a node across the tegminal surface should correspond to a higher, rather than lower frequency relative to vibration in the fundamental mode of Fig. 8A around 4,000 Hz. I believe the explanation lies in the fact that in Fig. 8A the membranes vibrate within the surrounding framework of veins, whereas in the modes of Fig. 9B and E the marginal veins participate in the deflection, with maximum amplitude at the distal margin of the tegmen rather than in its center. Theory predicts lower frequencies for plates with free edges than for identical plates with clamped edges (see, for example, Timoshenko and Young, 1955). Quantitative analysis of the problem is very difficult, because the presence and geometry of veins of varying mass and stiffness prevents treatment of the tegmen as a uniform vibrating plate.

It is clear that at the frequencies normally encountered as carriers of the song, vibration of a large part of each tegmen, rather than vibration of individual cell membranes, accounts for the fundamental mode. Visual observation of activity during mechanical stimulation of the file indicates that in most cases the harp membrane (*h*, Fig. 9A) vibrates as part of

a larger surface, so that while morphologically it appears as a well-defined unit, acoustically it is not.

The position of maximum amplitude of oscillation on each tegmen is frequency-dependent: above 3,800 Hz, amplitude is a maximum near the center of the tegmen, distal to the harp; below this frequency, two maxima exist simultaneously, one basal to the harp near the file vein, and another on the distal margin of the tegmen. At frequencies above 4,800 Hz, that is near the maximum and above the normal tooth-impact range, 3 maxima are present: one on or near the harp membrane, one near the hind margin of the tegmen on the first distal cell (Fig. 9A), and one near the apical end of the tegmen on the third distal cell.

Artificial Modification of Tegminal Resonance

I carried out several experiments to confirm that the nodal patterns discovered by artificial excitation of the tegmina correspond with those found in natural stridulation.

Frequencies in the range 5,200–5,750 Hz are found in rare specimens as anomalous carriers; the same frequencies are prominent tegminal resonances with characteristic nodal patterns (Fig. 8D, E, F). I modified the tegmina of several individuals by the addition of strategically placed artificial nodes, in order to obtain stridulation at anomalous frequencies experimentally: preliminary experiments with mechanical excitation had shown that the presence of a fine wire glued across the tegmen in an arbitrary position induces the formation of a stationary node, usually coinciding with the wire in position and direction, but sometimes crossing it at a small angle.

In one individual, I glued a fine wire to each tegmen in the position shown in Fig. 9F: this arrangement prevents vibration in the modes of Fig. 8A and B (3,800–4,600 Hz) and should encourage vibration with a node crossing the distal part of the tegmen: such a nodal pattern corresponds either to a low frequency below 3,800 Hz (Fig. 9E) or to a high frequency greater than 5,100 Hz (Fig. 8D, E, F). This specimen, at an estimated tooth-impact frequency of 3,480 Hz, stridulated yielding pulses similar to that shown in Fig. 3H, with a carrier frequency averaging 5,775 Hz.

Two specimens were modified by attaching a small weight to the center of each tegmen as in Fig. 9G: in this case the node forming on the tegmen is free to rotate about the middle, whereas in the experiment described above the position of the node was constrained within a narrow range of directions by the presence of the wire. One individual stridulated with

pulses almost entirely at the anomalous frequency: 3 records between 23 and 24 °C had average carriers of 5,460, 5,500, and 5,640 Hz. The other specimen produced mixed pulses (Figs. 3I and 4F), in which the initial portion (4.5–5.0 ms) was at the tooth-impact frequency (3,890 Hz average, although in most pulses instantaneous frequency varied considerably from cycle to cycle); the second, longer portion of each pulse (7–9 ms) was at 5,850 Hz. I conclude that each pulse began with vibration in a mode similar to that of Fig. 8A, with an antinode coinciding with the mass in the center of each tegmen, and ended with vibration in the pattern of Fig. 8F, with a nodal line lying on the center mass.

The above experiments demonstrate that the nodal patterns determined by artificial stimulation of the tegmina are consistent with those prevailing in stridulation, yielding similar frequencies for similar nodal geometries.

Resonance of Individual Tegminal Membranes

I carried out a few experiments to determine the contribution of individual tegminal membranes, particularly the harp (h, Fig. 9A). In one case, I coated the three distal cells of each tegmen with a heavy coat of varnish as shown in Fig. 9H. This specimen, in natural stridulation, produced mixed pulses (Fig. 3J) with the following frequencies: at 20.6 °C, 3,270 Hz and 6,070 Hz; at 27.8 °C, 3,560 Hz and 6,185 Hz: in each case the lower value represents the tooth-impact frequency. In another specimen, I removed the membranes of the three distal cells of each tegmen (d, d, d of Fig. 9A), leaving the harps and the framework of veins intact: this one gave essentially similar results, but a broader range of anomalous carriers, from 5,600 to 6,500 Hz, with a mean of 6,170 Hz. The difference between the two cases is that in the second individual the distal margin of the harp was free to vibrate, while in the first it was constrained to behave as a stationary node.

Removal of all 4 main membranes of each tegmen, including the harps, but without breaking the surrounding veins, practically silences the insect; removal of the harp membranes alone, leaving the three distal cells intact, reduces sound intensity somewhat, but leaves the carrier frequency equal to tooth-impact frequency. Varnishing not only the distal cells but also about one-third of the area of the harp membrane (Fig. 9I) raises the observed frequency to 8,950 Hz: under these conditions each tooth impact is followed by a short train of strongly damped vibrations, similar to the waveform of the song of some Tettigoniidae.

These results lead to the following conclusions:

1. If the 3 principal distal cells of the tegmen are absent or otherwise prevented from vibrating at their natural frequency, amplification of sound at the tooth-impact frequency is suppressed or strongly attenuated. 2. The natural frequency of the harp membrane is between 6,000 and 6,200 Hz, well outside the normal range of carrier frequencies for *O. nigricornis*.

By similar techniques I found that the triangular membrane of the first cell distal to the harp is tuned to about 6,900 Hz, while the second distal cell has an estimated natural frequency of 6,350 Hz; no data are available for the tuning of the apical cell, but it is probably in the same frequency range as the harp, being similar to it in size, shape, and in the nature of the membrane.

The initial high-frequency resonances found in the pulses of certain individuals (Fig. 3D), and the short high-frequency secondary pulses occasionally recorded are both probably due to vibration of single tegminal cells at their natural frequencies: these phenomena are particularly prevalent at tooth-impact frequencies near 3,100 Hz, when the resonance is excited as a second harmonic, giving rise to carrier frequencies around 6,200 Hz present for short periods during each pulse.

Published audiospectrograms do not normally show a resonance in the neighborhood of 6,000 Hz, but sound spectrograms of similar species do (see Dumortier, 1963, Fig. 215): it is likely that the small second peaks in sound spectrograms of *O. pellucens* (6,000 Hz) and *O. quadripunctatus* (6,300 Hz) also represent resonance of single tegminal membranes.

Discussion

Response to Rapid Temperature Change

The difference between the behavior of pulse rate and that of carrier frequency during rapid changes in ambient temperature (Fig. 5) indicates that the two parameters are controlled by two different mechanisms.

Pulse frequency has been shown, in other genera, to be controlled by impulses from the central nervous system (Huber, 1963); carrier frequency is equal to the tooth-strike rate, and thus depends on the velocity of contraction of the muscles actuating the tegmina during each pulse. The experimental results show that the speed of muscular contraction is thus controlled independently of wingstroke rate, and may depend on intrinsic muscular conditions less sensitive to changes in ambient temperature than the central nervous pacemaker controlling pulse rate.

Table 1. Ultra-subharmonic resonance in unmodified (a, b) and experimental *O. nigricornis* (c, d, e, f). The third column shows the smallest integers whose ratio is within 0.5% of the ratio of anomalous carrier to tooth-impact frequency

Anomalous carrier (Hz)	Tooth-impact frequency (Hz)	Ratio
a) Higher tegminal resonance		
5,679	3,797	3/2
5,691	3,895	16/11
5,682	4,266	4/3
b) Unidentified resonance (harp?)		
6,060	3,797	8/5
6,093	4,266	10/7
6,068	4,453	15/11
c) Artificial node (Fig. 9F)		
5,775	3,480	5/3
d) Artificial node (Fig. 9G)		
5,545	3,468	8/5
5,850	3,890	3/2
6,241	3,890	8/5
e) Harp resonance (Fig. 9H)		
6,196	3,553	7/4
f) Removal of cell membranes		
6,145	3,680	5/3
5,546	3,154	7/4

Ultra-Subharmonic Resonance

In specimens naturally exhibiting anomalous carrier frequencies, the latter appear discontinuously, at certain tooth-impact rates but not others: whenever anomalous carriers are present, and are equal to known prominent resonances, their ratio to the prevailing tooth-impact frequency is very nearly equal to the ratio of two small integers; the same is almost invariably true of specimens whose tegminal resonance has been modified artificially (Table 1). These observations mean that the anomalous carrier frequencies are excited as ultra-subharmonics of the tooth-impact frequency.

Ultra-subharmonic resonance is characterized by the fact that the ratio of resonance to excitation frequency is given by a ratio p/q , where both p and q are positive integers not equal to 1 and are prime relative to each other; if p equals 1, the resonance is designated as subharmonic (Levenson, 1949; Dincă and Teodosiu 1973: the latter use the term "supersubharmonics").

Subharmonic and ultra-subharmonic resonance are also evident in the data that Pierce (1948) obtained using completely different methods: his report does not differentiate between carrier frequencies and sec-

ondary resonances, but carrier frequencies for the species he discussed can be identified from other sources (e.g. Walker, 1962a, 1963). If I interpret Pierce's data for *O. nigricornis* correctly, they show a series of resonances equal to $1/3$, $2/3$, $4/3$, etc. of the carrier frequency (4,200 Hz); for both *O. pini* and *O. fultoni*,¹ the lowest resonance is almost exactly $4/7$ of the tooth-impact frequency, with an error of less than 10 Hz.

In the presence of damping, subharmonic and ultra-subharmonic resonance can only occur in nonlinear systems (Stoker, 1950, p. 8); in damped linear systems the resonance can only be equal to the excitation frequency, or be an integral multiple thereof. Since the tegmina are damped oscillators, the presence of ultra-subharmonic resonance implies that each tegminal resonator as a whole is a nonlinear system, in which the elastic properties of the vibrating structure vary with amplitude: it is probable that as deflection of the vibrating membranes increases, deformation of the surrounding rigid framework of veins comes into play, effectively increasing the stiffness of the system with increased amplitude of vibration. This is consistent with the observation, in free decay trains obtained by artificial excitation of the file, that the first few cycles (at maximum amplitude) are slightly higher in frequency than the rest of the train (Fig. 4E). Individual tegminal membranes may nevertheless be linear resonators, as has been shown for the harp membrane of *Gryllus* (Nocke, 1971).

The presence of subharmonic resonance may account for the very low frequencies reported by Fulton (1915) for various species of *Oecanthus*. Pierce (1948) assumed that only higher harmonics of the tooth-impact frequency may be present in the song (i.e. implicitly assumed linearity) and was thus misled into assigning very low values to the tooth-impact frequency of several species. The implicit assumption of linearity is commonly made in the literature whenever the relationship between tooth-impact rate and higher frequencies is discussed (for a recent treatment, see Michelsen and Nocke, 1974).

Comparison with Other Genera

A comparison of the present results on *Oecanthus* with published data on other genera is in order. The most complete study is that of Nocke (1971) on *Gryllus campestris* and related species. In *Gryllus* the harp is sharply tuned to a frequency near the tooth-impact frequency of the calling song (4–5 kHz), while

the mirror is tuned to a much higher value (7.2 kHz). In acoustic excitation at frequencies near the tooth-impact rate, the harp exhibits maximal amplitude of vibration, while the mirror is relatively inactive; in stridulation, sound pressure level of the 5 kHz component is a maximum over the harp, with relatively lower amplitudes in other regions of the tegmina. The primary frequency peak of the song (4–5 kHz) is drastically reduced by extirpation of the harp membrane, but can be restored to nearly normal intensity by replacement with a "prosthetic" harp membrane of synthetic material (Nocke, 1971).

These data identify the harp of *Gryllus* as the primary sound radiator, but also indicate that the characteristic profile of the sound spectrogram depends more on the existence and geometrical position of the harp than on its specific resonant frequency. In North American species of *Gryllus* and in *Acheta domesticus*, carrier frequency varies within each pulse (Lutz and Hicks, 1930; Alexander, 1957) reflecting variation in tooth-impact frequency: in a sound spectrogram this temporal variation is evidenced by a broadening of the primary frequency peak. During each pulse, whenever tooth-impact frequency equals the harp resonance, energy output is maximized: this probably explains the correlation found by Nocke (1971) between the position of the maximum of the first frequency peak and the natural resonance of the harp.

In *Oecanthus* the resonance of individual tegminal membranes is far removed from the normal range of tooth-impact frequencies: no single cell resonance of *Oecanthus* accounts for amplification of the carrier frequency of the song, a conclusion already reached by Walker (1962b). The concept of a primary sound radiator is elusive, because the stationary boundaries of the vibrating surface and the position of maximum oscillatory amplitude of the latter are both frequency-dependent: all that can be said is that the primary resonator of *Oecanthus* is a surface consisting of the 4 largest cells of each tegmen. These 4 cells are similar in size and tuning frequency, and form a continuous morphological unit capable of oscillating as a single membrane. By contrast, in *Gryllus* the harp and the mirror are morphologically sharply differentiated, being bounded by relatively stronger veins than in *Oecanthus*. (Both the harp and the mirror of *Gryllus*, incidentally, are compound structures, each being composed of more than one morphological cell.)

The tegmina of *Oecanthus* are particularly well suited to operate over a wide range of carrier frequencies, generally lower than those of *Gryllus* especially in such low-pitched species as *O. latipennis*, *O. fultoni*, and *O. niveus* (Walker, 1962a). Dumortier (1963) proposed two alternative mechanisms to ac-

¹ *O. fultoni* was formerly known as *O. niveus* and was so identified by Pierce (1948). See Walker and Gurney (1960)

count for the acoustic performance of crickets at variable tooth-impact frequencies: 1. the tegmen possesses a continuous series of natural frequencies, each of which may be excited in resonance with the prevailing tooth-impact frequency; or 2. the tegmina are passive surfaces which move perpendicularly to their planes when actuated by the file and scraper mechanism, at whatever frequency the latter generates, and without involving their own natural resonance. The present work demonstrates that the tegmina of *Oecanthus nigricornis* behave as continuously variable tuned resonators over much (possibly all) of the range of normal tooth-impact frequencies, showing that for this species Dumortier's first hypothesis is correct.

I thank Prof. T.J. Walker and two anonymous referees who reviewed the manuscript and provided many helpful suggestions.

References

- Alexander, R.D.: The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). *Ann. Ent. Soc. Am.* **50**, 584-602 (1957)
- Dincă, F., Teodosiu, C.: *Nonlinear and Random Vibrations*. București and New York: Academic Press 1973
- Dumortier, B.: The physical characteristics of sound emissions in Arthropoda. In: *Acoustic behavior of animals*. Busnel, R.G. (ed.), pp. 346-373. New York: Elsevier 1973
- Fulton, B.B.: The tree crickets of New York: Life history and bionomics. *N.Y. Agric. Exp. Stn. Tech. Bull.* **42**, 1-47 (1915)
- Huber, F.: The role of the central nervous system in Orthoptera during the co-ordination and control of stridulation. In: *Acoustic behavior of animals*. Busnel, R.G. (ed.), pp. 440-488. New York: Elsevier 1963
- Levenson, M.E.: Harmonic and subharmonic response for the Duffing equation $\ddot{X} + \alpha X + \beta X^3 = F \cos \omega t$ ($\alpha > 0$). *J. Appl. Phys.* **20**, 1045-1051 (1949)
- Lutz, F.E., Hicks, W.R.: An analysis by movietone of a cricket's chirp (*Gryllus assimilis*). *Am. Mus. Novit.* **420**, 1-14 (1930)
- Michelsen, A., Nocke, H.: Biophysical aspects of sound communication in Insects. *Adv. Insect Physiol.* **10**, 247-296 (1974)
- Nocke, H.: Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Z. vgl. Physiol.* **74**, 272-314 (1971)
- Pierce, G.W.: *The songs of insects*. Cambridge: Harvard University Press 1948
- Stoker, J.J.: *Nonlinear vibrations in mechanical and electrical system*. New York: Wiley 1950
- Timoshenko, S., Young, D.H.: *Vibration problems in engineering*. New York: Van Nostrand 1955
- Walker, T.J.: The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). I. The genus *Neoxabea* and the *niveus* and *varicornis* groups of the genus *Oecanthus*. *Ann. Entomol. Soc. Am.* **55**, 303-322 (1962a)
- Walker, T.J.: Factors responsible for intraspecific variation in the calling songs of crickets. *Evolution* **16**, 407-428 (1962b)
- Walker, T.J.: The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). II. The *nigricornis* group of the genus *Oecanthus*. *Ann. Entomol. Soc. Am.* **56**, 772-789 (1963)
- Walker, T.J.: Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: *Orchelimum*) and reanalysis of published data. *J. comp. Physiol.* **101**, 57-69 (1975)
- Walker, T.J., Gurney, A.B.: A new species of *Oecanthus* from the West Indies (Orthoptera, Gryllidae). *Fla. Entomol.* **43**, 9-13 (1960)