

Body Vibration and Sound Production in an Insect (*Atta sexdens*) Without Specialized Radiating Structures

W. Mitch Masters^{1*}, Jürgen Tautz¹, N.H. Fletcher², and Hubert Markl¹

¹ Fakultät für Biologie, Universität Konstanz, D-7750 Konstanz, Federal Republic of Germany

² Department of Physics, The University of New England, Armidale, N.S.W. 2351, Australia

Accepted October 21, 1982

Summary. 1. The leaf cutting ant *Atta sexdens* stridulates using a file-and-scrapers device (Markl 1968). The temporal and spectral characteristics of the cuticular vibration and airborne sound are fairly typical of the stridulatory sounds of insects that lack specialized radiating structures (Masters 1980). We used laser-Doppler vibrometry (LDV) to measure the velocity of different points on the ant's body during stridulation to determine what sorts of body vibration are produced by the impact of the scraper on the file, both in air and with mass-loading of the cuticle underwater, and how the vibration relates to this radiated sound.

2. The gaster, on which the file is located, appears to be the principal sound-radiating part of the ant. From theoretical considerations, we would expect four types of gaster vibration to be excited by the scraper impact: (I) dipole swinging of the entire gaster, (II) quadrupole distortion of the gaster shape due to volume flow of the gaster contents, (III) monopole pulsation of the gaster and (IV) bending waves travelling in the gaster shell. Each type of vibration has associated modal resonances whose frequencies are predicted in a semi-quantitative fashion from a simple mechanical model of the gaster.

3. Vibrometer measurement shows that each tooth strike typically excites low frequency (~1 kHz) and high frequency (~10 kHz) damped vibrations that can be detected at most points on the gaster. Broadband spectral energy can be detected up to about 30 to 40 kHz (in rare cases to ~60 kHz). The low frequency resonance appears to be due to type I rather than type II vibration, and the high frequency resonance due to type III rather than type IV vibration.

4. Underwater, both low and high frequency resonances were still present, but their frequencies were reduced by about 15% and 35% respectively. We expect the decrease to be even greater when the ant is buried underground.

5. The rate at which the scraper strikes the teeth of the file is close to the ~1 kHz modal frequency of the gaster, but in contrast to our expectation does not exactly match this frequency (Fig. 2). The reason for this discrepancy is not clear.

6. Below about 30 kHz there is fairly good correspondence between the energy spectra of the airborne sound recorded with a microphone and the gaster vibration recorded by LDV. Above this frequency the sound usually shows a complicated power spectrum that we can relate to the vibration of the body only in a qualitative fashion.

Introduction

Many insects and other arthropods possess specialized devices for producing sounds. Examples of the most common of such devices, in which opposable areas of the exoskeleton serve as file and scraper, can be found in scorpions, spiders, crustaceans, and many orders of insects (Haskell 1961; Dumortier 1963a, b). The scraper is drawn over the file, or vice versa, thus setting the exoskeleton into vibration and radiating sound. The vibration and sound may be used in both intra- and interspecific communication, for example as a courtship call or as an aposematic signal. While a fair amount is known about the properties of the radiated sound (mainly because of the availability of good microphones), comparatively little is known about the underlying vibration, the details of its production, and how it relates to the sound

* Present address: Department of Biology, University of Oregon, Eugene, Oregon 97403, USA

recorded by a microphone. In a few cases, sounds produced by insects with specialized sound-radiating structures have been examined (e.g., crickets whose wings have been modified to aid sound radiation [Nocke 1971; Sismondo 1979]), but almost no work has been done on the vast majority of phonic insects which do not appear to be highly modified or specialized for efficient sound radiation.

We have investigated sound radiation by one such seemingly unspecialized insect, the leaf cutting ant *Atta sexdens*, using laser-Doppler vibrometry (LDV) to measure the vibration of the insect's surface. This ant stridulates using a file-and-scrapers mechanism (Markl 1968). If buried underground as a result of a nest cave-in, stridulation attracts other members of the colony who may then dig out the trapped individuals (Markl 1967). Leaf cutting ants also stridulate when attacked or disturbed, and in this case stridulation may serve an aposematic function, as it apparently does in other insects (Masters 1979), warning perhaps of the painful bite these ants can inflict.

The mechanism of sound production and the nature of the sounds radiated by leaf cutting ants have been studied by Markl (1968). Briefly, the gaster is moved in such a way that a scraper attached to the posterior edge of the postpetiole moves across a striated file plate located on the first segment of the gaster (Fig. 1). The ridges of the file are roughly triangular in cross-section, are about 2 μm high and about 3 μm apart. The scraper delivers impulses (tooth strikes) to the file at a repetition rate of ~ 1 kHz. These impulse clicks appear in the radiated sound as a highly damped oscillation whose frequency is on the order of 10 kHz and with energy spread over a wide frequency bandwidth. Each stroke of the scraper across the gaster yields a train of these clicks lasting about 50 ms and the strokes are repeated about five times a second. Since in all these particulars leaf cutting ants appear to be rather typical of those stridulating insects that lack specialized radiating structures (Masters 1980), we decided that they would be good animals in which to study sound production by file-and-scrapers devices.

Materials and Methods

Large workers of *Atta sexdens* were obtained from a laboratory colony. Individuals ranged in length from about 7 to 11 mm and in gaster volume from about 1 to 10 mm³. We recorded both the airborne sound and the cuticular vibration from stridulating ants at a temperature of 22 to 25 °C. Vibration measurements were made with a laser-Doppler vibrometer (LDV) (DISA Elektronik A/S, DK-2740 Skovlunde, Denmark). This

instrument detects the Doppler frequency shift, proportional to velocity, undergone by light reflected from a moving target and produces an analog output voltage corresponding to the instantaneous velocity of the target. A laser beam is focused on the point to be measured, and light reflected back from that point is gathered by the focusing lens and its frequency compared with that of an unshifted reference beam. The component of target velocity along the axis of the laser beam is measured. On the velocity range setting we used, the frequency response is ± 1 dB from 0 to 100 kHz. (See Buchhave (1975), Michelsen and Larsen (1978) and Masters and Markl (1981) for further details on LDV).

Vibration was recorded dorsally from the postpetiole near the scraper and from the gaster near the file, and sometimes from additional positions (dorsal, lateral and ventral mid-gaster, gaster tip, and dorsal mid-thorax – see Fig. 1). Leaf cutting ants stridulate when held, and for recording, an ant was usually grasped by its head and thorax between thumb and forefinger. For thorax measurement it was held by its legs with forceps. The laser beam was aligned approximately perpendicular to the ant's surface so that the velocity component normal to the surface was measured. Due to the struggles of the ant, however, the beam could occasionally be as much as 45° off normal incidence, leading to possible errors of measurement of up to $\sim 30\%$. Points to be measured on an ant were painted with a small spot (diameter ~ 0.5 mm) of white type-writer correction fluid to improve the signal-noise ratio of the LDV signal and to make it easier to determine the point from which the vibration was recorded. The paint loaded the surface slightly (~ 30 $\mu\text{g}/\text{mm}^2$) but probably not significantly.

Airborne sound was recorded with a Brüel and Kjaer 1/4-inch microphone Type 4135 (± 1 dB from 1 to 100,000 Hz) located 5 mm from the ant. In a number of cases airborne sound and vibration signals were recorded simultaneously on two tracks of an instrumentation tape recorder (Hewlett Packard Model 3964A, frequency response at 38.1 cm/s ± 3 dB from 250 to 75,000 Hz).

Since these ants stridulate when trapped underground where radiation conditions are different than in air, we recorded vibration with the ant underwater to simulate the effect of earth loading on the cuticle. Water rather than sand or earth was used because it is possible to measure vibration by LDV in a transparent medium such as water. Preliminary observations indicated that shortly after submersion (within about 1 min), the ant's movements become noticeably weaker. Also, since it is possible that a water film might develop between the file and scraper thus lubricating the interface and causing unwanted changes, we tried to keep immersion as brief as possible. Ants were held underwater no longer than 45 s, were used only once, and only one point (near the file on the gaster) was measured.

Sound and vibration signals were analysed on the 100 kHz range of a fast Fourier transform (FFT) computing spectrum analyser (Nicolet Scientific Corp. Model 446A). On this range setting a 4 ms portion of the signal is digitized (1,024 points) and a 400 point power spectrum (i.e., frequency resolution of 250 Hz) of this time segment is produced. This study is based on ~ 250 spectra and ~ 350 time waveforms from 23 ants. The noise floor of the spectra was set by the LDV and varied somewhat between samples but in general was equivalent to a velocity of ~ 60 $\mu\text{m}/\text{s}$.

To measure the speed of propagation of a tooth-strike impulse through the ant's cuticle we mounted the ant by its thorax with beeswax on a small accelerometer (Brüel and Kjaer type 8307). Since the accelerometer was thus fixed in a stable position relative to the vibration-producing apparatus, its output could be used as a reference with which the time of arrival of the impulse at different points on the ant's surface

detected by LDV could be compared. The results are given with respect to the time of occurrence of the impulse at the near-file point of measurement, that is, the delay between the beginning of the accelerometer signal and the beginning of the impulse near the file was subtracted from all measurements.

The amount of air in the gaster tracheal system was determined by cycling the isolated gaster underwater a number of times through a sequence of evacuation and repressurization. This procedure forces most, although not all, of the air out of the trachea and replaces it with water. The fraction of air in the gaster was then estimated from the weight gain of the gaster, and the filled weight was used to estimate the total volume of the gaster, assuming its density to be that of water. Measurement of the gaster volume from its dimensions and its volume as determined by its filled weight were in good agreement.

Two-tailed probabilities are reported for all statistical tests.

Background Theory of Sound Radiation

Presentation and discussion of the results will be simplified if we first consider the vibration and radiation of sound from *Atta* from a theoretical viewpoint. Measurements of the airborne sound have shown (Markl 1968) that most of the energy is radiated from the gaster, since removal of the gaster (except for the file) reduces the total sound energy by > 50%, although the gaster itself forms only about one quarter of the ant by volume. For a first analysis, then, it is sufficient to consider only the vibration of the gaster. The anterior two thirds of the gaster is covered by dorsal and ventral plates, the dorsal plate being about twice as large and having the file on its anterior end (Fig. 1). The remainder of the gaster is covered by several overlapping pairs of plates, and thin, flexible membranes connect the plates to each other.

Vibration of the gaster shell is excited by passage of the scraper over the file. This would be expected to generate a low frequency wave in the cuticle due to the passage of the scraper over the file ridges, and a superimposed impulse as the scraper strikes each ridge (Markl 1968). The shape and amplitude of these two components would depend on the details of the file/scraper interaction.

Modes of Vibration

It is helpful to examine briefly the possible vibration modes of the gaster system in order to see what we should expect their frequencies and radiation characteristics to be. This can be done with the aid of a conceptual model of the gaster and its file/scraper excitation system which is on the one hand detailed enough to include most of the features of the real system and on the other hand contains virtually no unknown parameters so that

semi-quantitative predictions of resonance frequencies and radiation characteristics can be made.

Such a model treats the gaster as a roughly ellipsoidal body attached by the petiole and post-petiole, which are filled with springy muscle and cuticular tendons, to the thorax of the animal. The rigidity of the cuticular plates covering the gaster is appreciable but the flexible folds connecting them allow the gaster to expand, contract and deform relatively freely. To simplify the model still further we may take the gaster to be a simple sphere clad in a slightly stiff elastic skin. The gaster is filled with tissue containing, in capillary tubes, an air volume equal to about 20% of the total gaster volume (see Results). The gaster contents can therefore reasonably be approximated by a uniform fluid having 80% of the density of water and 20% of the compressibility of air, these values following immediately from the facts that the density of air is insignificant relative to that of water, while the compressibility of water is insignificant relative to that of air. This leads to an effective acoustic wave velocity c' within the gaster fluid of

$$\frac{c'}{c_{\text{air}}} = \left[\frac{K_{\text{air}} r_{\text{air}}}{K' r'} \right]^{\frac{1}{2}} \quad (1)$$

where c_{air} , K_{air} and r_{air} are the wavespeed, compressibility and density of air, and K' and r' are the effective compressibility and density of the gaster contents (Rayleigh 1896, p. 30). If the fraction of air is 20%, Eq. (1) predicts a velocity of about 30 m/s inside the gaster.

We can now identify the possible vibration modes of the gaster and estimate their frequencies.

Mode I. The gaster oscillates up and down, pendulum like (dipole motion), about its point of attachment to the thorax, the restoring force being supplied by the springy petiole/postpetiole. (In the real ant, of course, the center of mass of the whole insect must remain nearly fixed so there must be a contrary vibration of the thorax.)

Mode II. The gaster deforms in a 'tidal' oscillation without any change in volume, becoming successively prolate and oblate, with the symmetry axis passing through the postpetiole (quadrupole motion).

Mode III. The gaster undergoes spherically symmetric expansions and contractions – there are several possible modes of this type (monopole motion).

Mode IV. The gaster cuticle supports oscillations of small wavelength, not penetrating far into the interior (this type of mode is a higher order form of Mode II).

It is difficult to estimate the frequency of Mode I since this oscillation depends upon the muscular tension in the petiole/postpetiole during stridulation. This is presumably under the control of the insect and the frequency could range from a low value up to perhaps 1 kHz.

The frequency of Mode II tidal oscillations depends upon the value assumed for the average elasticity of the cuticular shell. As a minimum we can take the surface tension of water, in which case the oscillation frequency will be equal to that of a water drop of the same size; for a drop about 2 mm in diameter it is a few hundred Hertz (Rayleigh 1896, pp. 371–375). Even with its folds the cuticle is probably a good deal stiffer than this and, since the resonance frequency increases as the square root of the surface elastic modulus, we should expect a resonance frequency on the order of 1 kHz.

Mode III oscillations are the easiest to treat theoretically, though there are some subtleties in the mathematics (Morse 1948, pp. 311 ff.). These are compressive modes, in contrast to Modes I and II in which the gaster volume remains constant, and their frequencies are determined primarily by the wave propagation properties of the gaster contents. For the particular type III modes considered, the resonance frequencies are those for which the sphere diameter is an integral number of wavelengths. For a 2 mm gaster (roughly the size of a large worker) and a propagation velocity of 30 m/s, for example, we expect the first resonance at about 15 kHz with subsequent resonances at harmonics of this frequency.

The properties of type IV modes are determined largely by the cuticular plates. These modes will be important only if the plates are very stiff so that their behavior dominates that of the contained fluid, a situation which seems unlikely to apply at the relatively low frequencies so far considered. At higher frequencies, however, the plate stiffness becomes increasingly important and surface waves may propagate around the shell of the gaster or perhaps even within a single plate. These waves may be either longitudinal or transverse to the plates but in the latter case they will unavoidably couple to some extent to the contained fluid. In either case it seems unlikely that such modes will become dominant much below 50 kHz.

It should be pointed out that, because of the nature of biological tissues and particularly the air

included in the capillaries of the gaster, the quality factor (Q value) of these resonances will not be high. Indeed it is unlikely to exceed 10 and a value of 3 (or even less) may be more typical. Q is a measure of the sharpness of tuning and is defined as the center frequency divided by bandwidth across which the resonant response is within 3 dB of its value at the resonance peak. The lower the Q , then, the more the resonance peak is spread out.

The modes discussed above are, of course, highly idealized as far as the ant gaster is concerned. However, the 'non-ideality' of the real insect will modify the modes only in detail without altering their essential nature or greatly changing their frequencies.

The sharp impulses imparted to the gaster by the file and scraper will tend to drive all possible resonant modes but will favor those whose frequencies lie close to the fundamental or to one of the harmonics of the excitation frequency. Since the tooth strike rate is about 1 kHz it should lead to a relatively large amplitude for mode II and perhaps also for mode I if the petiolar support is stiff enough. All the mode III components are high enough in frequency and broad enough in bandwidth that they will encompass a number of harmonics of the excitation and thus emphasize them in the manner familiar in relation to vocal formants in human speech. Modes of type IV are not likely to be excited appreciably because there will be very little input energy at these frequencies.

Sound Radiation

The radiation of sound from a vibrating system such as the ant gaster is a moderately complex process to analyze (Morse 1948; Harris 1964). First we must recognize that the pressure field near the gaster (within about $\lambda/4$ where λ is the wavelength) is different from the true radiated sound field in which the radiated energy is lost to the system. Ideally measurements should be made in the far field since they are then easier to interpret, but in order to achieve an adequate signal-to-noise ratio it is necessary to place the microphone at a position that is in the near-field region for frequencies below ~ 20 kHz. Such placement gives much more emphasis to low frequency vibrations than would be apparent in the true radiated sound. We should remember, however, that the animal receiving the sound may itself often be located in the near field and the consequences of this fact depend on the type of detector (pressure, pressure gradient, velocity) the animal uses (see Michelsen and Nocke 1974).

The most efficient modes for sound radiation are the monopole modes of type III in which the gaster volume changes. If a is the gaster radius and λ the sound wavelength then, for a given surface velocity, the radiated sound intensity contains a factor $(a/\lambda)^2$. Since λ is small for the high-frequency type III modes, they radiate relatively effectively.

The wagging motion described as mode I constitutes an acoustic dipole and its radiated intensity contains a factor $(a/\lambda)^4$. The tidal motion of mode II is an acoustic quadrupole and contains the even stronger reduction factor $(a/\lambda)^6$. These two oscillations would occur, as we have discussed, at roughly the fundamental tooth-strike frequency of 1 kHz so that λ is large and radiation efficiency in air is almost vanishingly small.

In the very near-field region these radiation-efficiency factors disappear from the expressions for pressure variation so that, in the limit of a microphone placed very close to the gaster, the measured pressure contains only the single factor (a/λ) for all modes. Such near-field measurements therefore exaggerate immensely the importance of modes I, II and IV in the radiated sound. Nevertheless they provide a good check on surface vibration measurements and do show up the higher frequency type III modes that are primarily responsible for radiation.

Buried Insects

One of the purposes of the stridulation mechanism is apparently to facilitate the location of buried workers by rescue teams (Markl 1967). Several interesting aspects of sound production in this situation can be elucidated by preliminary theoretical analysis. For this purpose we can use the same model as before for the gaster but assume it to be immersed in an elastic medium with density about 3 times that of water and appropriately low compressibility. Solution of this problem for type III modes shows that, to a first approximation, a spherical jacket of the surrounding medium with thickness about equal to half the radius of the gaster effectively moves along with it. This added mass loading decreases the resonance frequency for each type III mode to about one third its value in air. The effect on dipole (type I) and quadrupole (type II) modes should be rather less but their resonance frequencies will also be decreased.

The amplitudes of all vibration types will be reduced underground. The increased impedance of the medium will have a stronger effect on type I and II vibrations, since now the motion must be accomplished against a high rather than a low re-

sistance. Type III and IV vibrations, on the other hand, must act against the relatively high internal impedance of the gaster contents even when the ant is in air, so the effect of moving from a low impedance to a high impedance medium will be less pronounced for these two types. The radiation efficiency at a given wavelength increases as the characteristic impedance of the medium increases (see Markl 1968), so radiation conditions are much better underground than in air. The energy coupled to the medium may therefore be larger underground even though the vibration of the exoskeleton is smaller.

Results

Typical velocity waveforms recorded from the gaster are shown in Fig. 1. Such waveforms usually show a sharp peak in the inward direction (downward in the figures) caused by the impact of the scraper on the file. At the postpetiole the direction of the impulse is always inward, and it was nearly always inward at points on the gaster (except generally outward at ventral mid-gaster). The impulse and its direction are sometimes difficult to see, especially on the thorax, at the gaster tip and on the ventral side of the gaster. The tooth-strike impulse may be followed by a high-frequency, damped oscillation with a frequency of about 10 kHz (e.g. Fig. 1c) and by a low-frequency, damped oscillation at about 1 kHz (e.g., Fig. 1d), which we will refer to as HF and LF oscillations respectively. The HF oscillation is not always distinguishable, especially at points distant from the file and scraper, but the LF oscillation is nearly always present and usually becomes more pronounced away from the file and scraper.

The spectra of vibration waveforms usually showed a low-frequency peak at ~ 1 kHz corresponding to the LF oscillation, and in about half the cases a peak or corner at roughly 10 kHz (e.g., Fig. 4b). Above 10 kHz spectra normally showed a steady decline in energy with no obvious resonance peaks, except rarely the file or scraper vibrations contained a broad peak at about 30 to 50 kHz (e.g., Fig. 4b). In general, the farther from the file and scraper, the less high-frequency energy was contained in the vibration signal as can be seen from the average signal energy at 10 kHz given in Table 1. The highest measurable frequency also decreased away from the file and scraper. At the gaster tip, for example, the highest frequency at which the signal was above the background noise level of $\sim 60 \mu\text{m/s}$ was 13.5 ± 1.5 kHz (mean and standard deviation) ($n=8$ ants) and at mid-

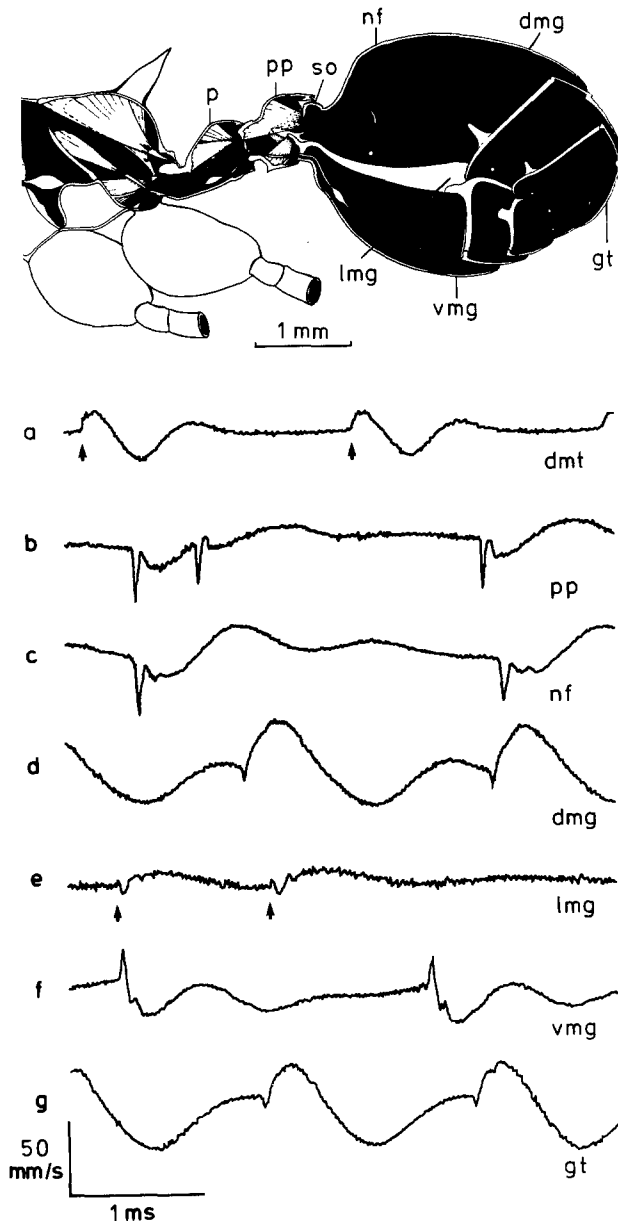


Fig. 1. Drawing of the abdomen and part of the thorax of a leaf cutting ant (modified from Markl (1968)) with typical stridulatory velocity waveforms recorded by LDV at different points on the ant. *dmg* dorsal mid-gaster; *dmt* dorsal mid-thorax (not shown in drawing); *gt* gaster tip; *lmg* lateral mid-gaster; *nf* near file on gaster; *p* petiole; *pp* postpetiole; *so* stridulatory organ; *vmg* ventral mid-gaster. Arrows in a and e mark the tooth strikes

thorax was 12 kHz ($n=2$), but near the file on the gaster it was 27 ± 4 kHz ($n=8$) and near the scraper on the postpetiole was 45 ± 16 kHz.

Modes I and II

Measurement of the average LF period for 15 ants gave a value of 0.94 ± 0.11 ms, which corresponds to a mean frequency of 1,050 Hz. The tooth-strike

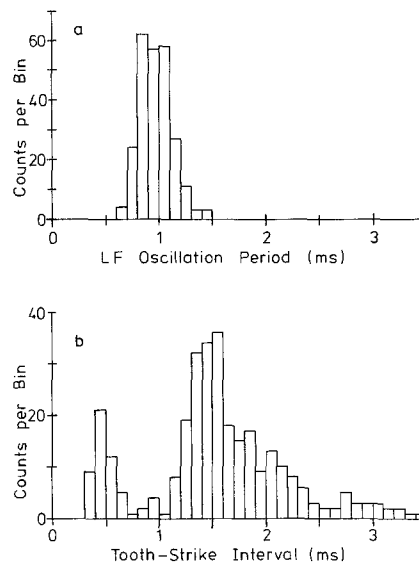


Fig. 2. Distribution of (a) low frequency (LF) oscillation periods ($n=249$) and (b) tooth strike intervals ($n=307$) determined from velocity waveforms such as those shown in Fig. 1

rate for these ants was lower, with an average inter-strike interval of 1.7 ± 0.4 ms. Furthermore, as can be seen by comparing the histograms of tooth-strike interval and period of LF oscillation (Fig. 2), impulses from the file and scraper only rarely occur with a spacing of 1 ms, that is, at a rate corresponding to the frequency of the LF component. In fact the tooth-strike distribution is bimodal, with 1 ms being a sort of 'forbidden zone'. The peak in the distribution at ~ 0.5 ms is due to 'double' tooth strikes such as shown in Fig. 1b. These occur intermittently in most stridulation signals although some ants tended to produce them more often than others. How these 'double' strikes arise is not clear. There was no correlation between the tooth-strike interval and the period of the LF oscillation; 249 paired observations where both could be measured gave a correlation coefficient of 0.04 ($df=247$, ns.). The period of LF oscillation also did not correlate with the gaster volume of the ant ($r=0.05$, $df=13$, ns.).

The LF oscillation occurs in a frequency range appropriate for either mode I or mode II. The fact that, as shown in Table 1, the amplitude of LF motion is generally small at the postpetiole and near the file, greater at dorsal mid-gaster and again small at lateral mid-gaster (all measured perpendicular to the surface) suggests the gaster undergoes an up and down oscillation in the vertical plane of the ant with a pivot point near the anterior end of the gaster. In addition, the fact that following an impulse the initial LF deflection is outward from the surface at dorsal mid-gaster and inward

Table 1. Average energy in the vibration spectra at 1 and 10 kHz. Values are given as mean \pm s.d. in dB re 1 mm/s; n is the number of ants used in determining the mean. Several spectra were used for each ant

Freq.	Dorsal mid-thorax (n=2)	Postpetiole (n=8)	Near file on gaster (n=9)	Dorsal mid-gaster (n=5)	Lateral mid-gaster (n=9)	Gaster tip (n=3)
1 kHz	9.4 ^a	10.4 \pm 4.1	8.2 \pm 4.6	13.1 \pm 3.6	3.5 \pm 7.9	19.6 \pm 3.4
10 kHz	-19 ^a	-6.7 \pm 3.2	-7.5 \pm 3.0	-11.0 \pm 3.6	-19.5 \pm 4.3	-17.2 \pm 3.9

^a Standard deviation not given due to small sample size (values were 7.4 and 11.4 dB at 1 kHz and -16.4 and -21.6 dB at 10 kHz)

at ventral mid-gaster (i.e., in the same direction in space, see Fig. 1 d and f) supports this interpretation. However, if the gaster behaved as a rigid pendulum we would not expect to see, as we do (Table 1), large amplitudes measured perpendicular to the tip of the gaster. We also find that the initial LF deflection is inward at the postpetiole and near the file (Fig. 1 b and c) but outward at dorsal mid-gaster and at the gaster tip (Fig. 1 d and g), which also conflicts with the idea of a simple, rigid pendulum.

These discrepancies could be explained if the gaster were not vibrating rigidly, but they might also be considered evidence of type II motion in which the shape of the gaster is distorted due to internal volume flow of its contents. To try to separate these two possibilities, we measured the period of LF oscillation before and after covering the gaster of one ant with nail varnish. The frequency of mode II depends principally on the average stiffness of the gaster covering and since nail varnish should make the expansion joints between segments much less compliant, it should raise the resonance frequency noticeably. We observed, however, a slight decrease in the LF frequency with the period increasing from 1.04 ± 0.08 ms to 1.17 ± 0.10 ms ($t=4.1$, $df=32$, $P<0.001$). The increase in period is about what we would expect for type I motion, since adding the nail varnish increased the mass of the gaster by about 20%. If the stiffness of petiole is assumed to remain constant, then an increase in the mass (moment of inertia) of 20% should lead to an increase in the period of about 10%, i.e., about what we observed. Analogously, we would expect reducing the gaster mass to lead to a decrease in period for mode I. Cutting off the distal half of the gaster of an ant lowered the period from 0.94 ± 0.08 ms to 0.37 ± 0.06 ms ($t=9.9$, $df=4$, $P<0.001$) corresponding to an increase in frequency from about 1 to 2.7 kHz. When immersed in water, the average LF period of 5 ants increased from 0.94 ± 0.14 to 1.08 ± 0.09 (paired $t=2.8$, $df=4$, $P<0.05$), the

change being in the direction expected for increased mass loading.

The evidence seems to indicate, therefore, that the LF oscillation is of type I rather than II, but that the motion of the gaster is not strictly perpendicular to the gaster axis, there being a component along this axis as well.

Modes III and IV

The average period of the HF oscillation for 17 ants was 95 ± 14 μ s, corresponding to a frequency of about 10.5 kHz. The period was correlated with the gaster volume of the ant ($r=0.78$, $df=12$, $P<0.01$), with larger ants tending to have a lower resonant frequency.

Based on our frequency estimates, the HF oscillation is probably of type III. The frequency of mode III is determined by the average wave propagation velocity within the gaster contents. This, according to Eq. (1), depends on the amount of air in the gaster tracheal system. We measured this for 17 ants whose gaster volume ranged from 2 to 7.5 mm³. The fractional content of air averaged $17.4 \pm 7.4\%$ and showed no correlation with the volume of the gaster ($r=0.007$, $df=15$, ns.). The true fraction of air is likely to be slightly greater than 17%, since it is not possible to replace all the air in the tracheae with water. Taking 20% as a reasonable estimate of the fractional air content, Eq. (1) gives a predicted velocity of about 30 m/s. This value is not strongly dependent on the precise fraction of air, values of 10% and 30% giving velocities of 40 and 26 m/s respectively.

The average gaster volume of those ants for which the HF period was determined was 6.8 mm³, equivalent to a sphere about 2.4 mm in diameter. For a sphere this size filled with a fluid whose wave velocity is 30 m/s, the predicted first resonance should occur at about 12.5 kHz. This is the undamped resonance frequency, but damping reduces the frequency of free oscillation by an amount related to the Q of the system. Q can be determined by the fractional change in height from

one peak in the oscillation to the next. For a Q of 3, the successive peaks show a ratio of 2.8 to 1, and this ratio increases with lower Q s. The HF oscillation generally shows a ratio of 3 or larger (for example, Fig. 1c and f), which indicates that Q is normally under 3, and in fact, since about half the time we do not see the HF oscillation, the damping in these instances may be so heavy that the free oscillation is completely suppressed. However, for those waveforms we were able to measure, Q was about 1 to 3. The free oscillation frequency is about 10% below the undamped resonance frequency for Q s of this magnitude, so the predicted resonance of 12.5 kHz must be reduced by this amount, bringing us quite close to the measured value of 10.5 kHz.

Viscous losses generally increase with increasing frequency, so the higher modes of type III predicted from theory probably will be even more strongly damped, and therefore their peaks even more flattened. This might explain why we found no consistent evidence of such peaks at multiples of 10 kHz in the vibration spectra.

Conceivably, the HF resonance could be of type IV, if the cuticular wavespeed were appropriate. The wavelength must be equal to the circumference for the lowest resonance of this type, which means that, for a sphere 2.4 mm in diameter, the wavespeed should be on the order of 75 m/s. To determine the speed of propagation in the cuticle, we measured the difference in arrival time of the tooth strike impulses at different points on the gaster. The delay between the near file and dorsal mid-gaster was $5.5 \pm 1.8 \mu\text{s}$, and between near file and gaster tip was $7.9 \pm 1.2 \mu\text{s}$. The distances travelled in the two cases were $1.8 \text{ mm} \pm 20\%$ and $3.2 \text{ mm} \pm 15\%$, translating into velocities of 330 and 400 m/s. The uncertainty in these estimates is rather large and arises mainly from the difficulty of determining the exact distance travelled, since the instantaneous point of measurement could not be precisely determined due to the ant's struggles. The velocities, nevertheless, are clearly higher than 75 m/s. We should remember, however, that this method of measuring wavespeed gives us the group propagation velocity rather than the phase velocity, and it is the phase velocity that is important in determining resonances. For a bending wave in a thin plate (a rough approximation of the gaster shell), the group velocity may be as much as twice the phase velocity (Cremer et al. 1973). The phase velocity might therefore be as low as 150 m/s, but this is still too high for a mode IV resonance at 10 kHz, and it seems most likely that the HF oscillation is of type III.

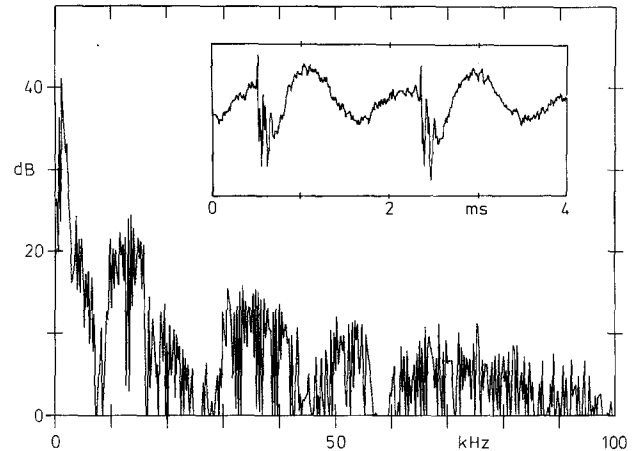


Fig. 3. Airborne sound recorded ~ 5 mm dorsal to the gaster. *Inset* shows the pressure waveform (maximum amplitude 0.17 Pa peak to peak, RMS sound pressure level 63 dB re 20 μPa). The 0 dB level in the spectral energy distribution of this waveform is at approximately the level of the background noise ($\sim 160 \mu\text{Pa}$ RMS)

When the ant is placed underwater the HF period increases, as would be expected due to the added mass of the water. The mean period for 5 ants measured before and after immersion changed from $97 \pm 9 \mu\text{s}$ to $135 \pm 8 \mu\text{s}$ (paired- $t = 5.3$, $df = 4$, $P < 0.01$), corresponding to a 35% reduction in frequency.

Airborne Sound

The airborne stridulation sound recorded about 5 mm above the file region showed evidence of the LF and HF components seen in the gaster vibrations. For example, in Fig. 3 the LF component is obvious in the time waveform, and the HF component, while overlaid in the time waveform by still higher frequencies making it difficult to recognize, is also present as can be seen by the spectral peak at about 10 kHz. With the microphone located lateral to the gaster, as was required for simultaneous recording of the airborne sound and cuticular vibration, the LF component is usually less pronounced in the airborne pressure waveform (Fig. 4a). This is to be expected if, as we believe, the LF component is type I (dipole) oscillation. For a dipole vibrating along the axis through its poles, the sound pressure radiated in the equatorial plane will be zero (see Harris 1964), and the microphone is approximately in this plane when it is lateral to the gaster. The HF oscillation, being of type III (monopole), should be about equally well radiated in all directions, and this energy is detected by both dorsally or laterally placed microphones (Figs. 3 and 4a).

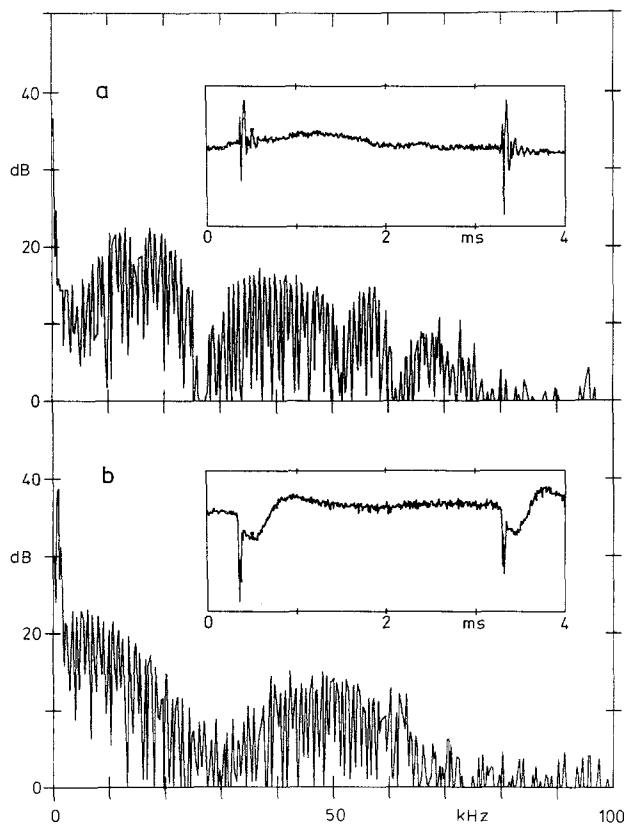


Fig. 4. **a** Airborne sound and associated energy spectrum as in Fig. 3 except that the microphone was located 5 mm lateral to the gaster. **b** Cuticular velocity waveform (*inset*) recorded near the scraper on the postpetiole and its energy spectrum. Maximum peak amplitude of the time waveform in **a** is ~ 0.31 Pa (total RMS sound pressure level 62 dB re 20 μ Pa) and in **b** is 47 mm/s. 0 dB is slightly below the noise level of the recording and is 200 μ Pa RMS in **a** and 33 μ m/s RMS in **b**. Upper cutoff frequency of the tape recorder was ~ 75 kHz, and spectral peaks above this frequency are due to recorder noise. In **b** the upper signal limit is ~ 65 kHz

Discussion

The usual motion that results from a tooth-strike impulse appears to consist of a low-frequency (~ 1 kHz) oscillation of type I and a high-frequency (~ 10 kHz) oscillation of type III. Type II motion seems to be relatively unimportant, and type IV motion, although not of great importance in the range we were able to measure ($< \sim 40$ kHz), may well be significant at higher frequencies. In other stridulating insects with different body structure the relative importance of these various types of vibration might well be different. Some beetles, for instance, have their stridulatory organs arranged so as to vibrate their elytra, and for these type IV vibration might be dominant.

We can divide the energy in the radiated airborne sound into three frequency regions, the first two corresponding to the LF and HF peaks of

the vibration spectrum, and the third extending above about 20 or 30 kHz. In the lower two regions energy in the sound spectrum can be interpreted rather directly in terms of the measured vibration. Energy in the range 0.5 to 1.5 kHz can be attributed to the LF oscillation and the tooth-impact rate. This low-frequency component has been found in other stridulatory insects and may be an important carrier of information (Broughton et al. 1975; Skovmand and Pedersen 1978). The amplitude of the LF oscillation which appears in the airborne pressure waveform appears to depend on the relationship between the point of measurement and the direction of the LF oscillation. In the range from about 5 to 20 or 30 kHz the energy comes mainly from the HF oscillation. Generally the vibration signal peak at about 10 kHz appears at a slightly higher frequency in the airborne sound pressure spectrum (e.g., Fig. 4a). The shift to higher frequencies is attributable to the increasing radiation efficiency of the gaster as frequency rises. Radiation efficiency reaches a plateau value at a wavelength of $2\pi a$, where a is the gaster radius, representing a frequency of about 40 kHz for a typical ant, and above this frequency radiation is about equally efficient at all frequencies, although of course the amplitude of vibration will be small at such high frequencies.

Atta radiates a large amount of sound energy in the ultrasonic range, in contrast to the results of Kermarrec et al. (1976) for a related species of ant, but in accord with measurements made on many other types of insects (e.g., Dumortier 1963b; Masters 1980). Relating sound to vibration in this upper frequency range is difficult, however. Only rarely was the vibration energy at frequencies > 30 kHz above the LDV noise floor. When we did record a signal with a great deal of energy in this range, for example in Fig. 4b, the sound spectrum envelope had roughly the same form as the vibration spectrum, but with a more complicated pattern of peaks and valleys (Fig. 4a). (The same effect could be seen below 30 kHz, but usually it was not as strong). Peaks in the sound spectra did not occur at the regular harmonic intervals we might expect from our simple model, but then of course the real system is more complicated than our model. For instance, the measurements of high-frequency energy in the signal given in Table 1 show that the vibration amplitude is not equal over the whole surface of the gaster, which is not surprising since it is essentially being driven at a point. At high frequencies, therefore, we would expect the radiation pattern to be directional (see Kinsler and Frey 1962, pp. 169 ff.), so the spectral

pattern we see will depend critically on the placement of the microphone. Modes of type IV will also start to play an increasingly important role as the frequency increases, and the radiation pattern of these modes will also be directional. In our model we also neglected radiation from the head and thorax because they contribute little to the total sound energy, but they will nevertheless have some effect on the spectral pattern. Furthermore, reflection of sound from nearby objects (e.g., the microphone diaphragm, our fingers and forceps) can lead to high-frequency standing waves that will also modify the envelope of the sound spectrum. For all these reasons predicting the spectral pattern at high frequencies, except in a qualitative fashion, is an extremely difficult task.

Simple mechanical considerations, applied to our model, lead in most cases to the prediction that the frequency of any particular mode should be inversely proportional to the linear dimensions of the ant. There is in fact a tendency for larger insects to exhibit a slightly lower HF oscillation, but the LF oscillation seems to be essentially independent of ant size. It is not surprising that this linear scaling law does not hold since it assumes that all parts of the anatomy scale similarly and this is known not to be correct (or physically reasonable) for other animals. The transverse dimensions of elastic supporting structures must increase more rapidly than linearly in order to bear the increasing weight. This applies in particular to the petiole, whose stiffness is important for mode I and to the cuticle for mode III. If the resonance at 1 kHz is important for some (as yet undetermined) reason, then it is easily possible for evolutionary modifications of the scaling law to have maintained it at this frequency for ants of different sizes.

One puzzling observation, however, is that the LF oscillation is at 1 kHz rather than closer to the tooth-strike rate (Fig. 2). Maximum amplitudes of LF motion would be achieved by driving the system at its resonance frequency of 1 kHz, but impulses seldom occur this fast even in the mid-portion of the stroke where the rate is about 750 Hz. The 'double' tooth-strikes which occur with an interval of <0.7 ms (Fig. 2b) are at too high a frequency for the LF oscillation.

One possibility is that the LF resonance would be found to match the tooth-strike rate if we could measure it in the situation where stridulation is probably of most importance to the ant, that is, when it functions as an 'underground SOS' to attract nest mates to a cave-in. The frequency of mode I would be reduced underground and the change would probably be a good deal more than

the 15% decrease we found with the ant underwater. However, the tooth-strike rate is also lower when the ant is buried (Markl 1970). The frequency of mode I also depends on the muscle tension within the petiole, and this too might be different in underground stridulation, so it remains an open question whether the resonance and driving frequencies would be equal in this case.

Further work on the details of the file/scrapper interaction might help clarify the situation. As mentioned earlier, we would expect, a priori, the excitation waveform to be composed of a low frequency component caused by the passage of the scrapper over the grooved file and a high frequency component caused by impacts of the scrapper against the file teeth. We have clear evidence for the presence of the impact component but the file contour component is difficult to separate from the LF resonance. One might even suppose that the LF oscillation is not a resonance at all, but rather simply a result of forced motion over the uneven file. This, however, seems unlikely because we often see two or more cycles of damped oscillation following an isolated tooth-strike (e.g., Fig. 1c). Furthermore, the displacement of the scrapper (Fig. 5b) which can be calculated from the velocity signal at the postpetiole (Fig. 5a), usually has an amplitude larger than the height of the file ridges, for example in Fig. 5b the displacement is ~ 7 μm , about three times the ridge height. Although this amplification could have other explanations, it tends to make us think that the LF oscillation is a true resonance.

The waveform in Fig. 5b does not exactly correspond to the ridge profile, which is roughly triangular. This is no doubt due in part to the LF resonance, but the flattened portion of the waveform just before each tooth strike suggests that the scrapper may be momentarily caught at the top of each ridge, i.e., that it moves in a jerky, catch-slip fashion. How this might be accomplished mechanically is not clear. If the feedback from the resonating gaster were strong enough, scrapper motion would tend to lock to the mode I (or mode II) frequency, just as the stick-slip motion under the bow of a violin is locked to the string's resonance frequency. For *Atta*, however, the feedback is apparently not strong enough for this explanation to hold (since the excitation and resonance frequencies are not equal). However, it might be accomplished though, catch-slip movement would permit storage of energy in cuticular deformation during the catch time and rapid release of this energy during the tooth strike, as in other examples of lock-release mechanisms (e.g., the jump of a flea [Alex-

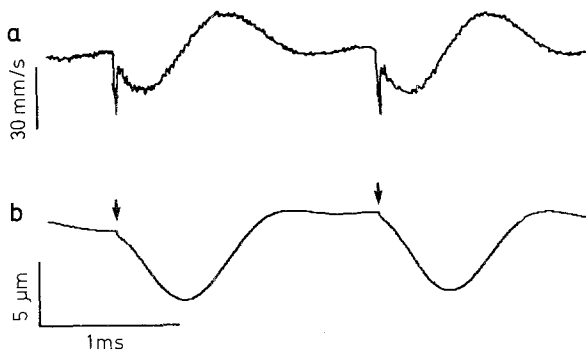


Fig. 5. **a** Velocity waveform recorded near the scraper on the postpetiole showing two tooth-strike impulses. **b** Displacement waveform at the same point, calculated by integrating **a**. The large velocity changes at the tooth strikes correspond to the small, rapid displacement changes marked by arrows in the displacement waveform

ander 1968]). In stridulation this process would tend to broaden the bandwidth of the signal (bandwidth is inversely proportional to the impulse duration) while generating maximum energy within this band (energy depends on impulse amplitude). The details of file/scraper interaction will need further study before these speculations can be verified.

Of course conditions are different underground. One result will be that the frequency of all modes will be lowered. For mode III we can calculate that the frequency should be reduced from ~ 10 kHz to ~ 3 kHz, rather than the ~ 7 kHz we measured underwater, and this would put the main energy in the range found by Markl (1968) for buried workers. But while shifts in the resonance frequencies are certainly important, there are also important changes in wave propagation behavior underground, since sand or earth has an appreciable shear modulus and can support propagation of transverse elastic waves. These waves are coupled quite effectively to the medium by motions of type I and will coexist with longitudinal waves of the type found in air, which are coupled especially well to type III motions. These effects, together with the attenuation properties of earth or sand at high frequencies, will tend to emphasize the low frequency part of the stridulation output, and it is precisely these frequencies to which leaf cutting ants are sensitive (50 Hz to 4 kHz, Markl 1970) and which attract excavators to a buried individual or to a nest cave-in.

Acknowledgements. We thank A.J.M. Moffat for her many contributions to this work. Supported by Deutsche Forschungsgemeinschaft grants Ma 374/11, Ma 374/13, Ma 374/14 and

Ma 374/15-2 to H.M. and a NATO postdoctoral fellowship to W.M.M.

References

- Alexander RM (1968) Animal mechanics. Sidgwick and Jackson, London
- Broughton WB, Samways MJ, Lewis DB (1975) Low-frequency sounds in non-resonant songs of some bush crickets (Orthoptera, Tettigoniidae). *Entomol Exp Appl* 18:44–54
- Buchhave P (1975) Laser Doppler vibration measurements using variable frequency shift. *DISA Information* 18:15–20
- Cremer L, Heckl M, Ungar EE (1973) Structure-borne sound. Springer, Berlin Heidelberg New York
- Dumortier B (1963a) Morphology of sound emission apparatus in Arthropoda. In: Busnel R-G (ed) Acoustic behavior of animals. Elsevier Amsterdam, London New York, pp 277–345
- Dumortier B (1963b) The physical characteristics of sound emissions in Arthropoda. In: Busnel R-G (ed) Acoustic behavior of animals. Elsevier, Amsterdam London New York, pp 346–373
- Harris GG (1964) Considerations on the physics of sound production by fishes. In: Tavolga WN (ed) Marine bioacoustics. Pergamon Press, Oxford, pp 233–248
- Haskell PT (1961) Insect sounds. Quadrangle Books, Chicago
- Kermarrec A, Mauleon H, Abud Antun H (1976) La stridulation de *Acromyrmex octospinosus* Reich. (Formicidae, Attini): Biometrie de l'appareil stridulateur et analyse du signal produit. *Insectes Soc* 23:29–48
- Kinsler LE, Frey AR (1962) Fundamentals of acoustics. Wiley, New York London Sydney
- Markl H (1967) Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. I. Die biologische Bedeutung der Stridulation. *Z Vergl Physiol* 57:299–330
- Markl H (1968) Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. II. Erzeugung und Eigenschaften der Signale. *Z Vergl Physiol* 60:103–150
- Markl H (1970) Die Verständigung durch Stridulationssignale bei Blattschneiderameisen. III. Die Empfindlichkeit für Substratvibrationen. *Z Vergl Physiol* 69:6–37
- Masters WM (1979) Insect disturbance stridulation: Its defensive role. *Behav Ecol Sociobiol* 5:187–200
- Masters WM (1980) Insect disturbance stridulation: Characterization of airborne and vibrational components of the sound. *J Comp Physiol* 135:259–268
- Masters WM, Markl H (1981) Vibration signal transmission in spider orbwebs. *Science* 213:363–365
- Michelsen A, Larsen ON (1978) Biophysics of the ensiferan ear I. Tympanal vibrations in bushcrickets (Tettigoniidae) studied with laser vibrometry. *J Comp Physiol* 123:193–203
- Michelsen A, Nocke H (1974) Biophysical aspects of sound communication in insects. *Adv Insect Physiol* 10:247–296
- Morse PM (1948) Vibration and sound. McGraw-Hill, New York Toronto London
- Nocke H (1971) Biophysik der Schallerzeugung durch die Vorderflügel der Grillen. *Z Vergl Physiol* 74:272–314
- Rayleigh JWS (1896) The theory of sound, vol 2. Reprinted by Dover, New York (1945)
- Sismondo E (1979) Stridulation and tegminal resonance in the tree cricket *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *J Comp Physiol* 129:269–279
- Skovmand P, Pedersen SB (1978) Tooth impact rate in the song of a shorthorned grasshopper: A parameter carrying specific behavioral information. *J Comp Physiol* 124:27–36