Modeling vibration and sound production in insects with nonresonant stridulatory organs

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Using a simple model for a nonresonant stridulatory organ, the intensities and shapes of the vibrations produced and the radiated sound were calculated. To test the results, the stridulation of femal multillid wasps (Mutillidae, Hymenoptera, Insecta) was investigated by the help of sound-analytical methods and with laser vibrometry. The model was shown to give good estimations for the sound spectrum and for the absolute power of the second to fifth harmonics. The wasps investigated, females of *Dasylabris maura* and ''*Smicromyrme*'' *praedatrix* with body lengths of about 10 mm, are able to make audible sounds with a power level of about 40 dB at a distance of 0.1 m. Stridulatory organs like those in mutillid wasps occur in several species of insects (e.g., beetles, wasps, and ants) and in other arthropods.
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INTRODUCTION

Stridulation is defined as sound emission by friction of two specialized surfaces against one another.[1] Stridulatory organs are widespread in insects and other arthropods. In most cases there is a scraper (plectrum, strigilator) on one part moving over a more or less regular structure (stridulatory file, stridulitrum, pars stridens, strigil) with periodically recurring elevations on another part. The structure and size of the stridulatory file are extremely variable; it may be made up of bristles, tubercles, teeth, or, frequently, of very broad ripples. Stridulatory organs have been found on virtually all regions of the body. According to the review of Dumortier,[1] there are many file-plectrum combinations in insects, virtually anywhere where two parts of the exoskeleton may touch each other.

Resonant structures may be associated with or attached to the stridulatory organ, especially if the sound is optimized for long-range intraspecific communication at distances of about 10 to 1000 m.[2] The benefits of using resonant structures are: limited bandwidth of the signal, optical sound radiation, and high energy produced with low energy per stroked bristle, tubercle, or tooth. Therefore, the stridulatory file is narrow if the resonator has a high quality Q. The width-to-period ratio of the stridulatory file is usually below 10:1.[1,3] Resonant structures are, for example, specialized areas of the forewings as in crickets[4,5] or air-filled cavities in the abdomen.[1]

For short-range intra- and interspecific communication, no resonant structures are necessary. Sometimes radiation far from the optimal sound impedance match is better, for example, to avoid the attraction of predators or to avoid the jamming of communication inside insect colonies. Stridulation without resonance is frequently used in distress situations, when the sound is presumably an aposematic signal aimed at discouraging predators from attacking the toxic, armed, or otherwise unpalatable sender. Some insects present acoustical signals together with optical (aposematic coloration) and/or chemical signals (allomones). A stridulatory file without associated resonant structures looks like a washboard and the width to ripple-period ratio of the file is above 10:1, usually in the order of 100:1. This paper deals with such stridulatory organs with broad files. They occur in different genera of many beetle families, like the cranioprothoracic organs, e.g., in Chrysomelidae, metathoracic organs in Cerambycidae, and abdominoelytral organs, e.g., in Scarabaeidae.[1] Abdominal organs occur in Hymenoptera in some genera of the wasp families Bradynobaenidae, Rhopalosomatidae, and Sphecidae, in almost all genera of Mutillidae,[6] and in several ant species.[7]

I. MATERIAL AND METHODS

A. Experimental animals

Measurements of stridulating female mutillid wasps were used to test the results obtained from computations based on the theoretical model (see below). In mutillids, the stridulatory organ occurs in both sexes on the abdomen dorsally between the second and third metasomal segments. The measurements were performed with three females of *Dasylabris maura*[8] (subfamily Sphaeropthalminae) from Germany and three females of ''*Smicromyrme*'' *praedatrix*[9] (subfamily Mutillinae) from South Africa. The mutillid wasps were kept in a terrarium where they had free access to water and a 50% solution of honey in water.

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B. Anatomical investigations

Dead dry specimens were rehydrated and softened in a pepsin solution (24 h, 40 °C). The expanding took place in distilled water. During washing in water and acetone (15′ each, 40 °C) the animals were treated with ultrasound to remove dust particles from the cuticle surface. After air-drying, the specimens were coated with gold (Balzers SCD 004 sputter coater) and examined in a Hitachi S-2400 scanning electron microscope (SEM). For all measurements the SEM was calibrated by using a Planotec silicon test object (Plano).

C. Sound and vibration recordings

Sound signals were recorded digitally with a computer sound board Pro Auido Spectrum 16 (Media Vision, settings: sampling rate 44.1 kHz; resolution 8 bit mono), and analyzed by the software Avisoft Sonagraph Pro 2.7 (Specht). A 1-in. condenser microphone MK 102 was mounted at a distance of about 0.1 m. The sound levels were measured with a precision pulse levelmeter 00 017 (Messelektronik ''Otto Schön'') which also served as a microphone amplifier.

The vibrations were measured with a laser vibrometer instrument containing a sensor head OFV300 (Polytec) and the vibrometer controller OFV2100 (Polytec, with enlarged frequency range, settings: displacement 1.62 μm/V, velocity 5 mm/s/V, 50-kHz low pass filter). Single small (diameter approximately 20 μm) half-mirrored spheres made from Scotchlite 7610 foil (3M) served as reflectors for the sensor head at a distance of 0.6 m. Displacement and velocity were digitized parallel to the sound signal with the help of a digital storage oscilloscope DS-8601A (Iwatsu, settings: sampling rates 75 and 300 kHz). The digitized signals containing 12 000 words each were accessed through a RS232-C interface SX-0111/0114 (Iwatsu) and converted using a PASCAL program to WAV format computer files.

II. RESULTS

A. Anatomy

In both species, the stridulatory file of the female is a shield-shaped area of approximately 160 very regular ripples with ripple distances of 2.4 to 4.8 μm. In the middle part of the file the ripple distance is 3.3 μm in *D. maura* (Fig. 1) and 2.6 μm in ''*S.*'' *praedatrix*, with depths of approximately 2 μm. The file is approximately 0.5 mm×0.5 mm in size, and the plectrum width is 0.20 mm in *D. maura* and about 0.15 mm in ''*S.*'' *praedatrix*.

B. Model

Figure 1 shows the movement of the plectrum relative to the file. If the file moves outward the plectrum goes from position 1 to position 2 in a short time down into the valley between the two ripples. The time taken to reach a position as in 1 on the next ripple (position 3) is much longer, because of the oblique angle of the plectrum. The up-and-down displacement of the plectrum is therefore not symmetrical and can be described using a sawtooth function over time as a first approximation. If the direction of movement is reversed, the sawtooth function is also reversed [Fig. 2(A) and

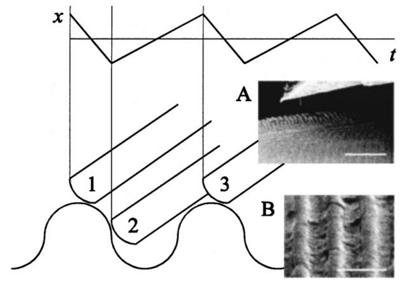

FIG. 1. The model for plectrum vibrations (right anterior, left posterior of the body). 1, 2, and 3 are the positions of the plectrum (above) relative to the stridulatory file while stroking one ripple during the movement of the file outwards. Above the plectrum, the displacement is plotted in simplified form. The time between 1 and 2 is t_b, and the period between 1 and 3 is T. Insets SEM pictures of *Dasylabris maura:* (A) Cross section of the plectrum (white bar: 100 μm). The plectrum is not in contact with the file below (artifact of preparation). (B) Three ripples of the file (white bar: 5 μm).

(B)]. The differentiation of x with respect to t gives the velocity u of the vibration. It is a periodic step function.

C. Vibration

Real displacement-time and velocity-time plots measured by laser vibrometry (Fig. 3) show waveforms very similar to the model. But the width of the high-speed part (between 1 and 2 in Fig. 1) is much shorter than in the model (Fig. 2). This can be explained by faster slipping of the plectrum into (or out of) the spaces between ripples during outward (or inward) movement of the file. This is possible because the plectrum is flexible and the forces causing inward and outward movements of the file with respect to the plectrum are weak compared with the forces causing the pressure of the file against the plectrum. During inward movement the duration t_b of the highest velocity remains relatively constant at a mean value of 0.16 ms. It is relatively independent of the observed period T, which ranges from below 1 ms to more than 2 ms in both species. Whereas T can easily be modified by the stridulating animal, the time t_b depends more on the mechanical properties of the stridulatory organ and to a lesser extent on the forces applied. The mean velocity u_0 usually reaches about 10 mm/s (Fig. 3). At that velocity the plectrum moves 1.6 μm in 0.16 ms, which is in the range of the ripple height of 2 μm observed anatomically and used in the model in Fig. 1.

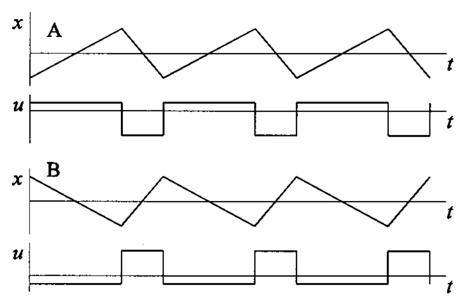

FIG. 2. Displacement x and velocity u of the plectrum during movement of the stridulatory file outward (A) and inward (B).

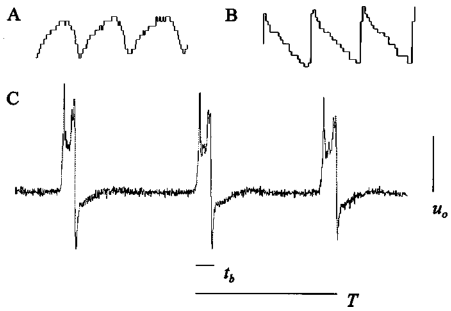

FIG. 3. Displacement x (A, B) and velocity u (C) of the vibrating plectrum of a female of ''*S.*'' *praedatrix* as a function of time. The plots show three ripples of the stridulatory file stroked by the plectrum during the movement of the third metasomal segment outward (A) and inward (B, C). See text.

D. Sound spectrum

Because of the small dimensions and the low frequencies produced by these insects, there is no optimal power transfer from the vibrating source to the surrounding air.[10] This causes an attenuation of the lower frequencies. The radiated sound power P may be expressed as the product of the squared effective velocity u_{eff} of the oscillating area and the real part of the acoustical radiation impedance, the resistance w_r

$$P = u_{\mathrm{eff}}^2 w_r . \tag{1}$$

The calculation of u_{eff} is easily possible if $u(t)$ is expanded into a Fourier series. A shift of the step function along the time axis allows the sine terms to be ignored. Because of the absence of any influence of constant terms on the sound radiation it is possible to write

$$u(t) = \sum_{n=1}^{\infty} u_n(t) = \sum_{n=1}^{\infty} \left[a_n \cos\left(\frac{2\pi n}{T} t \right) \right]. \tag{2}$$

If u is equal to u_0 between $-t_b/2$ and $t_b/2$ (the duration of highest velocity) and 0 in the other ranges in the period from $-T/2$ to $T/2$, the a_n can be calculated as follows

$$a_n = u_0 \frac{2}{T}\, 2 \int_0^{t_b/2} \cos\left(\frac{2\pi n}{T} t \right) dt, \tag{3}$$

$$a_n = \frac{2u_0}{\pi n} \sin\left(\frac{\pi n}{T} t_b \right). \tag{4}$$

According to Eq. (2) the expression for $u_n(t)$ is given by

$$u_n(t) = \frac{2u_0}{\pi n} \sin\left(\frac{\pi n}{T} t_b \right) \cos\left(\frac{2\pi n}{T} t \right). \tag{5}$$

For the calculation of the power P it is necessary to have the square of the effective velocity. This is the integral for all times over the square of $u(t)$. Because of the periodicity it is sufficient to integrate over one period T. The mean value of the squared cosine function is 0.5 and the term in the right-hand brackets does not depend on time. Therefore the result of the integral is

$$u_{n\ \mathrm{eff}}^2 = \frac{2u_0^2}{\pi^2 n^2} \sin^2\left(\frac{\pi n}{T} t_b \right). \tag{6}$$

It is more complicated to obtain a good estimate of the acoustical radiation resistance w_r. The laser vibrometry shows that the main area of vibration comprises about 0.03 mm^2 posteriorly on the plectrum. Furthermore, the females stridulate with the abdomen less than 1 mm above the ground. Therefore, as a first approximation, the far-field radiation may be that of an oscillating piston in a baffle,[11]

$$w_r = c\varrho \left[1 - \frac{J_1(2kR)}{kR} \right] A, \tag{7}$$

where c and ϱ are the speed of sound and the density of air, A and R are area and radius of the piston, k is the wave number

$$k = \frac{2\pi}{\lambda} = \frac{\omega}{c} = \frac{2\pi n}{cT}, \tag{8}$$

and J_1 is the Bessel function of the first kind an of order one. It can be expressed in a series expansion in the following manner:

$$J_1(x) = \frac{x}{2} - \frac{x^3}{16} + \frac{x^5}{384} - + \cdots . \tag{9}$$

For frequencies up to 50 kHz the wave number k is less than 1 mm^{-1} and R is about 0.1 mm. Thus $kR \ll 1$ is always true. Therefore Eq. (9) can be reduced to the first two terms of the series. Under these conditions Eq. (7) can be written as follows:

$$w_r \approx \frac{c\varrho k^2 A^2}{2\pi}, \tag{10}$$

or, according to Eq. (8):

$$w_r \approx 2\pi \frac{\varrho n^2}{cT^2} A^2. \tag{11}$$

Inserting Eq. (6) and Eq. (11) in Eq. (1) yields a sound power of line n in the line spectrum as follows:

$$P_n \approx \frac{4}{\pi} \frac{\varrho u_0^2 A^2}{cT^2} \sin^2\left(\frac{\pi n}{T} t_b \right) \tag{12}$$

or

$$P_n \approx \frac{2}{\pi} \frac{\varrho u_0^2 A^2}{cT^2} \left[1 - \cos\left(\frac{2\pi n}{T} t_b \right) \right]. \tag{13}$$

Because the expression in front of the square brackets depends only on the observed period T, the entire power spectrum depends only on T and t_b, the duration of the highest velocity. Figure 4 shows the variation of the logarithmic spectrum with T, assuming a constant t_b of 0.16 ms. Whereas T influences the line density in the spectrum and the power of all lines together, t_b causes attenuations only around $1/t_b$ (6 kHz) and integer multiples of that.

To compare a real sound pulse with an artificially made one and to estimate the maximal sound power, it is necessary to measure the period T. Because the fundamental frequency is of low power, cepstrum analysis was used to get the fundamental frequency f exactly. Figure 5 shows the minimal quefrency usually found in the middle part of each sound

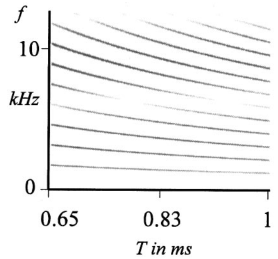

FIG. 4. Variation of the calculated acoustical spectrum with period T of the vibration. The period T is varied from 0.65 to 1 ms whereas the width t_b remains constat at 0.16 ms. The logarithmic sound power P is coded as a gray scale; the frequency scale is linear.

pulse. With the minimal value for $T=0.65$ ms and with $u_0=0.01$ m/s and $A=0.03$ mm^2, Eq. (13) yields

$$P_n \approx 0.2 n W \left[1 - \cos\left(\frac{2\pi n}{T} t_b \right) \right]. \tag{14}$$

Thus the first maximum of P can be found near $n=2(3$ kHz$)$ with a value of 0.4 nW. If T goes up to 1 ms the first maximum will be reached at $n=3(3$ kHz$)$ with only 0.2 nW because the factor in front of the square brackets goes down to 0.1 nW. The sound will be radiated in a hemisphere above the ground. At a distance of 0.1 m (approximately the wavelength of 3 kHz) the hemisphere has a surface area of 0.06 m^2. Thus the maximal sound intensity at this distance is approximately 7 nW/m^2, yielding a sound power level of 38 dB relative to 1 pW/m^2. The two species investigated produced sound power levels between 30 and 40 dB. Thus the estimation of sound intensity made above is quite good.

If the ripple period is constant, the time course of the fundamental frequency f represents the velocity of the plectrum relative to the stridulatory file. In a real sound pulse there are slow parts at the beginning and at the end (Fig. 6 left). The fastest movement occurs in the middle part. Using a self-written PASCAL program, it was possible to construct a synthetic sound pulse according to the model used (Fig. 6 right). Some characteristics are the same in both sonagrams. Typically, but not in all actual sound recordings, it is evident that in the middle of the sound pulse the $4f$ harmonic, and at the beginning and the end of the pulse the $5f$ harmonic, are attenuated near 6 kHz. This is because the frequency of the attenuation is relatively constant and depends mainly on the mechanical properties of the stridulatory organ. The most conspicuous differences in the real sound pulse compared with the synthetic one relate to the greater attenuation of the

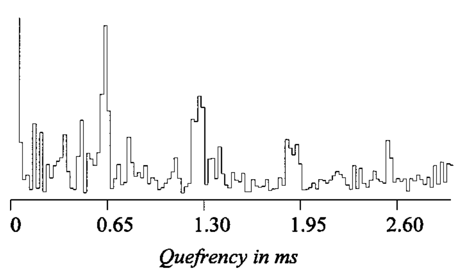

FIG. 5. Cepstrum of the middle part of one sound pulse of a femal of *D. maura*. The quefrency of 0.65 ms corresponds to the period T. The fundamental frequency is the reciprocal quefrency: $1/0.65$ ms$=1.54$ kHz.

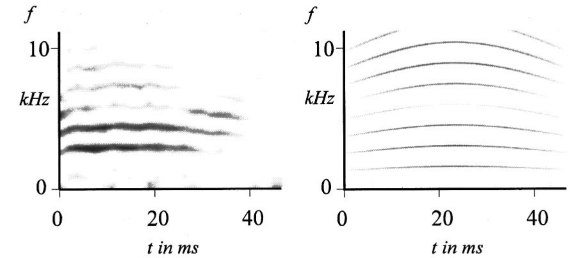

FIG. 6. Sonagram of an actual pulse produced by a stridulating femal of *D. maura* (left) and sonagram computed according to the model (right). The frequency scale is linear. For further explanation see text.

frequencies at f and above $4f$. The inaccurate power calculation at the fundamental frequency results from ignoring the reversed velocity course following the step function (Fig. 3). Further, because of limited acceleration of the plectrum, the time function of the velocity is not really a step function. Thus the model is inaccurate at higher harmonics. On the other hand, the model shows good agreement with the frequency of maximal sound intensity, and it allows an explanation of the broad frequency spectrum of the real sound ranging from approximately 1 to 10 kHz.

E. Oscillogram

The distress call contains several syllables, each made up of two sound pulses generated during the movement of the abdominal segment inward and outward (Fig. 7). The two pulses are usually readily distinguishable in the time function because of their asymmetry relative to the time axis (Fig. 8). Although the time function of the radiated sound pressure has a very different shape compared with the vibration velocity (Fig. 3), the asymmetry caused by the highly damped plectrum vibration is evident here also. The findings were confirmed both by the model and by actual recordings.

Whereas the syllable period and the pulse width remains fairly constant in the calls of female ''*S.*'' *praedatrix*, female *D. maura* are able to switch to faster syllable repetition with shorter sound pulses depending on the stress intensity (Fig. 7). Because the velocity of movement between plectrum and file does not change in the faster syllables, the fundamental frequency remains approximately the same. Thus the plectrum strokes a lesser number of file ripples in this case, but the produced spectra and time functions of the sound do not differ in the faster and slower parts.

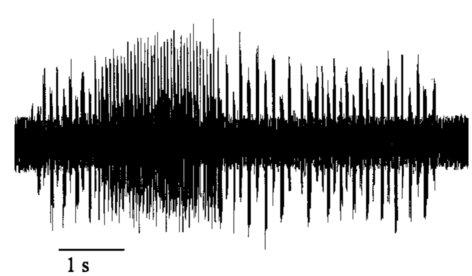

FIG. 7. Oscillogram of the distress call of a femal of *D. maura*. Note the discontinuous changes in the syllable period. One syllable consists of two sound pulses corresponding to the movement of the stridulatory file inward and outward.

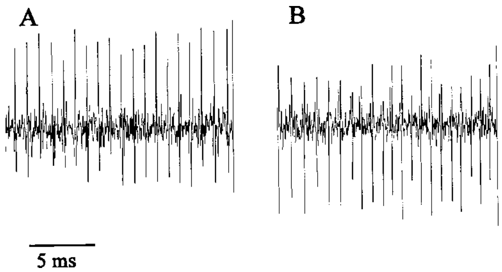

FIG. 8. Magnified detail of Fig. 7. Each ripple of the stridulatory file produces one spike in the sound pressure. The spikes are up and down corresponding to the direction of movement in the stridulatory organ (A) inward, (B) outward.

III. DISCUSSION AND CONCLUSIONS

The signals investigated in this paper have a broad spectrum with many harmonics. It may be that aposematic acoustical signals should have a broad frequency spectrum, for example, because the potential predators (e.g., lizards, mammals) are phylogenetically very different, or because the signals may have evolved in a Müllerian mimicry to hissing by vertebrates. But there is an unsolved problem. According to the model explored here, the sound power level of the stridulating insect depends on A^2/T^2, in addition to u_0^2. Assuming that a scaling down of the body size will influence A (the square of the length) more than T and u_0, the sound power level would be very low in small insects. While the investigated species have a body length of about 10 mm, there are many mutillid wasps and other insects with similar stridulatory organs only half the length or less. Half radius yields quarter radiating area and a reduced specific acoustic resistance, thus the sound power level will be reduced by 12 dB or more. The resulting sound, less than 26 dB, would scarcely be perceptible to many of the potential predators. But the sound power level is also not high enough to be used for intraspecific communication over a distance. This may provide a biophysical explanation of why some small insects may use the vibration signals for short-range intraspecific communication; some findings of Markl[12] suggest this. But there are many other possibilities for the use of stridulatory organs. In leaf-cutting ants the vibrations serve to reduce energy consumption during cutting,[13] and in mutillid wasps vibrations may aid soil manipulation.[14] However, there is still no good explanation why small insects also have stridulatory organs.

The model in this paper is a first approach to simulation of spectra and time functions of vibration and radiated sound. It has been shown to give good agreement with data taken from the investigated specimens of multillid wasps and with the data of Spangler and Manley.[15] The model will probably be useful for other arthropods with nonresonant stridulatory organs too, especially where they have similar file structures and approximately the same values of ripple-strike period T.[16,17] Furthermore, the results allow the synthesis of artificial vibrations and sounds. Therefore, the findings could be helpful for future investigations dealing with the effects of such signals in inter- or intraspecific communication.

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