SOUND EMISSION AND THE ACOUSTIC FAR FIELD OF A SINGING ACRIDID GRASSHOPPER (*OMOCESTUS VIRIDULUS* L.)

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Summary

An array of eight microphones, all at a distance of 15 cm, was used to make simultaneous recordings of the sounds emitted by courting male acridid grasshoppers of the species *Omocestus viridulus*. In this species, the movement pattern for sound production differs in the two hindlegs, and in most cases the leg facing the female moves with the larger amplitude. The sonic sound intensity (the total sound in the one-third octave bands with centre frequencies from 5 to 20 kHz) is maximal ipsilateral to the leg stridulating with the larger amplitude (the dominant leg). A spontaneous switch of dominance to the other leg may cause a significant change in the emitted sound power. The sound intensities contralateral to the dominant leg and frontal to the animal are, on average, approximately half (−3 dB) of the ipsilateral value, whereas the mean sound intensities behind and above the singer are approximately one-fifth (−7 dB) of the ipsilateral value. In most singers, the patterns of sound radiation are close to these mean values, but in some singers the radiation patterns are radically different. The sound radiated in various directions differs not only in terms of sound intensity but also with respect to the frequency spectrum, which was studied up to the one-third octave band with a centre frequency of 31.5 kHz. In particular, the ratio between the ultrasonic and sonic components is much smaller in the forward direction than in other directions. This may allow the courted female to hear whether the courting male is oriented directly towards her.

Key words: grasshopper, sound radiation, far field, singing, *Omocestus viridulus*.

Introduction

Sound communication in acridid grasshoppers has been extensively studied (Faber, 1953; Elsner, 1974; von Helversen, 1997), but little is known about the sound-radiating properties of singing grasshoppers. Values for 'typical' levels and frequency spectra of the communication sounds can be found in the literature, but the exact distance and direction of the microphone from the insect during the recordings are rarely stated. The spatial pattern of sound radiation has not been described, probably because it is very difficult to map a spatial pattern using only one microphone if the sound radiation does not remain constant. In the present study, an array of eight microphones at identical distances, but in different directions, from the singing animal was used to make simultaneous recordings. The main aim of the study was to describe the spatial pattern of sound radiation. Another aim was to develop methods for measuring the sound power emitted in the field and under acoustically well-defined conditions in the laboratory to facilitate future studies on the acoustic interaction between sound-emitting animals and their habitats.

Materials and methods

Sound fields and sound measurements

The sound level and sound spectrum measured at some distance from a sound source depend on the properties of the source and on the distance and possible presence of other objects (Pierce, 1981). The sound may behave in a simple manner at large distances from the source (in the far field), especially if no redirected sound components (e.g. echoes) are present (a situation called a free field). The front of the propagating wave is almost planar, and there is a simple relationship between the vibration velocity (v) of the 'particles' in the medium and the sound pressure (p):

$$v = p/\rho c, \tag{1}$$

where ρ is the density of the medium (approximately $1.2\,\mathrm{kg\,m^{-3}}$ for air) and c is the propagation velocity of the sound wave (approximately $340\,\mathrm{m\,s^{-1}}$ in air; so ρc is approximately $400\,\mathrm{N\,s\,m^{-3}}$). The power carried by the sound wave is given by pv. Sound intensity (I) is the sound power passing a unit area ($1\,\mathrm{m^2}$) perpendicular to the direction of propagation. In the free sound field, the sound intensity may be found simply by measuring p:

$$I = pv = p^2/\rho c. \tag{2}$$

A sound source in free space is free to radiate sound in all

directions. Ignoring attenuation caused by interactions with the medium, the power (P, in W) emitted by the source can be found by integrating the sound intensity measured at the surface of a sphere with the source at the centre. The mean sound intensity at the surface of the sphere is thus $P/4\pi r^2$, where r is the radius of the sphere. Similarly, the sound power emitted by a sound source situated on a hard, flat surface is distributed over the surface of a hemisphere, and the mean sound intensity at the surface is $P/2\pi r^2$, i.e. twice the value for the spherical case.

Calculations of sound intensities and sound power from measured values of sound pressure may be facilitated by referring to corresponding dB scales for pressure and intensity. A common reference for sound pressure (p_0) is $2\times10^{-5}\,\mathrm{N\,m^{-2}}$. From equation 2, the corresponding reference for sound intensity (I_0) is $(2\times10^{-5})^2/400=10^{-12}\,\mathrm{W\,m^{-2}}$. One has to remember that a factor of 10 corresponds to 20 dB for pressure, but only to 10 dB for power. The power emitted by the sound source is indicated by the mean sound intensity when the surface of the sphere or hemisphere is $1\,\mathrm{m^2}$ (that is, at a distance of 28 cm for the sphere and 40 cm for the hemisphere). At other distances, the following relationship applies:

$$10\log_{10}(P/P_0) = 20\log_{10}(p/p_0) + 10\log_{10}A , \qquad (3)$$

where A is surface area (in $\mathrm{m^2}$).

A complicated spatial distribution of sound pressure and medium flow often exists very close to the sound source (in the near field). The complications of near fields have several causes. One is the fact that the oscillating movements of the medium 'particles' are caused both by gradients of pressure and also directly by the vibrating surface of the source. The former component is in phase with the pressure (equation 1) and is responsible for the energy transported in the sound wave. The latter component, which is 90° out of phase with the pressure and 'wattless', decreases with the square of the distance from the source. At a distance of one-sixth of the wavelength, the two components are of equal magnitude. We performed our measurements at a distance (15 cm) corresponding to approximately two wavelengths of the lowest-frequency component being measured. At this distance, the latter component can be ignored, and equation 2 applies.

It should be noted that maintaining a distance of a few wavelengths to the source is not sufficient to ensure far-/free-field conditions. The source also has to be small relative to the wavelength of sound. Spatial interactions between sounds originating from different parts of the source may occur at considerable distances from the source if this is not the case. Further complications are found in the near field if the source is a dipole (e.g. the vibrating wing of a grasshopper). For example, the sound emitted by dipoles is very directional, and the sound power could be seriously overestimated if the sound pressure in the near field is measured and integrated over a sphere or hemisphere with the source at the centre (see Crocker and Price, 1975).

Omocestus viridulus *and its song patterns*

Male grasshoppers of the species *Omocestus viridulus* (L.),

caught in the vicinity of Göttingen, Germany, were kept in the laboratory and fed with grass for 1 or 2 days before being used for the experiments. *O. viridulus* belongs to the acridid subfamily Gomphocerinae, which is characterized by a femuro-tegminal stridulatory mechanism: a row of denticulate pegs on the proximal side of each hind femur is rubbed rhythmically against a vein on the ipsilateral tegmen. According to the behavioural context, the males produce calling, courtship or rivalry songs. For our study, we used the courtship song because it can easily be induced by the presence of a female close to the male. Although this is a typical near-field situation (see above), courtship song is suitable for the far-field measurements carried out in our study, because it differs very little from calling song. As described in detail by Elsner (1974), the courtship song consists of sequences of 45–60 s duration (calling song 15–30 s) separated by pauses of 10–15 s duration. In both calling and courtship song, each sequence is composed of numerous subunits produced by sonorous up- and downstrokes of the hindleg. The movements of the two hindlegs differ in amplitude and temporal features. The legs may change their role abruptly from one sequence to the next, but rarely within the course of a sequence. During courtship, the leg facing the female usually stridulates with the higher amplitude. In the present study, this leg will be called the dominant (or ipsilateral) leg.

Our experiments were started by placing a male next to a female. When courtship began, the relative position of the hemisphere carrying the microphones (see below) was adjusted so that the male was at the centre of the hemisphere. The female was free to move around (she just had to be within a few centimetres of the male to maintain his motivation). The results reported here are based on 335 measurements on 15 singing males. Most measurements were obtained in the laboratory, where the animals were walking on a polyvinylchloride (PVC) film on top of an acoustically hard PVC plate. The PVC film allowed small, rapid adjustments of the position of the male. Additional measurements were obtained with the hemisphere placed in a grassland habitat.

Design of the experiments

A fixed array of microphones is necessary for characterizing the spatial radiation of sound from time-variant sources such as singing grasshoppers. The sounds they produce are faint, so the microphones have to be fairly close to the grasshoppers but still in the far field. A distance of 15 cm was chosen as a reasonable compromise, since the lowest-frequency component analysed in this study was the one-third octave band centred at 5 kHz (wavelength 7 cm). We fastened the eight microphones to a hemisphere made of 4 mm steel rods and with a radius of 37 cm. The hemisphere (Fig. 1) could be easily rotated, since it rested on four toy train wagons running on a circular track (Märklin 29201). In each microphone, the active element (Knowles ET3169) was mounted at the end of a cylindrical acrylic tube (diameter 7 mm, length 30 cm). The tubes pointed towards the singing animal at the centre of the hemisphere. With a distance of 15 cm between the animal and the microphones, the steel hemisphere and the 1 cm×2 cm brass
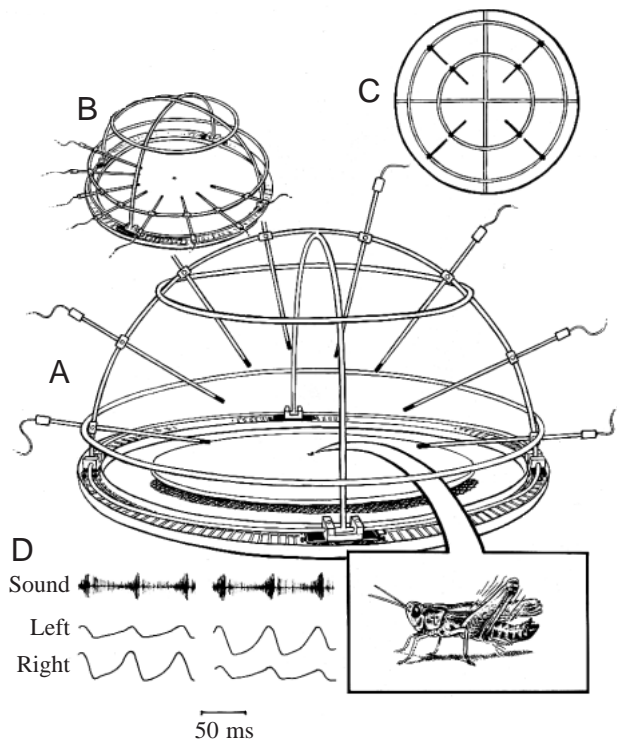
Fig. 1. The singing grasshopper was placed at the centre of a hemisphere (radius 37 cm; constructed from 4 mm steel rods) carrying the microphones. The microphones were mounted at one end of tubes 30 cm long, which were fastened to the hemisphere using brass holders (1 cm diameter) approximately 22 cm behind the microphones. The distance between the animal and the microphones was therefore 15 cm. The hemisphere could easily be rotated because it rested on four toy train wagons running on a circular track. (A) The median or transverse mounting of the microphones. (B) The horizontal mounting. (C) The total power mounting. (D) Sound oscillogram (upper trace) and the relative stridulation amplitude (lower traces) of the two hindlegs, which change their role from time to time. A–C were drawn by Per Erik Hedman; D is courtesy of R. Heinrich.

mountings for the microphones were 22 cm behind the microphones. The ceiling and walls of the laboratory were several metres away. The short distance between the sound source and the microphones (relative to the distances to other objects) ensured that we could ignore 'echoes', both from the hemisphere and mountings and from the walls and ceiling (when estimating the expected size of echoes, the size of the sound reflectors and the distance to them must be taken into account, since sound suffers a geometrical spreading loss before reaching the reflecting surfaces, and echoes suffer a similar loss on their way back to the microphones).

The positioning of the array of microphones relative to the singing grasshopper was carried out by hand and under visual control. We estimate that the singing grasshoppers were always within 0.5 cm of the centre. According to equation 3, a deviation of 0.5 cm from an aimed distance of 15 cm would cause the error in the measured sound intensity to be 7 % (0.3 dB). Errors of this size would not affect the conclusions of our study.

The inexpensive Knowles elements vary somewhat in sensitivity. From a larger sample, we selected eight microphones which had essentially similarly shaped frequency response curves and absolute sensitivity (they were matched to less than 1 dB in the frequency range 5–35 kHz). However, the sensitivity deviated from a flat frequency response by up to 5 dB when measured in one-third octave bands against an 1/8 inch Brüel & Kjær 4138 microphone. These deviations were entered into a spreadsheet and subsequently used to correct the data.

In most measurements, the signals from the eight microphones were stored on an eight-channel DAT recorder (O-5 Technology DSR-8/3) before being analysed in one-third octave bands (frequency analyser; Hewlett-Packard 35665A). The core of the DAT recorder is a Tascam DA-38 digital multitrack recorder, which uses a 16-bit linear quantization at 44 kHz and has a dynamic range better than 90 dB on each channel. The frequency analyser received a voltage proportional to the sound pressure and calculated the one-third octave power spectrum of the input voltage (i.e. values proportional to sound intensity). The values from the individual one-third octaves were entered into a spreadsheet, which was used both to correct the data for the deviations from a flat frequency response and to calculate the total sound intensity for the entire frequency range.

During the experiments, the performance of the singer and the possible occurrence of background noise were monitored by the experimenter, who marked periods suitable for analysis by saving a TTL pulse on the DAT recorder. During the subsequent analysis of the individual tracks, the TTL pulse was used to trigger the frequency analyser, thus ensuring that the eight tracks analysed had been recorded simultaneously. The one-third octave analysis was carried out on blocks of 8 s duration (preliminary analyses of blocks of various duration had indicated that 8 s was sufficient for ensuring a minimum of uncertainty in the computation of the spectral values). The selection of the analysed blocks is described in the Results section.

The DAT recorder is limited to frequencies below 22 kHz, so higher-frequency components of the song had to be studied in real time by connecting Knowles microphones (mounted on the hemisphere) or hand-held Brüel & Kjær microphones (1/2 inch type 4133 with preamplifier type 2669i; probe microphones 4182) directly to the frequency analyser.

Directionality of sound radiation

Three different mountings of the microphones were used to estimate the directionality of sound radiation. In the (almost) horizontal mounting (Fig. 1B), the eight microphones were placed in a semi-circle on the lower horizontal ring of the hemisphere, equally spaced with 22.5 ° separation. The lower ring was 14 ° above the animal's horizon; thus, the microphones were tilted by 14 ° relative to the horizontal plane. In the median mounting (Fig. 1A), the microphones were mounted equally spaced with 22.5 ° separation over the back of the singing animal. The two lowest microphones (facing the head and abdomen) were 11 ° above the animal's horizon. The transverse mounting was identical to the median mounting, but

the array had been rotated by 90° so that the two lowest microphones now faced the dominant (=ipsilateral) hindleg and the contralateral (non-dominant) hindleg.

By mounting the lowermost microphones 11° or 14° above the horizon, we avoided the complicated modes of sound propagation that often exist very close to a surface (Pierce, 1981). Furthermore, we reduced the possible influence on the recorded sound of the presence of a female fairly close to the male (this possible source of error is considered in the Discussion).

Total sound power

When estimating the total sound power radiated, several microphones have to be distributed over the surface of the hemisphere in such a manner that the microphones are associated with equal areas on the hemisphere. The number of microphones necessary depends on the complexity of the sound radiation pattern. Procedures exist for six, eight and ten microphones (Broch, 1971; Crocker and Price, 1975). In the total power mounting (Fig. 1C) used here, four equally spaced microphones were fastened to the lower ring of the apparatus (see Fig. 1A). The remaining four microphones were attached to the upper ring, again equally spaced. The upper microphones had the same azimuths as the four lower ones, but they were pointing at the singing animal from positions 51° above the horizon.

Results

It is obvious to human listeners that the sound intensity produced by male *O. viridulus* gradually increases during the initial 5–10 s of the 45–60 s song sequences. However, an analysis of the sound intensity measured at various times after the initial period demonstrates that the intensity increases by another 60 % (2 dB) during the 20–30 s following the initial period (Fig. 2). This rate of increase is below the human perception threshold and was only identified some months after the experiments had been completed. Fortunately, during the experiments, we had followed a rigid procedure of starting the DAT recorder as soon as the sound intensity seemed to be constant after the initial period. In the later analysis of the data and especially in the comparisons, we could therefore make sure that the selected data were not biased by the gradual increase in intensity shown in Fig. 2.

Radiation patterns

In the horizontal plane, the largest sound intensities were found in the direction of the dominant leg, which we identified as the leg that moved with the larger amplitude. Most often, the dominant leg faces the female. The dominant leg and the non-dominant (contralateral) leg also have slightly different movement patterns (Fig. 1D; and see Elsner, 1974). The sound intensity measured in the direction of the dominant leg varies considerably among individuals (Fig. 3). In one case (male B), a change in the position of the female caused the male to switch the dominance from the left to the right leg. The sound intensity measured in the direction of the left leg before the
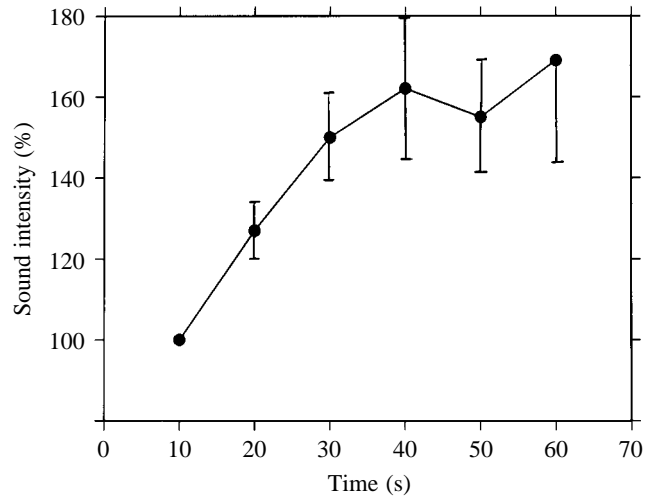

Fig. 2. The increase in sound intensity during the first minute of the song. During the initial phase of 5–10 s, humans perceive a gradual increase in intensity. The first recording (at 10 s, N=16) was made when the experimenter judged the song to be of constant intensity. The sound intensities (means ± S.E.M.) of later recordings (N=16, 16, 14, 7 and 4, respectively) are expressed relative to that at 10 s. Human ears detect the weak beginning of the song before the first recording, but not the later increase in intensity.
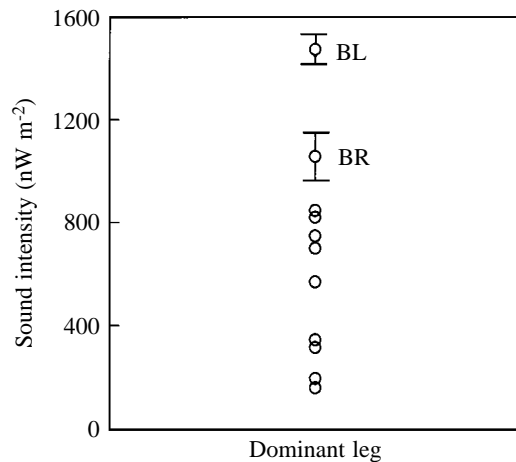

Fig. 3. The total sound intensity for the one-third octave bands centred at 5–20 kHz, measured using an almost horizontal microphone in the direction of the dominant leg. Data from 10 animals. Except for male B, each point is from a different animal. Male B first sang with a dominant left leg (BL) and later with a dominant right leg (BR); the values for this male (means ± S.D., N=3) are significantly different (P<0.001; t-test).

switch was significantly larger than that measured in the direction of the right leg after the switch (Fig. 3).

On average, the sound intensity behind the animal is approximately 20 % (−7 dB) of the intensity at the dominant leg (Fig. 4). In the frontal and contralateral directions, the intensities are approximately half (−3 dB) of the intensity at the dominant leg. Some animals deviated greatly from the average pattern: male E had ipsi- and contralateral intensities of similar magnitude and very little sound radiation to the front and back.
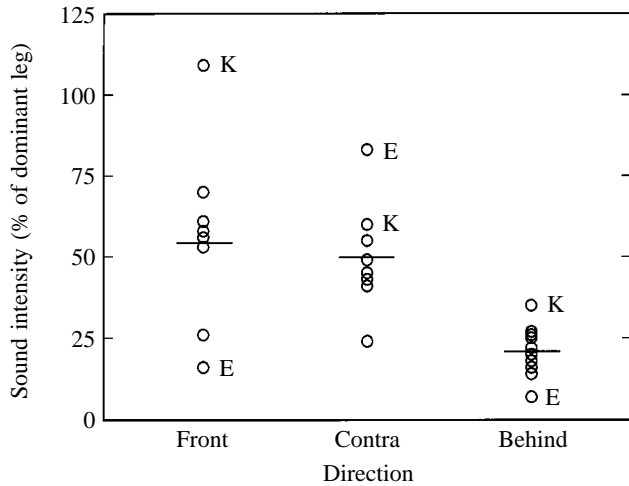
Fig. 4. The total sound intensity in the 5–20 kHz frequency bands measured using microphones in front of the singer, contralateral to the dominant leg (Contra) and behind the singer. The data points indicate the intensity relative to that at the dominant leg in each of the 7–8 animals. The horizontal lines indicate the mean intensity. Males E and K had atypical directional patterns (for details, see the text).
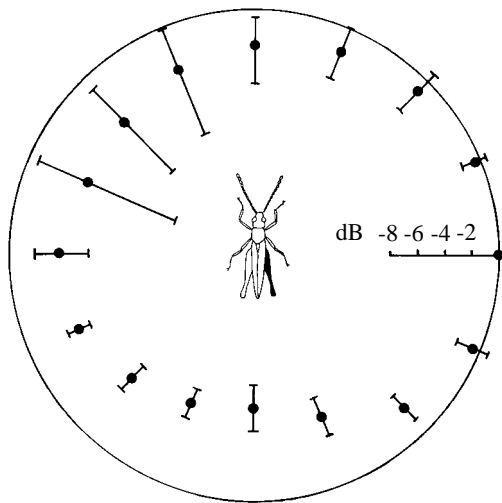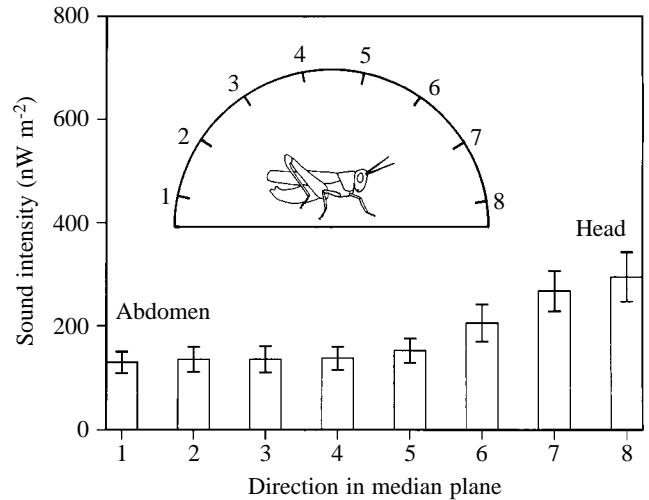

Fig. 6. The total sound intensity in the 5–20 kHz frequency bands measured for eight directions in the median plane (see inset). Mean values and standard deviations are based on data from three animals.

Fig. 5. The total sound intensity in the 5–20 kHz frequency bands measured for 16 directions in the horizontal plane. Values are means ± S.D. from 10 animals (none of which contributed data for all directions) and are plotted relative to the intensity in the direction of the dominant leg, which is shaded black.
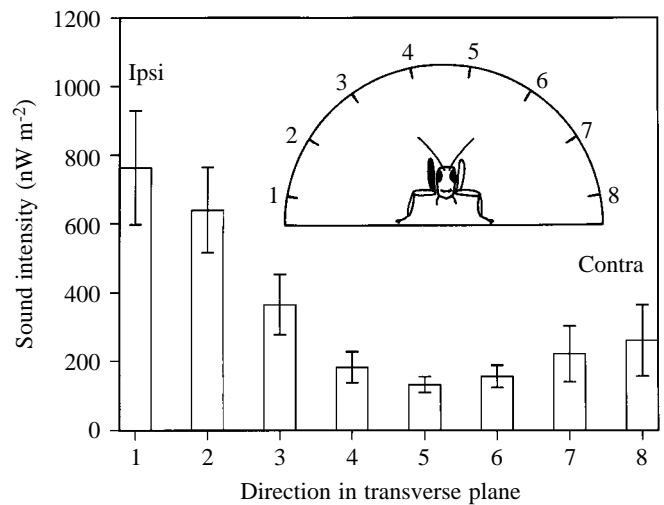

Fig. 7. The total sound intensity in the 5–20 kHz frequency bands measured for eight directions in the transverse plane (see inset). Mean values and standard deviations are based on data from three animals. The dominant leg is shaded black. Contra, contralateral; Ipsi, ipsilateral.

In contrast, in male K, sound radiation was similar in the frontal and ipsilateral directions. The mean sound intensities measured in these four main directions are similar to values that one would obtain by interpolation from a more complete analysis (Fig. 5). For some unknown reason, the variation was very large for the three positions measured between frontal and contralateral (Fig. 5).

The measurements performed with the median and transverse mountings (Figs 6, 7) reveal the existence of a minimum in sound radiation dorso-caudally. The sound

intensity above the singer appears to be at the same level as behind the animal (approximately 20 % or −7 dB relative to the sound intensity at the dominant leg). Again, the sound intensities measured at intermediate directions are similar to the values that would have been obtained by interpolation of the values in the main directions. The three-dimensional radiation pattern therefore appears to be so regular that the total radiated sound power can be estimated reliably using a limited number of microphones (eight in this case).

Total sound power

The total sound power radiated from singing males was determined from four animals on an acoustically hard surface

in the laboratory and from three animals in a grassland habitat at approximately the same temperature (approximately 25–30 °C). In the laboratory, three animals had mean power outputs of 16 nW, 23 nW and 45 nW. The fourth animal had a mean output of 49 nW with the right leg dominant and 61 nW with the left leg dominant (the difference was significant; $P=0.05$, t-test). In grass, the mean power outputs measured from three animals were 10 nW, 10 nW and 18 nW. These values are the total for the frequency bands centred at 5–20 kHz. Experiments in which the sound was measured using a 1/8 inch Brüel & Kjær 4138 microphone and displayed as a frequency response by the frequency analyser confirmed the presence of an ultrasonic component below 35 kHz. Measurements of the sound power in the one-third octave bands centred at 25 and 31.5 kHz (bypassing the DAT recorder) suggested that, in order to estimate the total radiated power, 50 % should be added to the total values calculated for frequency bands centred at 5–20 kHz.

Spectral directionality

The sound recorded from different directions differs not only with respect to intensity but also with respect to the frequency spectrum. The real-time measurements for centre frequencies up to 31.5 kHz revealed a marked directional dependence of the relative amount of ultrasound present (Fig. 8). In the frontal direction, ultrasound contributes approximately one-quarter of the radiated sound intensity, whereas in the other directions the sonic and ultrasonic contributions are approximately equal. Fig. 8 shows such a pattern for one male; very similar results were obtained from two other males.

Discussion

The spatial pattern of insect sound radiation has been measured only in crickets and mole crickets (Nocke, 1971; Paul and Walker, 1979; Bennet-Clark, 1989). Unlike these Orthoptera, which make use of one stridulatory apparatus, i.e. the elytra moving against each other, singing grasshoppers are endowed with two instruments: the left and the right hindleg each rubbing sonorously against a vein of the corresponding forewing. The acoustics of sound radiation in these grasshoppers is not easy to understand, especially in species such as *Omocestus viridulus* which perform different movement patterns with the two hindlegs. Nevertheless, we chose this species for our initial study to obtain a better insight into the problems of sound radiation in grasshoppers which will be addressed in future detailed studies.

Because of the ease with which it can be elicited and the long-lasting sequences produced, we investigated courtship song. To a large extent, courtship song resembles calling song, which is far less easy to observe in the laboratory. However, courtship song has to be elicited by a female, and the presence of a female close to the singing male constitutes a possible source of error in the measurements of the spatial patterns of sound radiation. The magnitude of this possible error can be estimated by considering the relationship between the size of the insect body
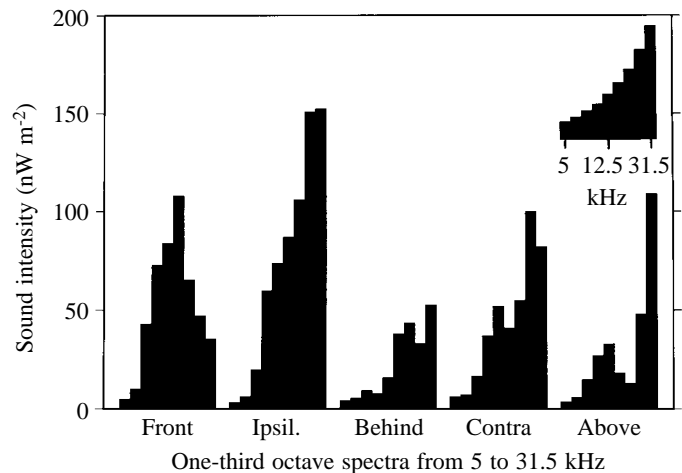

Fig. 8. Frequency spectra of sound measured in five directions. Each spectrum indicates the intensity within nine one-third octave bands with centre frequencies of 5, 6.3, 8, 10, 12.5, 16, 20, 25 and 31.5 kHz, respectively. Note that bandwidth increases with frequency, which means that white noise (constant intensity per Hz) would give rise to a frequency spectrum of the shape shown in the inset. Mean values are shown for four fairly similar spectra in each direction, measured from a single animal. Note the small relative proportion of ultrasound ($\geqslant 20$ kHz) in the frontal direction.

and the wavelength of the sound. To a first approximation, the body of a grasshopper can be modelled a cylinder with a diameter of 3 mm. The wavelengths of the sounds measured in this study vary from approximately 8 cm for the lowest frequencies to 1 cm for the highest. The body is known to cause some diffraction of sound over most of the frequency range studied (Michelsen and Rohrseitz, 1995), but it is too small to reflect the sound, even at the highest frequencies measured. The presence of a 3 mm diameter cylinder fairly close to the sound source is likely to have moderate acoustic effects at close range, but not in the far field. In accordance with this prediction, we observed smooth changes in both sound intensity levels and frequency spectra when we compared the sounds recorded by neighbouring microphones.

The main finding of our study is that the radiated sound intensity is strongly dependent on direction. It reaches a maximum ipsilateral to the leg stridulating with the higher amplitude, whereas it is only half this value on the contralateral side and in front of a singing male. Both behind and above the grasshopper, it is 20 % of the ipsilateral value (Figs 4–7). It should be noted that the sound level of the songs emitted by courting male *O. viridulus* varies over time and among animals. Some individuals (e.g. males E and K in Fig. 4) may have directional patterns that are far removed from the average. Such interindividual variability is probably associated with differences between the movement amplitudes of the two stridulating legs, which vary from animal to animal and during courtship (in some individuals, the non-dominant leg may almost stop stridulation during the final part of courtship). It is not known whether this variability reflects genetic variation or differences in levels of motivation. Changes in motivation are

unlikely to cause the significant changes in radiated intensity and total emitted sound power when, during a song of long duration, the legs switch dominance.

The radiated sound intensity increases not only during the first 5–10 s, when the increase can be perceived by humans, but also during the subsequent 30 s, when human observers believe that the level is constant. Such imperceptible changes are a possible source of error in studies involving comparisons of measured sound levels. Although not large (approximately 60 % or 2 dB), this change is sufficient to cause a significant difference in sound intensity level. In this study, we were aware of this time effect and made sure that the data used in comparisons were not biased.

The observation that the relative amount of ultrasound emitted in the forward direction is only half that in other directions (Fig. 8) may have behavioural significance. The ears of grasshoppers contain three groups of low-frequency receptors and one group of high-frequency receptors (Michelsen, 1971; Römer, 1976) sensitive mainly in the ultrasonic range (Meyer and Elsner, 1997). It is therefore likely that actively orientating females (most often virgins) can use the directionality of frequency radiation for orientation towards the male.

The results of the present study enable future biophysical and behavioural investigations to be made. Biophysically, it would be of great interest to analyse the correlation between the patterns of leg movement and spatial sound radiation in a more detailed manner, particularly as far as the contribution of each hindleg is concerned. Such a study should be performed on a comparative basis in species such as *Omocestus viridulus* and *Chorthippus mollis*, which have asymmetrical stridulation patterns, and in species with symmetrical leg movements, for example *Stenobothrus lineatus*. Attention should also be paid to the phase shift of the stridulatory movements found in these groups.

Behaviourally, it is of interest whether the animals make use of the directionality of sound radiation. To avoid attracting other males during courtship, it might be advantageous to keep the overall sound intensity as low as possible, concentrating the radiation of sound towards the female.

The relationship between the far field and near field

In this study, we have measured the acoustic far field of a song that is used only for near-field communication. Although we believe that our results are also valid for the long-distance calling song (see above), our data cannot be used to predict the nature of the courtship song in the near field. The few existing studies of acoustic near fields in insects demonstrate great complexity. For example, the song of the grass cicada (*Tympanistalna gastrica*) has a complicated near field (Fonseca and Bennet-Clark, 1998), but a much simpler far field (A. Michelsen and P. Fonseca, unpublished data). This is not surprising, given the relationship between the wavelengths emitted and the size of the sound emitter (body). In these studies, only the sound pressure amplitudes were mapped. However, the ears of most insects respond not only to the amplitude component of sound but also to gradients of pressure amplitude and phase (Michelsen, 1998), which are very different in the near and far fields, even for simple sound sources. Furthermore, other very different mechanoreceptors sensitive to air currents rather than to pressure are likely to be involved in short-range communication. The complexity of the fields of air currents surrounding dancing honeybees (*Apis mellifera*) (Michelsen, 1993) may illustrate the challenges to be expected when attempting to understand the near field of singing insects.

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