

DIRECTIONAL SOUND PROCESSING AND INTERAURAL SOUND TRANSMISSION IN A SMALL AND A LARGE GRASSHOPPER

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Accepted 26 May 1995

Summary

Physical mechanisms involved in directional hearing are investigated in two species of short-horned grasshoppers that differ in body length by a factor of 3–4. The directional cues (the effects of the direction of sound incidence on the amplitude and phase angle of the sounds at the ears) are more pronounced in the larger animal, but the scaling is not simple.

At high frequencies (10–20 kHz), the sound pressures at the ears of the larger species (*Schistocerca gregaria*) differ sufficiently to provide a useful directionality. In contrast, at low frequencies (3–5 kHz), the ears must be acoustically coupled and work as pressure difference receivers. At 3–5 kHz, the interaural sound transmission is approximately 0.5 (that is, when a tympanum is driven by a sound pressure of unit amplitude at its outer surface, the tympanum of the opposite ear receives a sound pressure with an amplitude of 0.5 through the interaural pathway).

The interaural transmission decreases with frequency, and above 10 kHz it is only 0.1–0.2. It still has a significant effect on the directionality, however, because the directional cues are large.

In the smaller species (*Chorthippus biguttulus*), the interaural sound transmission is also around 0.5 at 5 kHz, but the directionality is poor. The reason for this is not the modest directional cues, but rather the fact that the transmitted sound is not sufficiently delayed for the ear to exploit the directional cues. Above 7 kHz, the transmission increases to approximately 0.8 and the transmission delay increases; this allows the ear to become more directional, despite the still modest directional cues.

Key words: grasshopper, hearing, sound localization, locust, *Schistocerca gregaria*, *Chorthippus biguttulus*.

Introduction

In many animals, the body is much smaller than the wavelengths of sounds of interest, and the differences in sound pressure at the ears are too small to be sufficient as cues for directional hearing. Nevertheless, in most of these animals, the amplitude of vibration of the tympanum varies greatly with the direction of sound incidence. The reason is that the tympanum receives sound at both its external and internal surfaces and thus operates as a pressure difference (gradient) receiver (Autrum, 1940).

We recently described a method for measuring the changes in amplitude and phase angle of sounds entering the body and propagating through internal pathways to the internal surface of the tympanum (Michelsen *et al.* 1994a). In addition, we devised a method for obtaining precise data on the directional dependence of the amplitude and phase angle of the sounds at the ears (Michelsen *et al.* 1994b). It was thus possible to determine all the data needed for calculating the directional dependence of the tympanal vibrations. This has been done in crickets, in which we also measured the tympanal vibrations by means of laser vibrometry and found a reasonable

agreement between the calculated and measured directionalities (Michelsen *et al.* 1994b).

In crickets, we found that the ears (which operate as pressure difference receivers) obtain most of their directional sensitivity by exploiting the variation of the phase of sound that occurs as the direction of sound incidence changes. Most of this phase variation reflects the different times of arrival of sound at the two sides of the body and thus depends on the size of the animal. It might be expected, therefore, that very small animals would have poor directional hearing at sonic frequencies, even when their ears operate as pressure difference receivers.

In the present paper, we test this possibility in two species of acridid grasshoppers of different size. Males of the desert locust *Schistocerca gregaria* and the European short-horned grasshopper *Chorthippus biguttulus* are 46–55 mm and 13–15 mm long, respectively, and the diameter of their thorax and abdomen also differ by a factor of 3–4. Much is known about the directional hearing of these two species from earlier investigations, but nothing is known of the function of hearing in locusts. In gomphocerine grasshoppers, acoustic communication is used mainly for the attraction and courtship

of mates. To achieve pair formation, the male *C. biguttulus* sings its calling song, to which a receptive female may answer with her own song. The male then makes an abrupt turn towards the direction of incidence of the female song. This orientation turn is based only on a simple left–right decision. After this lateralization, the male walks a short distance in the new direction and starts a new sequence by singing again. Using this strategy, the male eventually reaches the female (von Helversen, 1972; von Helversen and von Helversen, 1983). In behavioural experiments with males placed between two loudspeakers emitting female song, it was found that a difference in sound level of only 1–2 dB elicits a turn towards the side stimulated with the louder sound (von Helversen and Rheinlaender, 1988).

Locusts and grasshoppers have an ear on each side of the first abdominal segment. It consists of a sclerotized ring forming a recess in the abdomen and encircling a tympanal membrane, to which 60–80 receptor cells are attached. Between the ears are air-filled tracheal sacs, which permit interaural sound transmission (Fig. 1). In locusts, the air sacs act as an acoustic low-pass filter, suggesting that the ears are pressure difference receivers at low frequencies and mainly pressure receivers at high frequencies (Michelsen, 1971*b*). This view was supported by later studies that used biophysical (Miller, 1977) or electrophysiological (Römer, 1976) methods. These studies did not reveal, however, how such a mechanism allows the animal to exploit cues in the incident sounds to determine the direction of sound incidence.

In the present study, we measured the directional cues; that is, how the amplitude and phase of sound at the ears vary with the direction of sound incidence. We also measured the changes in amplitude and phase during interaural sound propagation. These data are used for calculating how the force driving the tympanum varies with sound direction. The result is compared with the directional dependence of the amplitude of tympanal vibrations (measured in a part of the tympanum in which the vibration is linearly related to the force). The results confirm that small animals with ears that act as pressure difference receivers may have difficulty in determining the direction of sound at low frequencies.

Materials and methods

Adult male grasshoppers *Schistocerca gregaria* (Forskål) and *Chorthippus biguttulus* (L.) were used at least 2 weeks after their final moult. The specimens of *S. gregaria* came from a culture in the Zoological Institute, Göttingen, Germany. Specimens of *C. biguttulus* were caught near Erlangen, Germany. All animals were fed on fresh grass.

The animals were anaesthetised with CO₂; all legs and wings were removed, and the animal was glued to a cork platform by means of beeswax. A small platform was used for the determination of the interaural transmission gain. For the determination of directional cues and tympanal vibrations at various directions of sound incidence, the grasshopper was fixed ventral side down at the centre of a 20 cm diameter cork

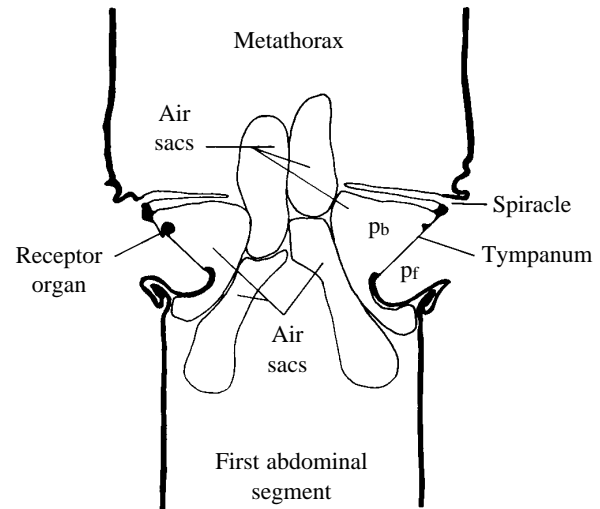


Fig. 1. Horizontal section through the auditory region of a male grasshopper, *Oedipoda coerulescens* (schematic, redrawn after Schwabe, 1906). The ears are connected by tracheal air sacs associated with the spiracles. Each ear drum (tympanum) receives sound both at its external (front) surface (sound component *pf*) and at its internal (back) surface (sound component *pb*). The anatomy of the tracheal air sacs varies somewhat among the species.

platform. The tympanal organ of *C. biguttulus* is hidden behind a narrow slit in the cuticle, so for laser vibrometry, it is necessary to open this slit with a cut and to remove some of the cuticle. The frequency response of the tympanal vibrations (measured in an operated animal at the internal surface of a tympanum driven by sound at its external surface) did not change as a result of this operation. Earlier reports of an effect of this operation and of the position of the hindlegs on the directionality of the ear (Römer, 1976; Adam, 1983) were based on measurements at 20 kHz in the much larger *Locusta migratoria* and thus do not contradict our findings.

Physical measurements

The experimental apparatus and the methods have been described before (Michelsen *et al.* 1994*a,b*), so only a short summary is given here. The acoustic stimuli were brief (4.5 ms) swept sine-wave pulses ('chirps') generated by a frequency analyzer (Hewlett-Packard 3562A) that also received the sound or vibration signals. The tympanal vibrations measured were linearly related to sound pressure for all sound levels used in this study (up to approximately 100 dB relative to $2 \times 10^{-5} \text{ N m}^{-2}$). We have restricted our analysis to frequencies up to 20 kHz, since phonotactic behaviour in *C. biguttulus* can be released by sounds below 15 kHz (D. von Helversen, personal communication).

The directional cues in the sounds reaching the ears are the variations in amplitude and phase angle that occur as the direction of sound incidence changes. The variation in sound amplitude is due only to diffraction, whereas the variation in phase is also (and mainly) caused by the different times of arrival of the sound at the two ears. In order to be useful in calculations of directional hearing, the amplitudes and phase

angles must be measured against the same reference. Our reference is the sound pressure at the external surface of the right tympanum when the sound arrives from the front (0°). In the calculations, this sound pressure is assumed to have an amplitude of 1 and a phase of 0° at all frequencies. All other sound pressures are indicated relative to this reference.

The directional data were collected with the large cork platform on top of a stationary stand situated at the centre of a roundabout carrying a loudspeaker (Dynaudio D28AF). We first ensured that the sound field near the centre was homogeneous in the absence of an animal (i.e. that the sound pressure at various frequencies differed by less than 1 dB when measured at different positions and directions of sound incidence). We then determined the exact position of the centre of the roundabout by measuring the time of arrival of sound from various directions at the tip of a probe microphone (Brüel & Kjær 4182) and by moving the tip until the arrival times differed by less than $2 \mu\text{s}$.

A grasshopper was now placed on the cork platform with its right ear below the tip of the probe microphone (so that the right ear was at the centre). We then lowered the probe tip to a position just in front of the right ear and measured the sound pressure and the tympanal vibrations (in the area of the pyriform vesicle, see below) for 12 directions of sound incidence. Finally, we moved the tip of the probe to the external surface of the left ear and measured the sound pressure for the same 12 directions. Note that the right ear was still at the centre of the roundabout and that the differences in phase

between the sounds measured at the right and left ears now included the effects of the different times of sound arrival at the ears as well as the effects of diffraction.

These data represent the actual directionality and the directional cues in the sounds at the two ears. The next step was to determine the gain (the change in amplitude and phase) for sounds entering one ear and propagating through the interaural pathway to the internal surface of the other ear. A local sound source (positioned several millimetres from the ear, see Michelsen *et al.* 1994a) was used to restrict the sound stimulation to one of the ears (a further reduction of the sound at the other ear was obtained by placing a wall of beeswax on the dorsal side of the animal). The sound at the external surface of the ear was measured with the probe microphone, and the sound at the internal surface of the other ear was estimated from the vibrations of its tympanum (we thus used the tympanum as a microphone).

The first step was to calibrate the 'tympanal microphone'; that is, to measure the vibrations of the tympanum when the ear was activated by sounds at its external surface (Fig. 2A). The calibration was expressed as a transfer function (the vibration spectrum divided by the sound spectrum). We then moved the local sound source and probe microphone to the other ear (Fig. 2B). From the vibrations of the 'calibrated' tympanum, we calculated the sound pressure at its internal surface. This sound spectrum was divided by the sound spectrum at the other ear to give the transmission gain. The amplitude component of the gain function shows how well

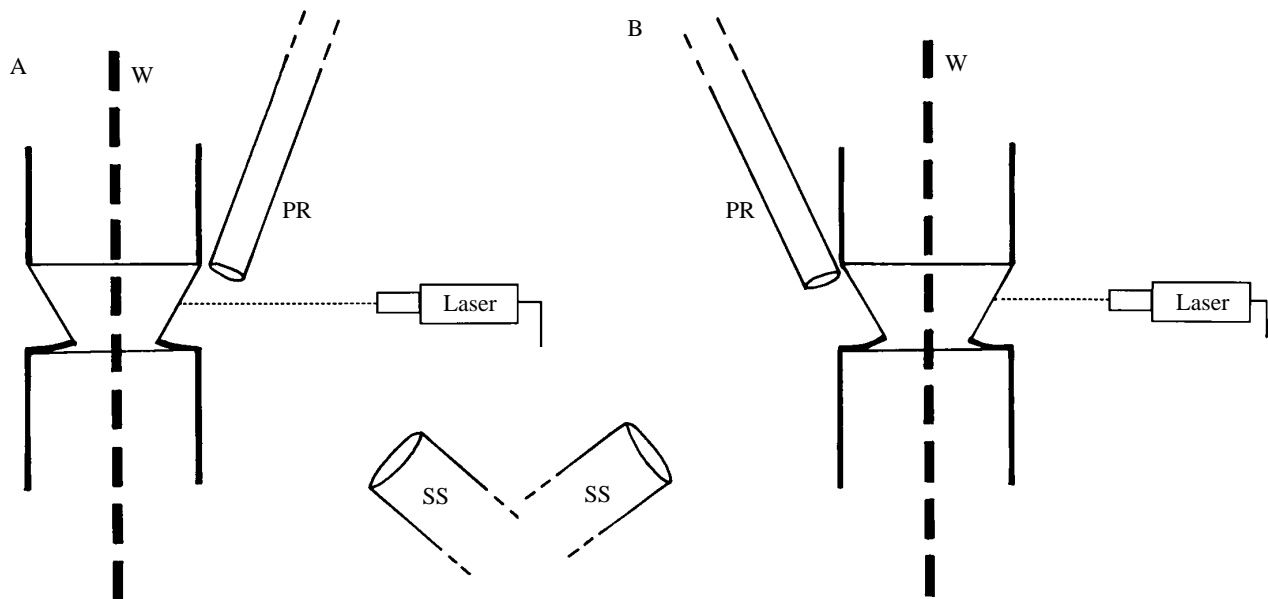


Fig. 2. Schematic drawing (not to scale) of how the transmission gain (the changes of amplitude and phase) of sounds arriving at the tympanum from the other ear were estimated by using the tympanum as a microphone. (A) Calibration of the 'tympanal microphone'; tympanal vibrations caused by a local sound source (SS) are measured with laser vibrometry, while the sound pressure at the ear is measured with a probe microphone (PR). Sound transmission around the body is attenuated by a wall (W) of beeswax on the dorsal side of the animal. (B) The tympanum is activated by sound from the other ear. The tympanal vibrations measured by vibrometry reveal the sound pressure at its internal surface and thus the transmission gain. Diameter of probe, 1 mm; diameter of sound source, 2.5 mm; diameter of tympanum, 0.9 mm in *Chorthippus biguttulus* and 1.5×2.5 mm in *Schistocerca gregaria*; distance between probe and ear, less than 1 mm; distance between sound source and ear, 6–8 mm; distance between laser and ear, 30 cm.

sound propagates through the interaural pathway at various frequencies, whereas the phase component shows how long the transmission takes. Note that this procedure added 180° to the phase angles, since we calibrated the tympanum from the outside, but used it to estimate the sounds at its internal surface.

All measurements of tympanal vibrations were performed in the area of the pyriform vesicle (the attachment area of the d-cells, see Michelsen, 1971a). This part of the tympanum vibrates with a reasonably large amplitude at all frequencies, and the vibration amplitude is linearly related to sound pressure over a wide range. The amplitude and phase of vibration vary with position on the tympanum (Michelsen, 1971a), so the laser beam must be focused at exactly the same spot throughout the experiments. This was achieved by placing a small reflecting sphere (taken from 3M reflective tape) on the tympanum. The mass of the sphere (approximately $0.5 \mu\text{g}$) was too small to affect the vibration of the tympanum (but our use of the results of the measurements was not dependent on whether this was the case; the only important point was whether the measured vibrations faithfully reflected the driving force).

Calculation of directionality

The directional sensitivity of the right ear was calculated by means of a model in which it was assumed that the tympanum is driven by two components of the sound wave: one component (p_f) propagates directly to the external surface, whereas the other component (p_b), from the other ear, is incident on the internal surface (Fig. 1). p_f was measured for 12 directions of sound incidence. p_b could be calculated by multiplying the sound pressure at the left ear (measured) by the gain of the interaural sound pathway (calculated from our measurements). Both p_f and p_b can be thought of as acting on the external surface, because the 'tympanal microphone' had been calibrated with sound at its external surface (adding 180° to the phase of the gain). These two sound pressures (conveniently represented as vectors) could therefore be summed to estimate the total sound pressure (P) driving the tympanum. The calculation was repeated for each of the 12 directions of sound incidence investigated (Fig. 3).

Results

Four kinds of data were obtained in both species: the directional cues (i.e. the amplitude and phase of the sound at the two ears for various directions of sound incidence); the gain of the interaural sound pathway; the directional patterns of the driving force calculated from these data; and the directional patterns of tympanal vibration measured with laser vibrometry. The directional patterns for force and vibration can be compared directly, because there is a linear relationship between sound pressure and tympanal vibration. These data are presented separately for each species.

Schistocerca gregaria

We illustrate data obtained at 5 kHz and 12 kHz, which are

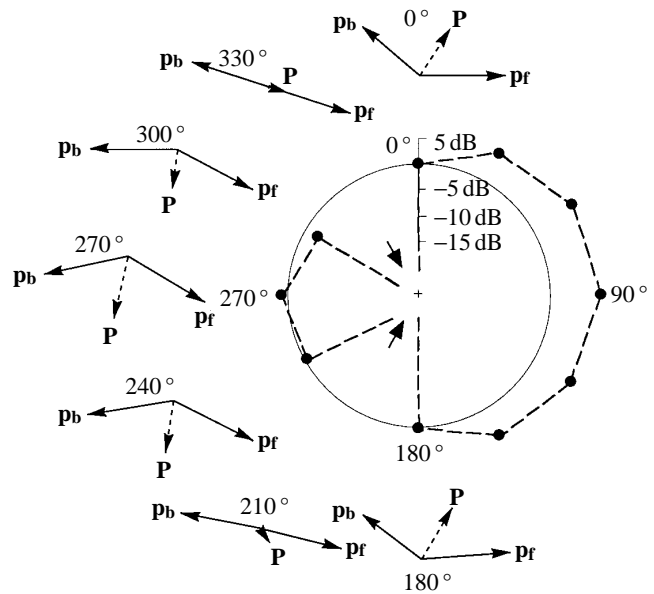


Fig. 3. Representation of a directional pattern (at 10 kHz in *Chorthippus biguttulus*), in which the sounds have been drawn as vectors. p_f is the measured sound pressure at the external (front) surface of the tympanum, and p_b is the calculated pressure at the internal (back) surface. 180° has been added during the estimation of p_b (the sound that originated at the other ear), thus 'moving' p_b to the external surface. The resulting pressure (P) driving the tympanum can thus be calculated simply by summing the two vectors. At 210° and 330° (arrows within the polar plot) the values of P are -26 dB and -30 dB , respectively. In the vector diagrams for these directions, the P component indicates only the phase, not the amplitude. The amplitude and phase relationships of the vector diagrams are determined by the following definition: p_f for sound incident from the front (0°) is given an amplitude of 1 and a phase of 0° , and all other vectors are expressed relative to this. In the vector plots, negative phase values (c.f. Figs 4, 7) are plotted clockwise.

close to the best frequencies of the low- and high-frequency receptor cells in the ear (Römer, 1976); these data are representative of those obtained at other frequencies. Fig. 4A shows the amplitude of sound at the external surface of the locust tympanum for 12 directions of sound incidence. 0° indicates that the sound source was in the anterior (forward) direction, 90° is ipsilateral, 180° is posterior and 270° is contralateral to the ear under consideration (the values for the right and left ears are, of course, mirror images relative to the length axis). The values are indicated relative to that measured in the 0° direction (this amplitude is defined as 1 in our calculations). At both 5 and 12 kHz, a greater pressure is seen for ipsilateral directions, and this difference is larger at 12 kHz than at 5 kHz. The data measured at 5 kHz for contralateral directions are very close to 1, whereas a 'shadow' is seen in the 12 kHz data. This dependence on sound frequency was expected, since diffraction depends on the size of the body (relative to the wavelength of the sound).

Fig. 4B shows the phase angles (with the sound at the right ear for 0° direction of sound incidence defined to have a phase of 0°). The variation in the phase angle at the right ear is caused

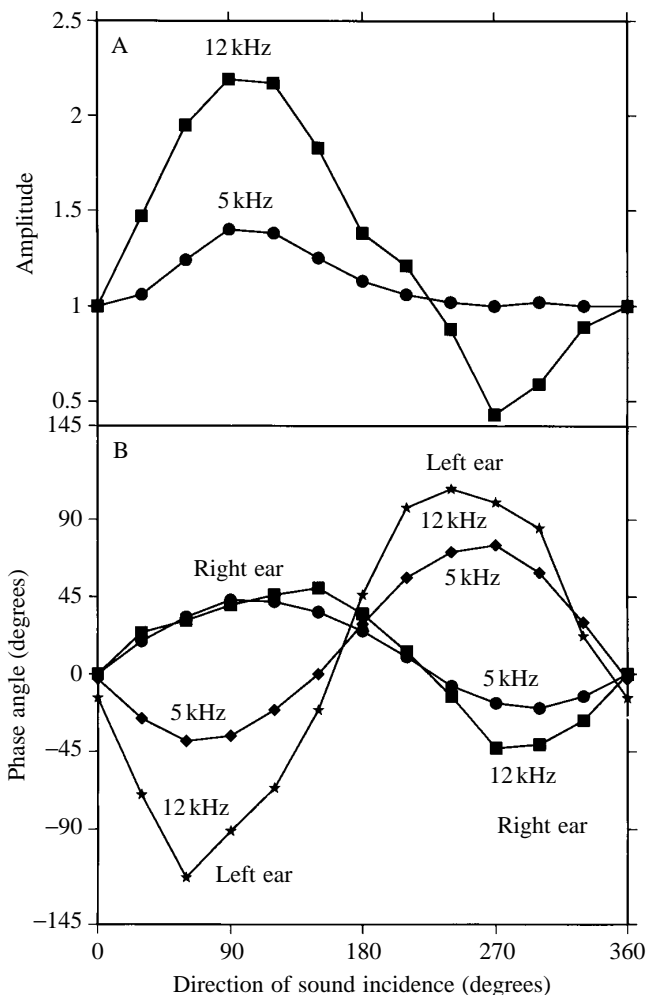


Fig. 4. Amplitude (A) and phase angle (B) of the sound pressure at the external surface of the tympanum in *Schistocerca gregaria* as a function of the angle of sound incidence (where 0° is the front and 90° is ipsilateral to the right ear). The amplitude and phase are defined to be 1 and 0° , respectively, when sound arrives at the right ear from the front (0°). The amplitude data have been plotted for the right ear only; values for the left ear are the mirror-image of those shown. The phase angles for the left ear reflect the different time of arrival of the sound at the two ears.

entirely by diffraction. In contrast, the much larger variation in the phase angle at the left ear is due both to diffraction and (mainly) to the different times of arrival of the sounds at the two ears (remember that all sound pressures are expressed relative to that at the right ear).

The amplitude and phase characteristics (gain) of the sound pathway from the external surface of the tympanum in one ear to the internal surface of the tympanum in the other ear are shown in Fig. 5. An amplitude of 1 means that the tympana in the two ears vibrate with the same amplitude when only one of them is receiving sound at its external surface. Here, the amplitude is approximately 0.5 at 3–5 kHz and 0.1–0.2 between 10 and 20 kHz. A phase angle of 180° (not 0° , see Materials and methods) means that the sound has propagated

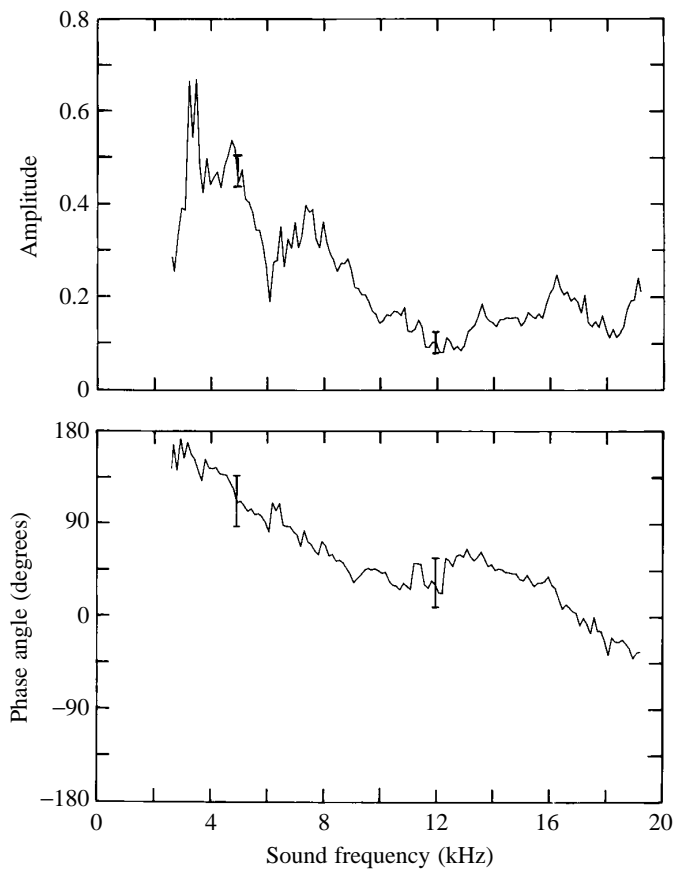


Fig. 5. Transmission gain for sound arriving at the tympanum from the contralateral ear in *Schistocerca gregaria*. An amplitude of 1 and a phase angle of 180° indicate that the amplitude and phase have not changed during the transmission. Averaged data (and standard deviations at 5 and 12 kHz) from three animals.

from one ear to the other instantaneously. Smaller (or negative) phase angles mean that the sound propagation through the animal takes a certain time (values expressed as degrees indicate this delay relative to the period of the sound). Here, there is a fairly smooth decrease of phase between 3 kHz and 20 kHz.

From the data in Fig. 4 and the transmission gains in Fig. 5 (0.45, 112° at 5 kHz, and 0.10, 24° at 12 kHz, respectively), it is possible to calculate how the tympanic vibrations should vary with the direction of sound incidence, provided that the force driving the tympanum is determined only by the sound at the external surface and by the sound at the internal surface arriving from the other ear (the two-sound-input model). In Fig. 6 the dashed lines show the calculated directionalities of the tympanic vibrations and the solid lines the actual values (measured with laser vibrometry). The agreement between the curves suggests that the model is a valid description of the acoustics of the ear, both at 5 kHz and at 12 kHz. In other words, there is no need to postulate that sound arriving at the internal surface through other routes (e.g. through spiracles) should play any significant role.

The dotted curves in Fig. 6 show the amplitude of sound

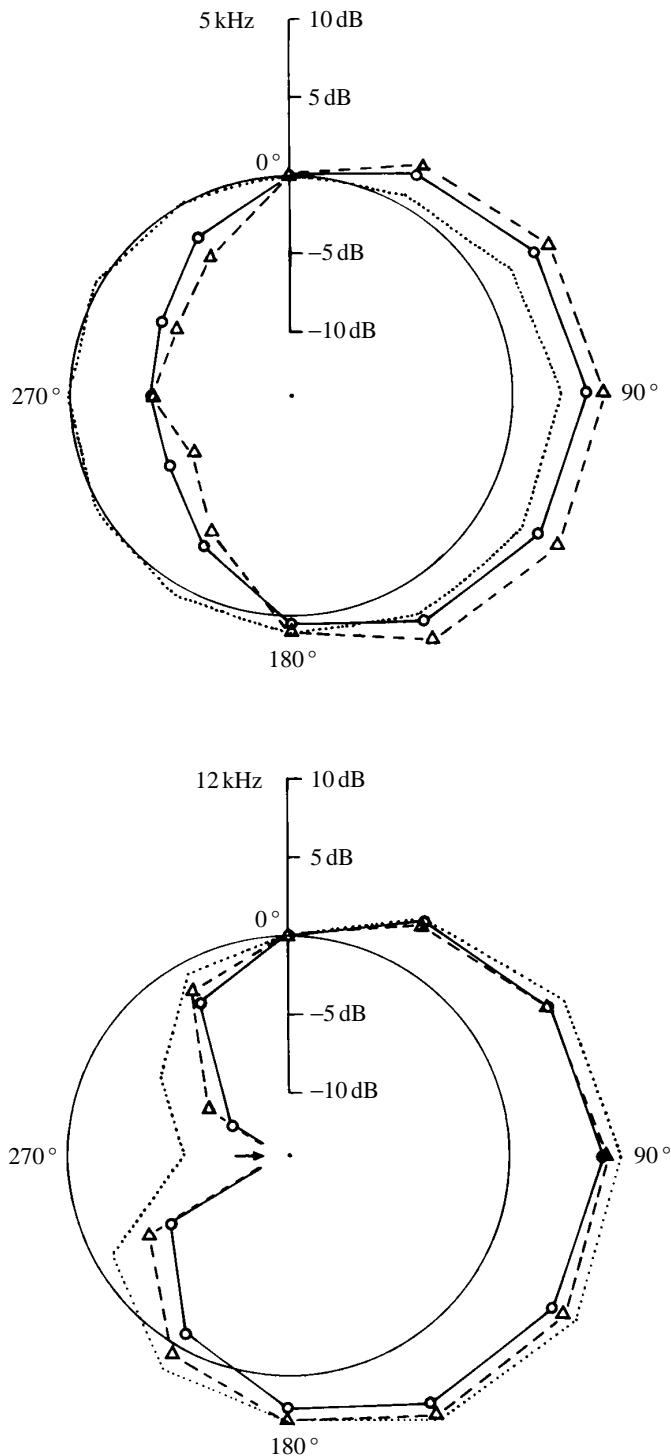


Fig. 6. Directional patterns at 5 kHz and 12 kHz in *Schistocerca gregaria*. Solid and dashed lines: observed and calculated vibration amplitude of the tympanum, respectively. Dotted lines: amplitude of sound pressure at the ear (same data as in Fig. 4A). The arrow marks an amplitude minimum.

pressure at the external surface of the tympanum. These curves thus show the directionality that would exist in the absence of a pressure difference mechanism. This mechanism is clearly

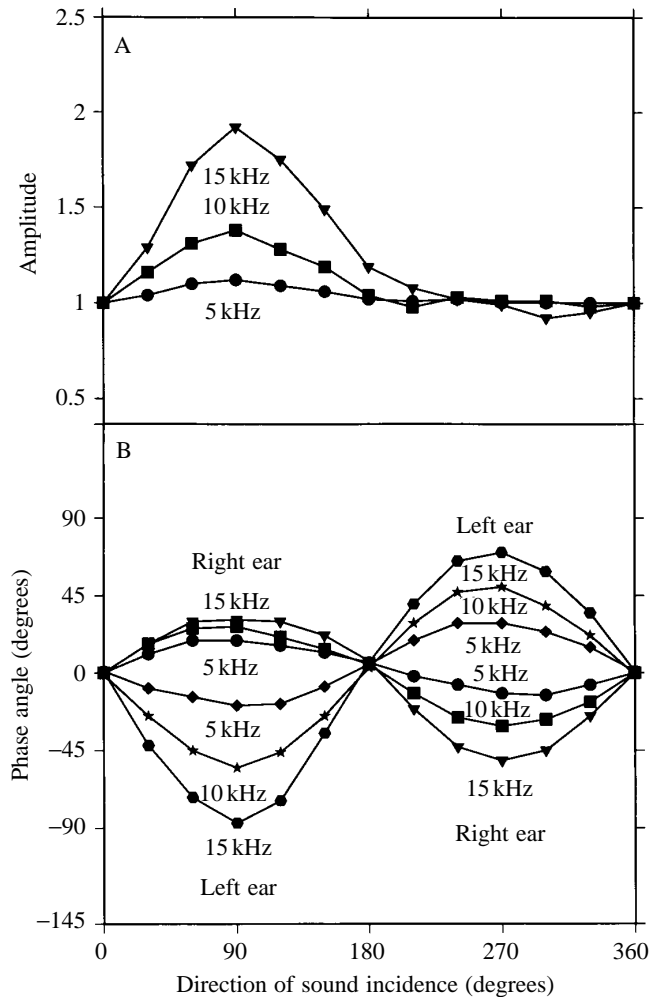


Fig. 7. Amplitude (A) and phase angle (B) of the sound pressure at the external surface of the tympanum in *Chorthippus biguttulus* as a function of the angle of sound incidence. Definitions as in Fig. 4.

essential at 5 kHz, but at 12 kHz, where the amplitude of the transmission gain is only 0.1, it plays a minor, but not insignificant, role (see Discussion).

Chorthippus biguttulus

The data for *C. biguttulus* in Figs 7–9 are equivalent to those for *S. gregaria* in Figs 4–6 and are therefore presented without detailed explanations of how they were obtained.

Fig. 7 shows the amplitudes and phase angles measured at the external surface of the ears for 12 directions of sound incidence (cf. Fig. 4). Again, all values are indicated relative to sound at the right tympanum at 0° sound incidence (amplitude 1, phase angle 0°). The relatively greater pressure for ipsilateral directions depends on the frequency of the sound, as in the locust (although the amplitudes are surprisingly large, see Discussion). For contralateral directions, the amplitudes are close to unity at all frequencies (there is no ‘shadow’ at 12 kHz as there is in the locust). The dependence on frequency and direction seen in the phase angles at the right and left ears is similar to the data from the locust.

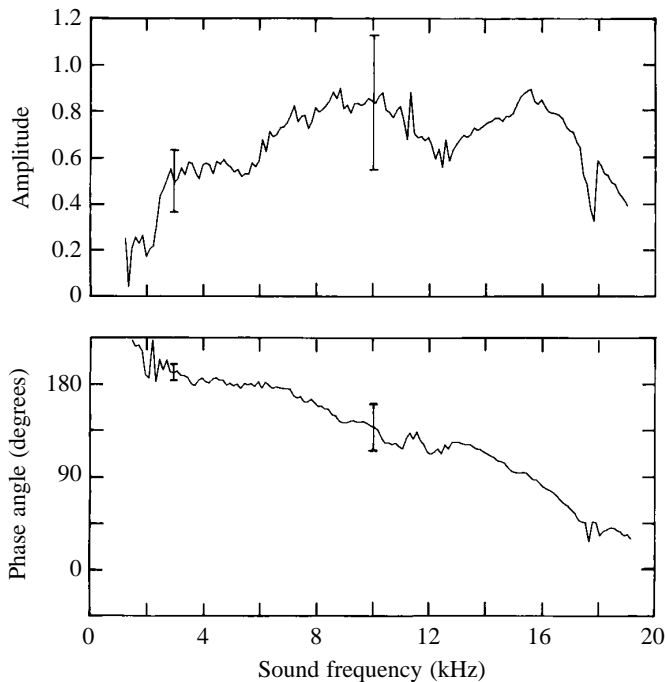


Fig. 8. Transmission gain for sound arriving at the tympanum from the contralateral ear in *Chorthippus biguttulus*. Averaged data from six animals. Standard deviations are indicated at 3 and 10 kHz. Further explanation in the legend to Fig. 5.

The gain of the interaural sound transmission is shown in Fig. 8. The amplitude at 4–5 kHz is approximately 0.5, which is about the same as in the locust, but it then increases with frequency to a remarkably high level (approximately 0.8). The phase angles decrease with frequency (as expected), but below 5–6 kHz the values are obviously too large, both in this averaged plot and consistently in the individual results. (Values above 180° are physically meaningless, since the time used for sound propagation cannot be negative. In the Discussion, we argue that the phase angles measured between 10 and 20 kHz are more reliable.)

Observed and calculated directional patterns are shown for 5 kHz, 8 kHz, 10 kHz, 12 kHz and 17 kHz in Figs 9 and 10. Again, the overall agreement suggests that the two-sound-input model approximately describes the acoustics of the hearing organ.

At 12 kHz, the directional patterns are fairly similar in the large *S. gregaria* and the small *C. biguttulus* (Figs 6, 10C), despite the difference in the directional cues. The reason for this paradox becomes apparent if the amplitude component of the interaural transmission gain is varied in the calculation of the directional pattern in *C. biguttulus* (Fig. 11A). Using the measured value (0.68), the calculated directional sensitivity for the forward direction (expressed as the difference between the values for the 30° and 330° directions of sound incidence) is 14 dB. In contrast, this difference becomes 7 and 4 dB when the transmission is assumed to be 0.5 and 0.25 of the measured amplitude (0.34 and 0.17), respectively. Apparently the large interaural transmission in the small animal compensates for the

modest directional cues. The observed pattern at 5 kHz is obviously less directional in *C. biguttulus* (Fig. 9A) than in *S. gregaria* (Fig. 6). The amplitude of the interaural transmission at 5 kHz is very similar in the two species. The calculations reveal, however, that the modest directional cues are not the main cause of the smaller directionality in *C. biguttulus*. By assuming a transmission phase angle of 112° (the value found at 5 kHz in the locust), a dramatic improvement of directionality is obtained (Fig. 11B). Apparently, the system of air sacs between the ears does not allow the small grasshopper to obtain such a transmission delay at 5 kHz.

Discussion

In *Schistocerca gregaria* and *Chorthippus biguttulus*, tympanal vibrations (observed with laser vibrometry) depend very much on the direction of sound incidence. The observed directional patterns are in reasonable agreement with those calculated from measured values of sound pressure at the ears for various sound directions and the gain of the interaural sound transmission. For the calculations, we assumed that two sound pressures act on the tympanum: the sound at the external surface and the sound that has propagated from the external surface of the other ear, through the interaural air sacs, to the internal surface. The approximate agreement between the observed and calculated directional patterns suggests that this assumption (the two-sound-input model) is a reasonable description of the acoustics of the ear.

Such a system is an example of a pressure difference receiver, in which sound can reach both sides of a membrane. The idea that directional hearing in small animals may be caused by such a mechanism was first proposed by Autrum (1940), who referred to the inherently directional nature of pressure gradient receivers. In recent years, this concept has become the standard explanation for directionality, almost a magic formula, but very little has been done to investigate the problems and limitations of such systems.

The ideal pressure gradient receiver is so small (relative to the wavelength of sound) that it does not cause any diffraction. It is driven by the small differences in phase that are caused by the different times of arrival of sound at its two surfaces, which are equally exposed to sound. The driving force is proportional to the pressure gradient, hence the name. Such devices are not very sensitive, and their directional patterns have the ambiguous shape of a figure-of-eight. Obviously, these properties are far from those of typical ears.

Animals need sensitive ears with 'useful' directional patterns. Directional patterns that emphasize ipsilateral sounds can be processed by means of a few neurones in the central nervous system, and such patterns are thus much more useful for small animals than, for example, figure-of-eight patterns. Grasshoppers obtain such directional patterns over a broad range of frequencies partly by allowing sound to reach both sides of their tympanal membranes, but they also need some directional cues in the sounds reaching their ears (that is, the

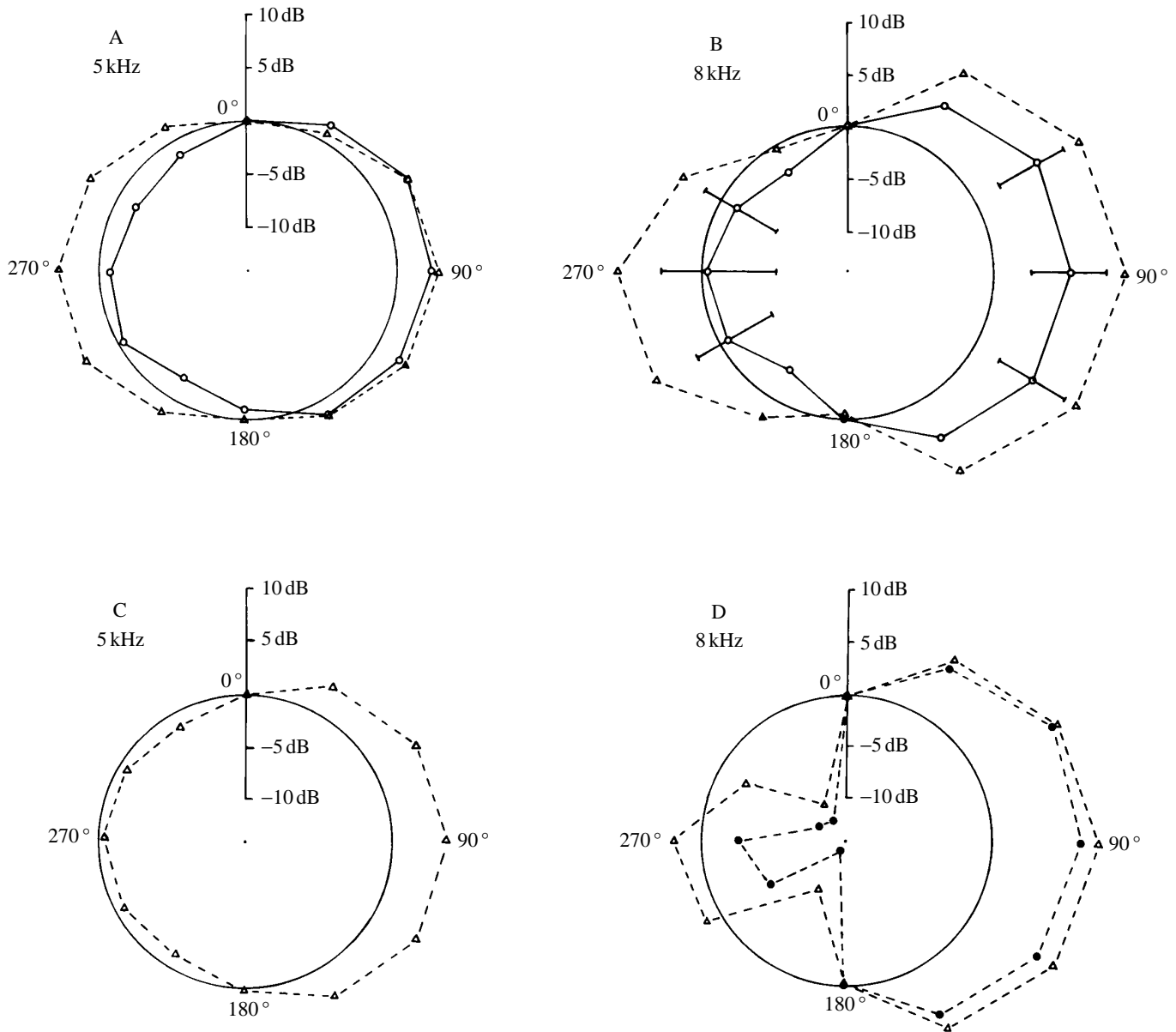


Fig. 9. Directional patterns in *Chorthippus biguttulus* at 5 kHz (A,C) and 8 kHz (B,D). (A) 5 kHz. Solid line: observed values, averaged from three animals. Dashed line: values calculated from data. (B) 8 kHz. As for A, but the ranges of the observed values are indicated for six directions. (C,D) Calculated patterns obtained by assuming somewhat lower transmission phase angles than those measured. (C) Assuming a phase of 158° at 5 kHz, where the measured value was 182° . (D) Assuming phase values of 152° (open triangles) and 140° (filled circles) at 8 kHz, where the measured value was 164° . See the Discussion for comments on the patterns shown in C and D.

amplitude and phase angle of the sound at the ears should change with the direction of sound incidence).

The amplitude of the transmitted sound decreases with frequency in *S. gregaria*, but increases in *C. biguttulus* (Figs 5, 8). At 5 kHz, *S. gregaria* needs a pressure difference mechanism for obtaining marked directionality, whereas at 12 kHz the directionality of the ear is similar to that in a pressure receiver (compare the dotted and dashed curves in Fig. 6).

Note that, although the pressure difference mechanism is not essential for *S. gregaria* at 12 kHz, it still causes a significant decrease in the sensitivity to contralateral sounds. This may

seem surprising, since the transmission amplitude is only 0.1 (i.e. -20 dB). The reason is seen in Fig. 4: when 12 kHz sound arrives from the contralateral direction, the contralateral ear experiences a sound amplitude of 2.2, and the sound transmitted to the internal surface of the ipsilateral ear is ($2.2 \times 0.1 = 0.22$), which is almost half of the sound amplitude at the external surface (0.5). Small sound transmissions may thus have significant effects at frequencies where the diffraction effects are large.

C. biguttulus exploits smaller directional cues than those available to *S. gregaria*. Nevertheless, the directional pattern

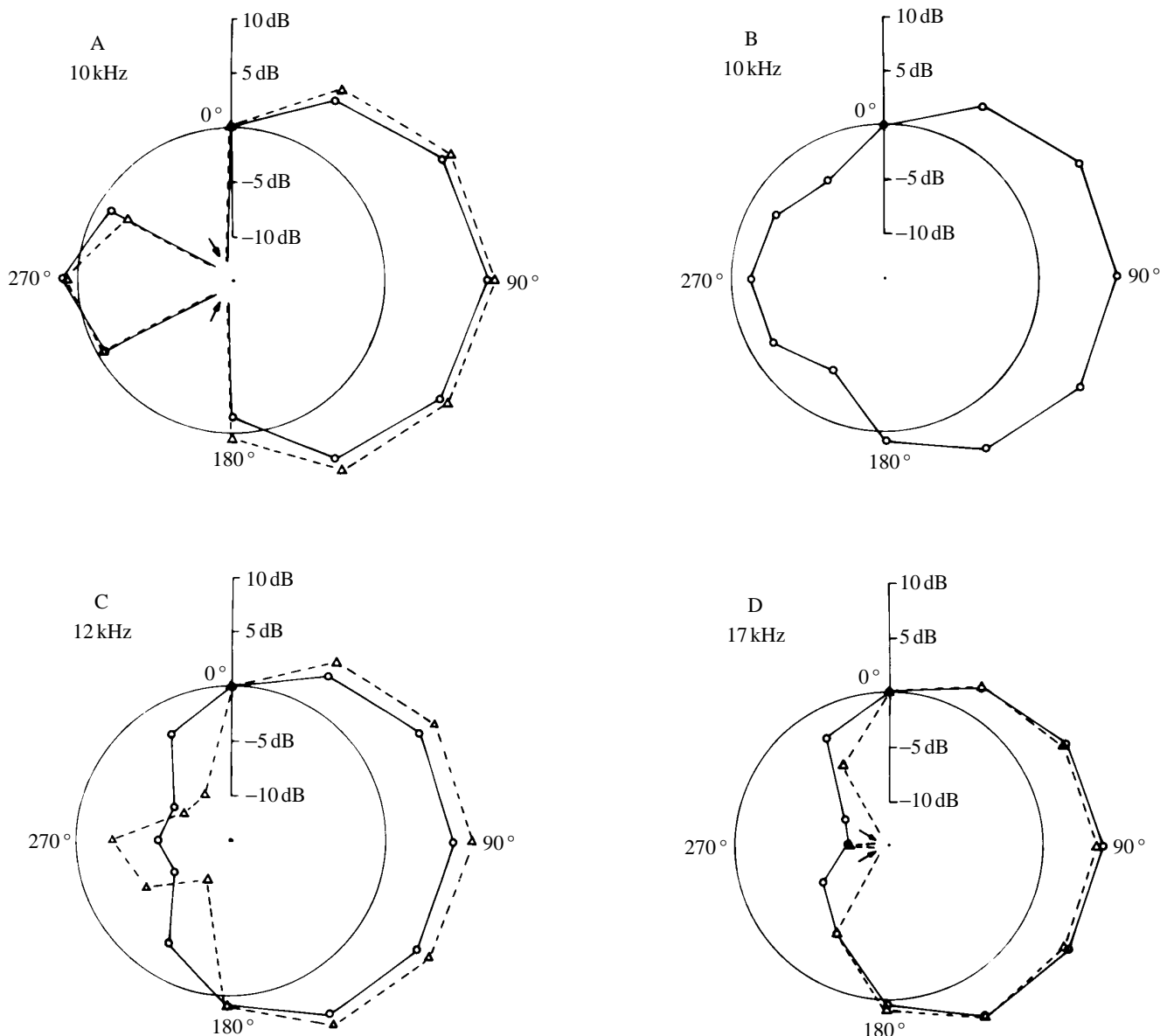


Fig. 10. Directional patterns in *Chorthippus biguttulus* at 10, 12 and 17 kHz. (A) Observed pattern at 10 kHz in one animal (solid line) and calculated pattern (dashed line). (B) Observed pattern at 10 kHz; averaged for four animals. (C) Observed pattern at 12 kHz (solid line; averaged for four animals) and calculated pattern (dashed line). (D) Observed pattern at 17 kHz (solid line; averaged for three animals) and calculated pattern (dashed line). Arrows mark amplitude minima.

at 12 kHz (Fig. 10) is not inferior to that of *S. gregaria* (Fig. 6). The calculated results shown in Fig. 11A suggest that *C. biguttulus* uses the large interaural transmission to compensate for the small directional cues. It remains to be determined whether this is also the strategy of other small animals.

As expected, the directional cues become more prominent as the size of the animal increases, but the relationship is not that of simple scaling. The two species differ by a factor of 3–4 with respect to body length and the diameter of thorax and abdomen, but the change of sound amplitude at a particular frequency only differs by a factor of 2 (compare Figs 4 and 7). In the case of pure diffraction around an inflexible object, one would expect simple scaling according to size and frequency,

but grasshoppers are not inflexible objects. Their acoustic impedance is likely to change with frequency, and there is no simple relationship between, for example, body length and the thickness of their cuticle.

It is not known how directional the hearing must be to allow the animals to locate singing conspecifics in their natural habitats. The strategy used by short-horned grasshoppers for locating a sound source is to turn their body towards the side of the more loudly stimulated ear. A 1–2 dB difference in the level of stimulation is sufficient for this decision (von Helversen and Rheinlaender, 1988). The directional pattern observed in *C. biguttulus* at 5 kHz (Fig. 9) should thus be sufficient in a free sound field in a laboratory. It is doubtful, however, that it will

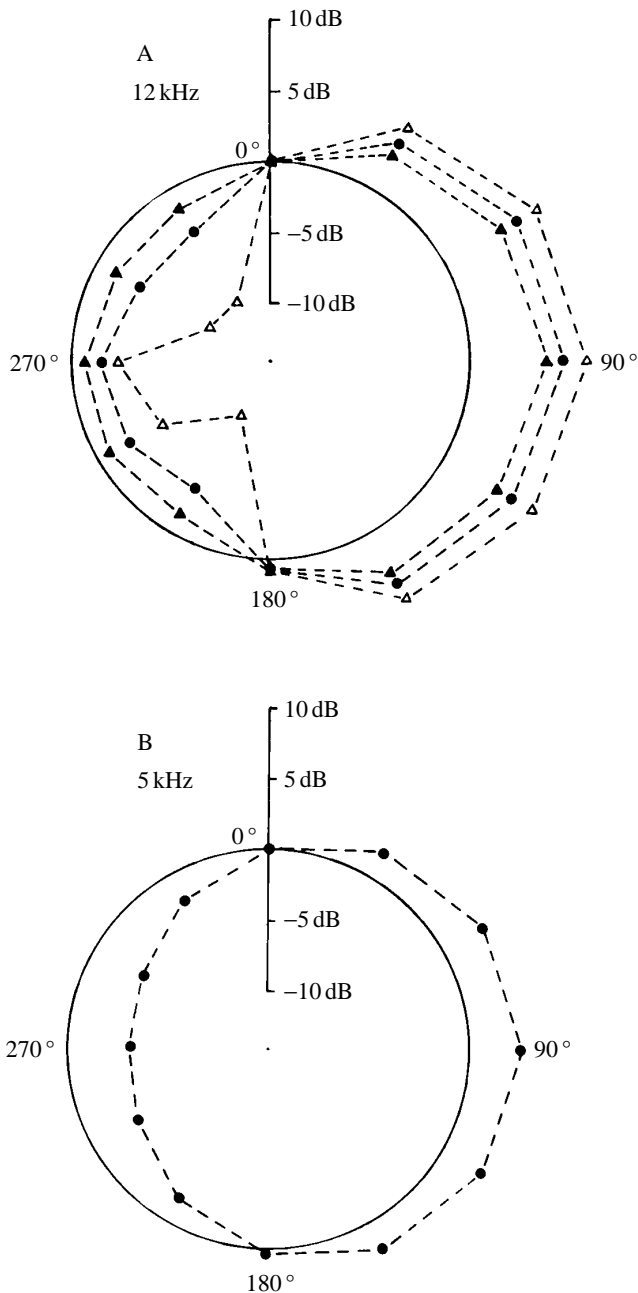


Fig. 11. (A) Directional pattern in *Chorthippus biguttulus* at 12 kHz, calculated from the measured data, but assuming various amplitudes of transmission gain. Open triangles: assumed gain of 0.68, equal to the measured value (this pattern is also shown in Fig. 10C). Filled circles and filled triangles: assumed gain values of 0.34 and 0.17, respectively. (B) Directional pattern in *C. biguttulus* at 5 kHz, calculated by assuming a transmission phase angle of 112° , the value found at 5 kHz in the locust.

suffice in the more diffuse sound fields found in natural habitats. The directional patterns observed at 5 and 12 kHz in *S. gregaria* (Fig. 6) and the patterns observed at 12 and 17 kHz in *C. biguttulus* (Fig. 10) should be more useful under the acoustic conditions in the field. It remains to be shown whether the potential ambiguities in the patterns observed at 8 and 10 kHz

in *C. biguttulus* (Figs 9, 10) cause the animals to make mistakes. Studies of this problem and of the directional cues in sound fields in natural habitats are in progress.

The importance of phase relationships

In a previous study of the physics of directional hearing in crickets (Michelsen *et al.* 1994b), it was found that proper phase relationships are essential for the directional patterns. In crickets, sound reaches the tympanum from three or four different inputs, and changes in the phase relationships between these sounds may cause large changes in the sensitivity of the ear, even though the amplitudes remain constant.

A similar situation has been found in the present study. At 10 kHz, there was a perfect match between the calculated directional pattern and the pattern observed in one of the animals studied (Fig. 10A). The amplitude was a minimum for the 210° and 330° directions. At these minima, the sounds acting at the external and internal surfaces of the tympanum are almost in phase (and thus totally out of phase when p_b 'moves' to the external surface, see Fig. 3). By chance, the same situation must have existed in this particular animal at 10 kHz and at these two directions. Of course, one cannot expect such a perfect match of phase to occur very often. The measured directional patterns show considerable scatter, and the average pattern for 10 kHz (Fig. 10B) has only slight indications of minima for these directions.

Note that the agreement between the calculated and observed directional patterns in Fig. 10 is much better for ipsilateral directions ($30\text{--}150^\circ$) than for contralateral ones. This is not surprising, since the two sound components are in phase for ipsilateral directions, but more or less out of phase for contralateral directions; the result is critically dependent on the exact phase relationships in the latter case, but not in the former.

The hypothesis that the magnitude of the transmission delay is a critical parameter in determining the directional patterns is supported at several frequencies in the data from *C. biguttulus*. For unknown reasons, the measured phase angles for interaural transmission (Fig. 8) were obviously too high below 6 kHz, where the measured values above 180° suggest that the sound travelled across the body in a negative time. We therefore calculated the directional patterns corresponding to lower and physically more realistic phase values. This resulted in an improved agreement between the measured and calculated directional patterns, both at 5 kHz (Fig. 9A,C) and at 8 kHz (Fig. 9B,D). At 10–17 kHz, however, reasonable agreement was obtained between the observed directional patterns and those calculated using the observed values of the transmission delay (Fig. 10). We therefore believe that these values are more reliable than those below 10 kHz.

The pattern for 5 kHz calculated with the measured transmission phase angle (Fig. 9A) is almost bilaterally symmetrical along the length axis of the animal. With this pattern, the two ears experience very similar driving forces for each direction of sound incidence. The conditions leading to this apparently useless pattern are an interaural transmission delay close to zero (180° , Fig. 8) and the mirror-image nature

of the 5 kHz phase curves for the sound at the two ears (Fig. 7). Introducing a transmission delay of just 13 μ s (corresponding to 24° at 5 kHz) changes the 5 kHz pattern from the shape illustrated in Fig. 9A to that shown in Fig. 9C.

At 12 kHz, an increased transmission amplitude caused an improved directionality (Fig. 11A), but this was not so at 5 kHz. Here, the transmission delay was small, and larger transmission amplitudes would result in a reduced absolute sensitivity of the ear (which would become almost a pressure gradient receiver). The calculations show, however, that further increases in the assumed transmission delay (reduction in phase angle) lead to further improvements of directionality (Fig. 11B).

In order to obtain a good directionality at low frequencies, the animal apparently needs to have a large transmission delay. This is not possible with a short, simple delay line, in which the phase is proportional to the sound frequency. Crickets appear to have solved this problem: the tracheal tube connecting the two ears causes a dramatic phase shift (Michelsen *et al.* 1994b), but only when the central membrane is intact (Michelsen and Löhe, 1995). Crickets can thus achieve a remarkable directionality, but only within a very narrow range of frequencies (generally around the frequency of the calling song, where the transmission phase is suitable for directional hearing).

We have no explanation for the small discrepancy in the estimate of the phase component of the transmission gain in *C. biguttulus*. The method was designed in such a manner that most systematic errors should cancel, and it has been used in both insects and vertebrates without such problems. We hope to be able to solve this mystery in the future.

The Centre for Sound Communication is financed by the Danish National Research Foundation. We are grateful to Knud Rasmussen, Brian Lewis, Dagmar and Otto von Helversen, Norbert Elsner and two anonymous referees for help and comments on the manuscript.

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