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Physics of directional hearing in the cricket *Gryllus bimaculatus*

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Abstract In the cricket ear, sound acts on the external surface of the tympanum and also reaches the inner surface after travelling in at least three pathways in the tracheal system. We have determined the transmission gain of the three internal sound pathways; that is, the change of amplitude and phase angle from the entrances of the tracheal system to the inner surface of the tympanum. In addition, we have measured the diffraction and time of arrival of sound at the ear and at the three entrances at various directions of sound incidence. By combining these data we have calculated how the total driving force at the tympanum depends on the direction of sound. The results are in reasonable agreement with the directionality of the tympanal vibrations as determined with laser vibrometry.

At the frequency of the calling song (4.7 kHz), the direction of the sound has little effect on the amplitudes of the sounds acting on the tympanum, but large effects on their phase angles, especially of the sound waves entering the tracheal system at the contralateral side of the body. The master parameter for causing the directionality of the ear in the forward direction is the sound wave entering the contralateral thoracic spiracle. The phase of this sound component may change by 130–140° with sound direction. The transmission of sound from the contralateral inputs is dominated by a very selective high-pass filter, and large changes in amplitude and phase are seen in the transmitted sounds when the sound frequency changes from 4 to 5 kHz. The directionality is therefore very dependent on sound frequency.

The transmission gains vary considerably in different individuals, and much variation was also found in the di-

rectional patterns of the ears, especially in the effects of sounds from contralateral directions. However, the directional pattern in the frontal direction is quite robust (at least 5 dB difference between the 330° and 30° directions), so these variations have only little effect on how well the individual animals can approach singing conspecifics.

Key words Cricket · Directional hearing · Sound localization · Laser vibrometry · Pressure gradient

Abbreviations CS contralateral spiracle
CT contralateral tympanum · IS ipsilateral spiracle
IT ipsilateral tympanum · P the vectorial sum of the sounds acting on the tympanum

Introduction

In many animals the body is much smaller than the wavelengths of the sound signals used in social communication, and diffraction is therefore not likely to cause much difference in sound pressure at the ears. Nevertheless, both neural recordings and measurements of tympanal vibrations often show that the individual ear is much more sensitive to sounds from certain directions than to sounds from other directions. The ears of crickets are a good example: they are much more sensitive to calling song (wavelength c. 7 cm in European field crickets) arriving from the ipsilateral side of the body than from contralateral directions.

A mechanism that could be responsible for the directional sensitivity of such ears has been known since the pioneering work of H. Autrum (1940). He pointed out that the observed directionality could be accounted for if the ears were pressure difference (pressure gradient) receivers, i.e., if the sound waves were able to reach both the external and internal surfaces of the tympanal membrane. This principle is now generally accepted, and a large number of examples of ears operating according to this mechanism have been reported in the literature.

The criteria used in many of these reports have been: the existence of air-filled passages between the ears or

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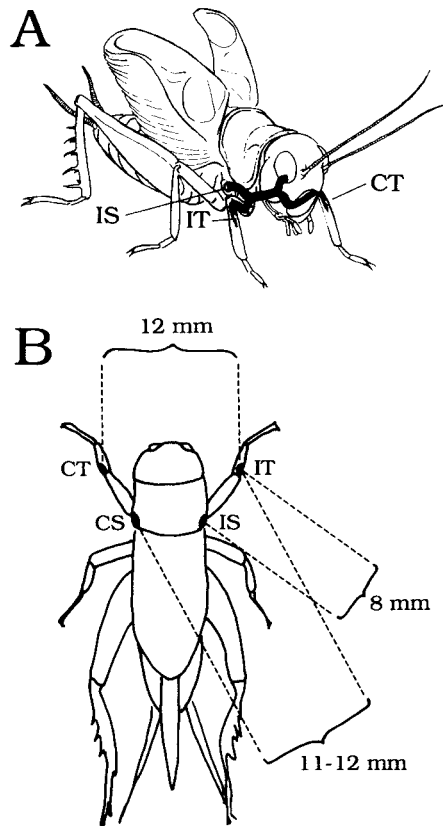


Fig. 1 A Schematic diagram of the hearing organ of the cricket with an indication of the position of the tympanum and the acoustic spiracle at each side of the body. B Approximate distances between the acoustic inputs during the measurements of diffraction, time delays and tympanal vibrations. *IT* and *CT*, ipsi- and contralateral tympana. *IS* and *CS*, ipsi- and contralateral acoustic spiracles

from another sound-input to the internal surface of the tympanum; the effects of blocking potential sound inputs; and measurements of sound propagation through the internal pathways. However, such observations are not sufficient, if the aim is to understand the directional sensitivity of the ear. In this paper we give examples of pressure difference receivers which do not provide the animal with any useful directionality (see Discussion). One aim of this paper, then, is to pinpoint the criteria that need to be applied in future investigations.

The directional hearing of the cricket has been studied intensively by many different investigators (for a review see Larsen et al. 1989). Crickets have their ears in the front leg tibiae, and all investigators agree that the tympanum receives sound at both its external and internal surfaces. The internal surface is connected with the ipsilateral acoustic spiracle (*IS*) on the thorax through a horn-shaped tracheal tube known as the acoustic trachea (Fig. 1). The acoustic trachea is also linked, through a connecting trachea, with the acoustic trachea on the other side of the body. Therefore, sound may propagate from the contralateral ear and acoustic spiracle, across the midline, to the internal surface of the ipsilateral tympanum.

However, very different opinions are held of the importance of these contralateral inputs for creating the directional characteristics of the ear. Some investigators have favoured the sound from the contralateral ear (Hill and Boyan 1976; Fletcher and Thwaites 1979) and others the sound from the contralateral spiracle (Larsen and Michelsen 1978; Schmitz et al. 1983). Finally, the observation that disrupting the central tracheal connection does not hinder sound localization in very homogeneous sound fields has been claimed to "toll the death of all such cross-body theories" (Weber and Thorson 1989).

In this paper we demonstrate that the sound from the contralateral spiracle plays a key role in creating the directional pattern in forward directions, which is crucial when the individuals approach singing conspecifics. Sound from the ipsilateral spiracle is also essential, whereas the sound from the contralateral ear plays only a minor role.

Materials and methods

Animals

The experiments were carried out in Odense in April-July 1992. The crickets (*Gryllus bimaculatus* de Geer) came as eggs from a culture in the laboratory of Franz Huber, Seewiesen and were raised at Odense. Animals of the last instar were kept isolated from each other in single glass containers, and the day of the adult moult was noted. The results reported here were obtained from 7-15 days old adult crickets (mainly females).

The crickets were anaesthetised with CO_2 and glued to a platform of cork by means of sticky wax. The two thoracic spiracles were held open by means of sticky wax. For the determination of the diffraction of sound by the cricket's body, the cricket was mounted in the normal walking position in the middle of a horizontal cork platform of 20 cm diameter. The platform was mounted on a stand in an anechoic room and at the middle of a roundabout carrying a loudspeaker (Fig. 2). For the determination of the transmission gains the cricket was mounted on a smaller piece of cork in such a way that there was an easy access for the probe microphone and local sound source to the tympana and the thoracic spiracles. In both cases the tympanal vibration velocity was measured by focusing the laser beam on a small reflective sphere on the tympanum of the right ear.

Acoustical measurements

1. Diffraction

A determination of the changes of sound amplitude and phase due to diffraction requires that the sound field is reasonably homogeneous (i.e., without major reflected sounds at the position of the animal). This may be difficult to achieve, even in an anechoic room, when large instruments have to be present. In these experiments, swept-sine sound pulses of 3.5 ms duration were used; the signal analyser (Hewlett-Packard 3562A) was also set to analyse received signals within a 3.5 ms time window, ignoring reflected sound signals arriving later. Reflected sounds from objects more than 60 cm behind the animal were therefore ignored (sound travels at approx. 340 m/s).

At the centre of the platform and at 2-20 kHz the sound field was homogeneous within ± 1 dB before the cricket was mounted.

The phase of the sound at the tympana and acoustic spiracles must be determined accurately and indicated in such a way that the results can be used in the later calculations. This means that

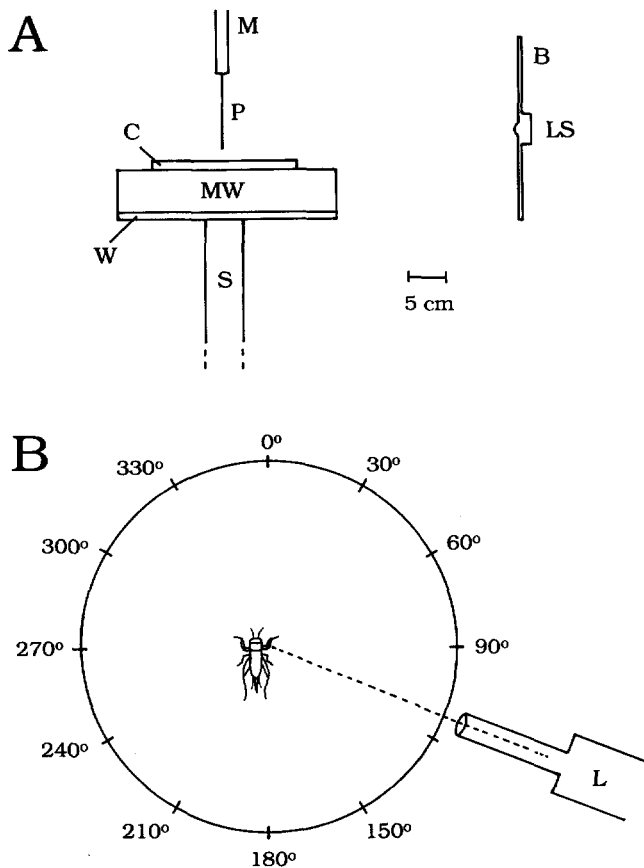


Fig. 2A,B Experimental set-up during the measurements of diffraction, time delays and tympanal vibrations. **A** Vertical section through the platform carrying the cricket. **B** Definition of the angles of sound incidence when the right ear is considered. *B* baffle; *C* cork; *L* laser vibrometer; *LS* loudspeaker; *M* microphone; *MW* mineral wool; *P* probe; *S* stand; *W* wood

the position of the animal in the middle of the round-about must be well defined. We first determined the exact position of the centre of the round-about: the tip (1 mm diameter) of a probe microphone (Brüel & Kjør 4182) mounted above the platform was placed at the middle of the round-about, and the times of arrival of sounds from the loudspeaker were measured for various directions of sound incidence. The tip of the probe was then moved until the times of arrival differed by less than 1–2 μ s (corresponding to an error of 2–3° at 4–5 kHz). The cricket was then brought into the set-up, and its right tympanum was placed very near to the tip of the probe. The right (ipsilateral) tympanum was now at the centre, and the tip of the probe monitored the sound at its outer surface. In order to simplify the calculations, *at all frequencies 0° and 0 dB sound level are defined as the phase and amplitude of the sound at the outer surface of the right tympanum when the sound arrived from the frontal direction (the 0° direction, see Fig. 2). All other phase angles and sound levels were indicated relative to this reference.* In practice, this was achieved by dividing all sound spectra by the spectrum of the sound measured at the outer surface of the tympanum when sound arrived from the frontal direction. This was true both for the sound spectra measured at the outer surface of the tympanum at other directions of sound incidence and for the sound spectra measured at the contralateral tympanum and at the two thoracic spiracles.

In the measurements of diffraction, the loudspeaker was moved in 30° steps around the animal. In the first session, at each direction of sound incidence the sound spectrum was measured at the external surface of the tympanum, and the vibration velocity of the

tympanum was determined. In the following three sessions the cricket remained in the set-up with its right ear exactly at the centre of the round-about. The tip of the microphone was now moved, first to the contralateral tympanum and then to each of the two thoracic spiracles. Vibration data were obtained from 11 directions only, since the laser vibrometer occupied the 120° direction.

2. Transmission gains

The transmission gains from the contralateral tympanum and the two thoracic spiracles were measured as described by Michelsen et al. (1994). In brief, a local sound source was used for delivering sound at one of the auditory inputs, and walls of bees' wax between the auditory inputs ensured that the sound level at the other inputs was at least 20 dB down (this was confirmed by moving the probe microphone to the other inputs). We first determined the transfer function of the tympanum by applying sound at its outer surface. The transfer function is the tympanal velocity divided by the sound pressure; it has an amplitude and a phase part. We then determined the transfer function for each route to the inner surface of the tympanum, but this time the sound was measured at the input in question. This transfer function consists of the gain of the transmission path times the transfer function of the tympanum. The gains of the transmission paths could then be obtained by dividing these transfer functions with the transfer function of the tympanum.

It should be noticed that in determining the gains of the transmission paths we divided the respective transfer functions with the transfer function obtained with sound at the *outer* surface of the tympanum. By this procedure we added 180° to the phase angles of the transmission gains (remember that a surplus pressure forces the tympanum to move inwards when applied to the outer surface, but outwards when applied to the inner surface). In other words, although the sounds from the other auditory inputs really act at the *inner* surface of the tympanum, our phase angles correspond to these sounds acting at the *outer* surface. Since all sounds now act (virtually) on the outer surface of the tympanum, we can reduce the sounds to a total sound pressure at the outer surface, simply by adding the vectors representing the sounds.

Furthermore, we made the assumption that sounds acting at the outer surface of the tympanum cause the same vibrations as sounds acting at the inner surface. We do not know, whether this is true. If not, then the difference is included in the measured transmission gains. This uncertainty does not affect the calculations of directionality.

3. Calculation of directionality

The aim of this part of the study was to investigate whether the directional dependence of the four sound waves that reach the tympanum and add to provide a pressure proportional to the driving force can account for the directional dependence of the tympanal vibrations. For each direction of sound incidence and each sound input the amplitude and phase of the sound at the input (caused by diffraction and time delays) was multiplied by the transmission gain to give the amplitude and phase of the sound at the tympanum. The sounds were then added (see above), and the directional dependence of the resulting pressure was compared to that of the tympanal vibrations.

Results

During these experiments we collected data within the frequency range 2–25 kHz. From the data and our calculations it is obvious that the mechanisms responsible for directional hearing vary very much with frequency. A detailed discussion would cause the paper to increase to

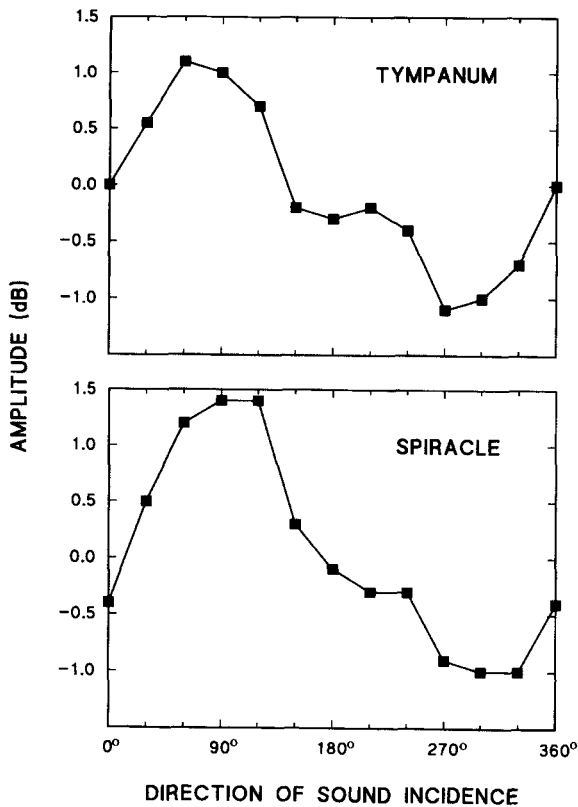


Fig. 3 Amplitude of sound pressure at the tympana and acoustic spiracles at 4.5 kHz, as a function of the angle of sound incidence. 0 dB is defined as the sound pressure at the external surface of the tympanum when sound arrives from the frontal direction (0°). The scale of sound angle is for the right side of the body (cf. Fig. 2B). For the left side, a mirror-image of Fig. 2B has to be used

an unacceptable size. The calling song of the cricket *Gryllus bimaculatus* is at 4.6–4.7 kHz, and we have therefore chosen to restrict the main description to the frequency range 4–5 kHz.

Diffraction and time delays

The presence of the body of the cricket in a sound field gives rise to some diffraction of the sound waves. At the frequency of the calling song the body is substantially smaller than the wavelength of sound (73 mm), and the change in sound amplitude is therefore moderate. Figure 3 shows the amplitude of sound at the tympana and thoracic spiracles as a function of sound incidence for a cricket standing on a plane substrate (see Fig. 2). Note that all values are indicated relative to the amplitude of sound at the ipsilateral (right) tympanum with sound coming from the frontal direction. The values plotted in Fig. 3 are for 4.5 kHz sounds, but only little change of amplitude is observed (and expected) when the sound frequency changes to 4 kHz or to 5 kHz.

According to Kleindienst (1978), the change of phase due to diffraction is also moderate (see Discussion and Fig. 13). However, the phase values of interest to calcu-

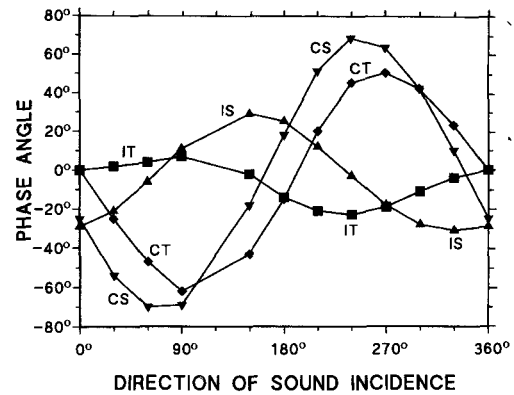


Fig. 4 Phase angles for 4.5 kHz sound at the four acoustic inputs. The phase includes the effects of diffraction and differences in the time of sound arrival. 0° is defined as the phase of the sound at the right (ipsilateral) tympanum when sound arrives from the frontal direction (0°)

lations of directionality of hearing are larger, since sound arrives at the four inputs at different times. In Fig. 4 is shown the combined effects of diffraction and time of arrival on the phase of sound at each input at 4.5 kHz. The reference (0°) is the phase at the ipsilateral (right) tympanum with sound coming from the frontal direction. The phase angles change somewhat with frequency, but the effects of a change to 4 kHz or 5 kHz are always below 12° . From Fig. 4 it is obvious that the sounds arriving at the tympanum from the two contralateral inputs (CS and CT) show much more variation of phase than does the sound from the ipsilateral spiracle (IS).

Transmission gains

The diffraction and time delays are determined by the size and external morphology of the body, and the values obtained from different individuals do not vary much. In contrast, we found a substantial inter-individual variation in the transmission gains. Furthermore, the cricket's auditory system is not always bilaterally symmetrical: substantial differences between the transmission gains and tympanal vibrations measured at the left and right side of the body are quite common.

For the transmission of sound from the *ipsilateral spiracle* (IS), the amplitude gain is close to 1 at low frequencies and increases to reach a maximum around 6–8 kHz and again at 17–19 kHz (Fig. 5). The phase changes almost 360° between 1 and 20 kHz. When interpreting the value of the phase angles one should keep in mind that 180° was added in the calculation of the gain function (see Methods). One therefore has to subtract 180° from the values in Fig. 5 in order to obtain the phase of sound at the inner surface. Per definition, the phase at the outer surface is 0° at all frequencies. As expected, at low frequencies the phase is close to 0° at the inner surface. With increasing frequency the sound at the inner surface gets progressively delayed (the phase becomes increasingly negative).

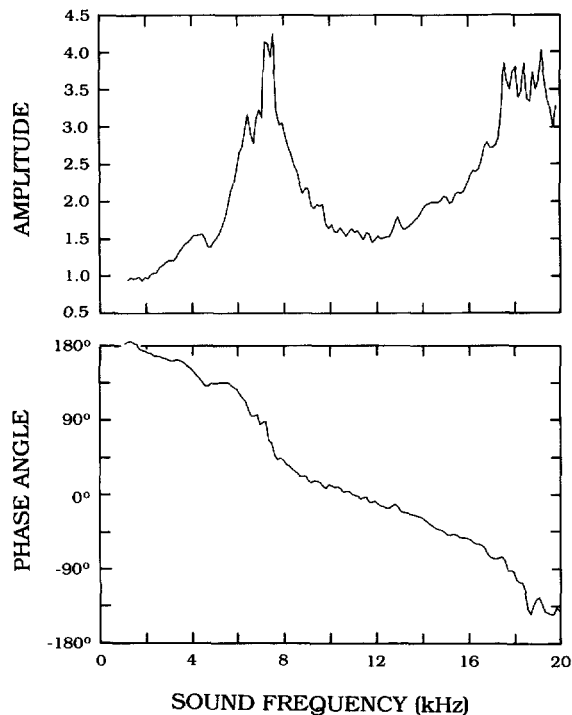


Fig. 5 Transmission gain for sound arriving at the tympanum from the ipsilateral spiracle (IS). Note that the amplitude is plotted in a linear scale (not dB). An amplitude of 1 and a phase angle of 180° indicate that the amplitude and phase have not changed during the transmission

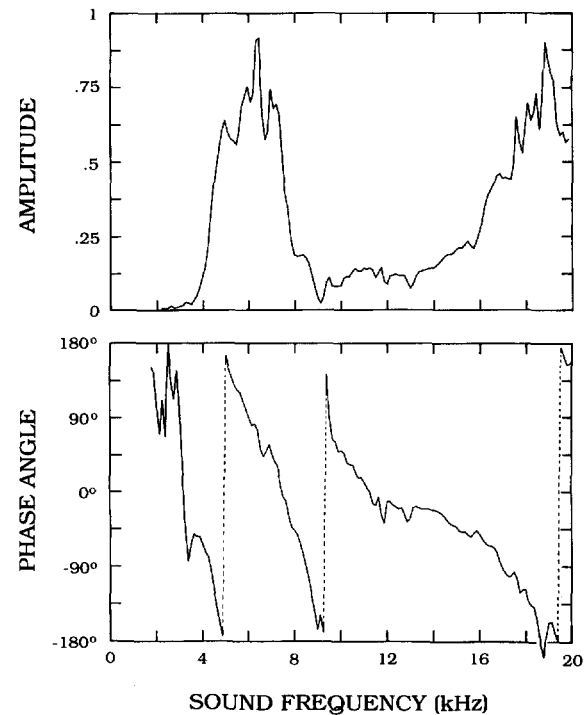


Fig. 6 Transmission gain for the sound arriving at the tympanum from the contralateral spiracle (CS). The phase curve is continuous, but has been cut at the position of the *broken lines* in order to save space. For further explanation see the legend to Fig. 5

The transmission of sound from the *contralateral spiracle* (CS) differs very much from this simple pattern (Fig. 6). The amplitude is at a maximum at 5–7 kHz and again around 18 kHz (much like the sound from IS), but it is virtually zero below 3.5 kHz. In the frequency range 4–5 kHz (around the frequency of the calling song) the amplitude of the sound from CS varies drastically with frequency. Between 4 and 4.5 kHz the amplitude increases by a factor of 4. In some animals the increase levels off above 4.5 kHz, whereas in others the steep slope continues up to 4.75 kHz. The average increase between 4.75 kHz and 5 kHz is only 10%. The strong frequency dependence of the amplitude is accompanied by a large change of phase. From 2 to 10 kHz the phase angle of the sound from CS decreases by approximately 800° (for comparison: the phase of the sound from IS shows a decrease of only 180°). Above 10 kHz the rate of decrease approaches that observed in the sound from IS.

The amplitude gains for sound transmitted from IS and CS in different animals vary in amplitude with a factor of 3 (at 4.5 kHz), and the IS-gains and CS-gains in different animals are positively correlated (Fig. 7). It remains to be learned whether the morphology and physical properties of the tracheal tubes show a similar inter-individual variation. The phase curves for the sound transmitted from IS are fairly similar in different animals. In contrast, large variations in phase were found in the sound from CS measured in different animals. This is

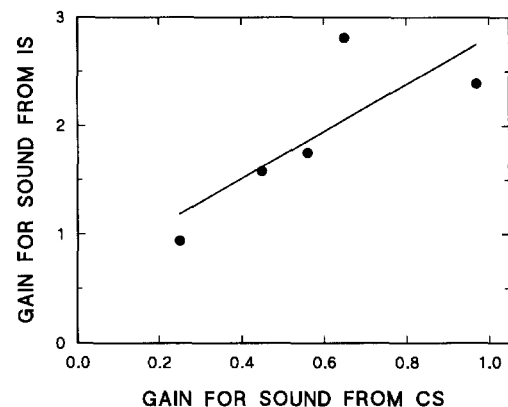


Fig. 7 Correlation between the amplitudes of the transmission gains from the ipsi- (IS) and contralateral (CS) spiracles at 4.5 kHz and 5 animals

not surprising: the drastic change of phase means that small variations in the frequency characteristics of the filter are accompanied by large differences in phase. The variation is especially large at frequencies close to 4.7 kHz, the frequency of the calling song.

The transmission from the *contralateral tympanum* (CT) follows the pattern observed in the transmission from CS. However, the amplitude of the sound arriving at the tympanum is considerably smaller, and the measured phase curves are thus more noisy (Fig. 8).

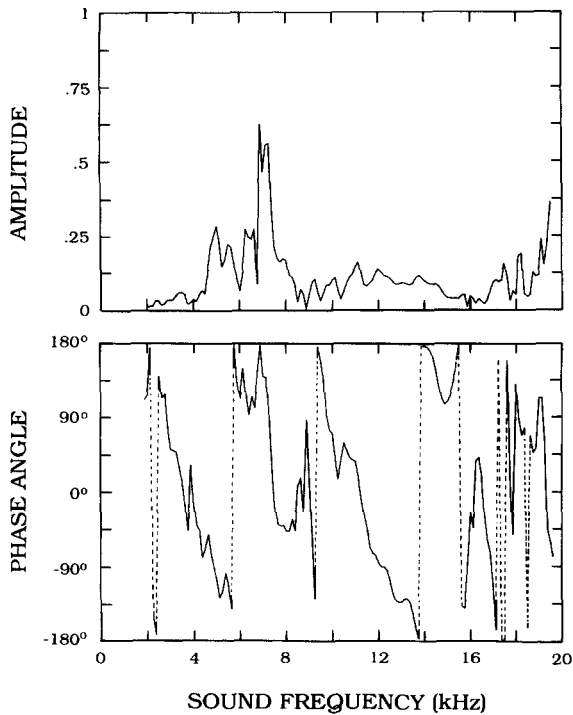


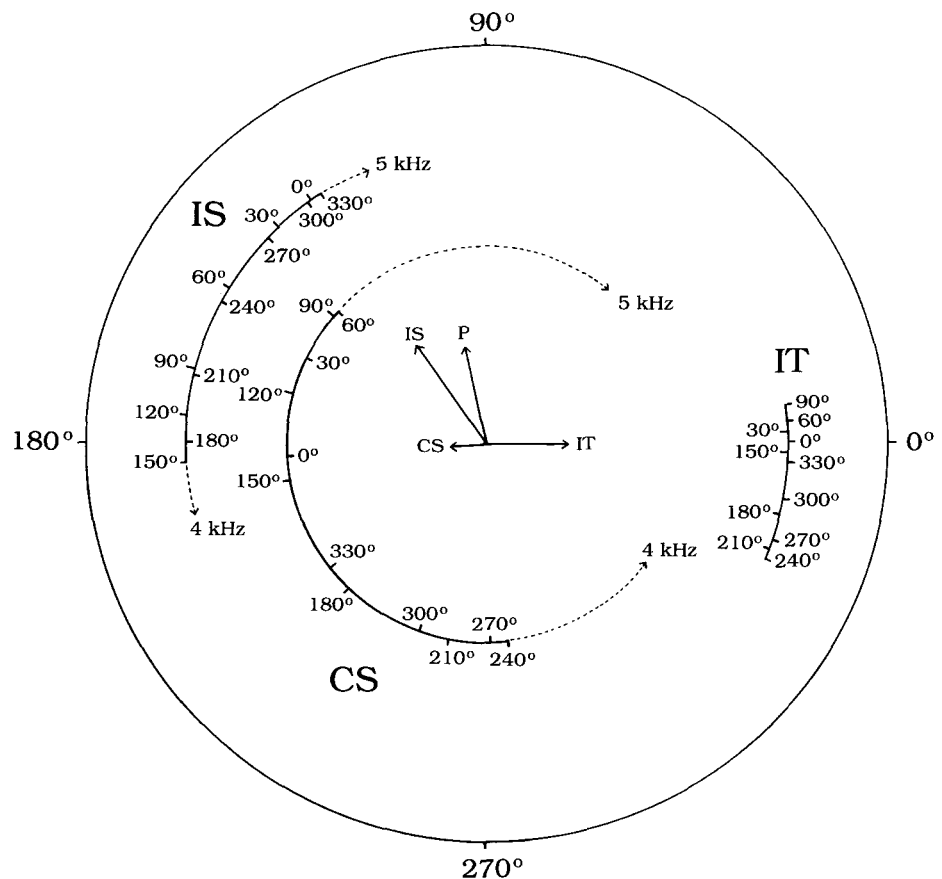
Fig. 8 Transmission gain for the sound arriving at the tympanum from the contralateral tympanum (ear). For explanation, see legends to Figs. 5 and 6

Calculated directionality

The measured diffraction, time delays and transmission gains of the four sounds acting on the tympanum can now be combined in an attempt to account for the dependence of the tympanal vibrations on the direction of sound incidence. The calculations are fairly straight-forward, but the large inter-individual variations (especially in the tracheal transmission gains) present a problem. We tried to get around this problem by collecting all the necessary data from a single animal, but found the scatter to be unacceptable. In the following, we have used averaged data for the diffraction and time delays (these data show only moderate scatter). For the transmission gains we have chosen “typical” values for the amplitudes and varied the phase values within the ranges observed in the experiments. In this way we have obtained an impression of how robust the directional patterns are.

The average amplitudes and phase angles for the sounds at the four sound inputs and at 4.5 kHz are shown in Figs. 3 and 4. At 4.5 kHz the amplitude of the sound from the contralateral tympanum (CT) is so small in most animals that it does not have much effect on the directional pattern, with the possible exception of the magnitude of the contralateral null. In these calculation we ignore the sound from CT. The problem is then reduced to three vectors: the sound at the external surface of the

Fig. 9 Polar plot of the phase angles of three sounds at the tympanum (indicated as if all the sounds were acting at the external surface) at 4.5 kHz and at various angles of sound incidence. The phase angles for the sound at the external surface of the (ipsilateral) tympanum (*IT*) are those from Fig. 4. The phase angles for the sounds from the ipsi- (*IS*) and contralateral (*CS*) spiracles are the sum of the values in Fig. 4 and the phase angles for the transmission (Figs. 5 and 6). The vector diagram at the centre of the figure shows the situation with sound from the forward (0°) direction. *P* is the sum of the three other vectors



tympanum (IT) and the sounds at the inner surface arriving from the ipsilateral and contralateral spiracles, respectively (IS and CS).

The amplitude and phase of IT for sounds arriving from the frontal direction are, as a matter of definition, 1 and 0°. At 4.5 kHz, a typical value of the gain of the sound from IS is 1.5, and at this value one expects the gain from CS to be 0.44 (cf. Fig. 7). The average phase angles of their transmission gains are 147° and 246°, respectively. By adding the three vectors, sound components acting on the internal surface (IS and CS) are subtracted from the sound component acting at the external surface (IT), since the IS and CS were phase-shifted 180° when they were measured (see Methods). The sum of the three vectors can be thought of as a sound pressure (P) which is acting at the external surface and is proportional to the force that causes the tympanum to vibrate.

We shall first present a combination of values, selected within the observed range of variation, which produces a “nice” directional pattern (the phase angles 154° and 208° for the sounds from IS and CS, respectively). In order to represent the three sounds as vectors it is convenient to plot the phase angles in a polar diagram. In Fig. 9 the phase angles of the transmission gains have been added to the phase angles in Fig. 4. The three full lines show the phase angle of each vector at the 12 different directions of sound incidence. The phase angle of the sound at the external surface (IT) is seen to vary between +7° and -23° (as in Fig. 4). The phase angles of the sounds from IS and CS vary between 123° and 183° and between 137° and 276°, respectively. At the centre

of the figure, the three vectors and their sum (P) are shown for 0° (frontal) sound direction. The lengths of the three vectors at each angle of sound incidence are determined by multiplying the gain amplitudes (here 1, 1.5 and 0.44) with the relative amplitudes of the sounds at the respective inputs (Fig. 3).

The result of this model calculation is shown in Fig. 10. The directional pattern at the centre is surrounded by the 12 vector diagrams (similar to that at the centre of Fig. 9). The calculated directional pattern has the most important of the features seen in the measured patterns reported in the literature: The driving force is at a maximum at the ipsilateral directions 30° and 60°; the force decreases by approximately 5 dB from 30°, through 0° to 330°; and the force is at a minimum at 270° (contralateral sound). The minimum is 15 dB below the value in the frontal direction (0°).

From the vector diagrams for the three forward directions of sound incidence (330°–0°–30°) it can be seen that the slope of driving force in the forward direction is caused almost entirely by changes of the phase angle of the sound from CS. In contrast, the contralateral minimum is caused mainly by changes of the phase angle for the sound from IS. At the minimum the sum (P) is almost in phase with the sound from IS. A deeper minimum (more perfect null) would therefore only require a slight reduction in the amplitude of the sound from IS. As mentioned, the amplitudes of the transmission gains for the sounds from IS and CS vary very much and in proportion in different animals (Fig. 7), whereas the amplitude of the external sound (IT) varies only little. Ob-

Fig. 10 Directional pattern at 4.5 kHz for driving force (or tympanal vibration amplitude) calculated from the sound at the external surface of the tympanum (IT) and the sounds transmitted from the ipsi- (IS) and contralateral (CS) spiracles. The sound from the contralateral tympanum has been ignored. The phase angles of the three sounds are those in Fig. 9. The amplitudes of the three vectors are those of Fig. 3 times (for IS and CS) the amplitude of the transmission gains which have been chosen to be 1.5 and 0.44, respectively (cf. Fig. 7). Note the role of the sound from CS in shaping the directional pattern in the forward directions (around 0°), and that of the sound from IS at the contralateral directions (around 270°)

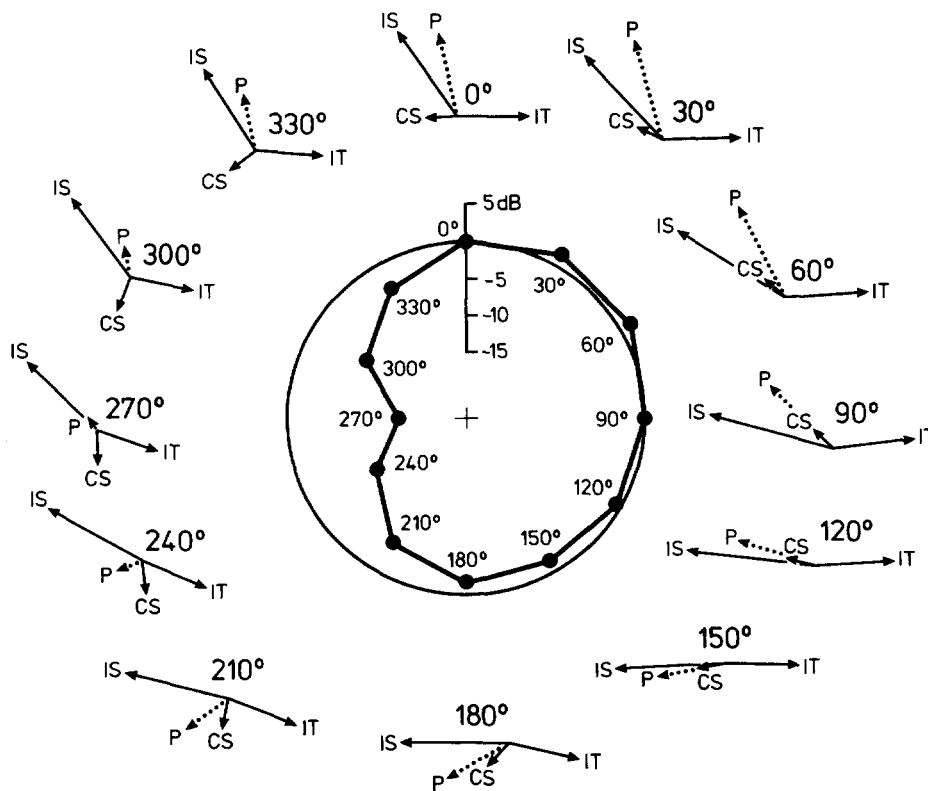
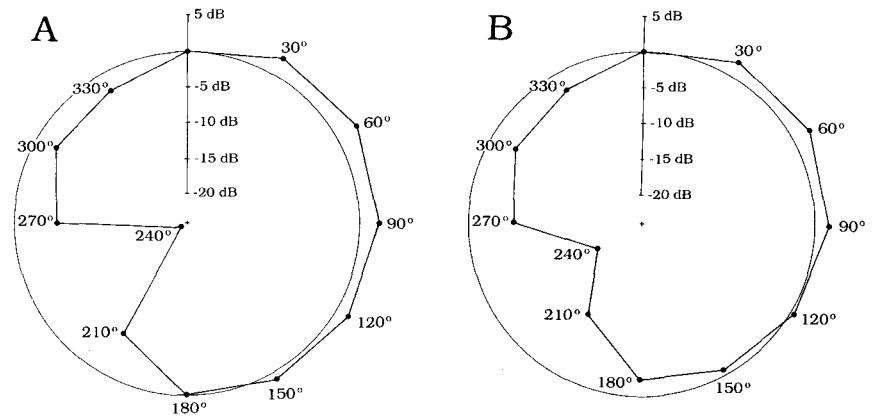


Fig. 11A,B Directional patterns for driving force (or tympanal vibration amplitude) calculated like that in Fig. 10. **A** 50° has been added to the phase of the sound from the contralateral spiracle (CS) in order to explore the effect of varying this parameter within the range observed in the experiments. **B** The phase angles for CS and IS (the sound from the ipsilateral spiracle) chosen as the average of the measured values



viously, a deep minimum can only be obtained if the amplitudes of the sounds from IS and CS match that of IT.

The largest variation in the measured data was observed in the phase angle of the transmission gain for the sound from CS (and CT). Values other than those used in the calculation of Fig. 10 would cause a rotation of the range of phase angles for CS in Fig. 9. The phase angle chosen for CS was 208°, which is at the lower end of the range observed in different animals (202°–284°). Changing the phase to, for example, 258° (a 50° counterclockwise rotation) leads to the directional pattern shown in Fig. 11A. The minimum has become deeper and has moved to the 240° sound direction, but not much has happened to the slope of the driving force in the forward directions (the difference between the amplitudes at 330° and 30° is 5.2 dB in both Fig. 10 and Fig. 11A).

The directional pattern calculated by using the average values for the phase angles of the sounds from IS and CS (Fig. 11B) also has its minimum at a sound direction of 240°, and the slope in the forward direction is almost the same as in the two previous cases (4.9 dB difference between the amplitudes at 330° and 30°).

Several other directional patterns have been calculated. With the values for 4.5 kHz mentioned, a clockwise rotation of the phase angles for the sound from CS causes the minimum to move towards 270°, whereas a counterclockwise rotation causes the minimum to move towards 180°. This is the change expected when the sound frequency decreases towards 4 kHz.

An increase of frequency should cause a clockwise rotation of the phase angles for the sounds from IS and CS, but above 4.5 kHz it is no longer realistic to leave out the sound from the contralateral tympanum (CT). Several calculations considering all four sound inputs have shown, however, that the minimum still moves forward with increasing frequency, and it may even reach 300°.

Despite these variations in the position of the minimum, the slope of driving force in the forward directions remained large and robust within reasonable variations in the parameters used in the calculations. Only in a few cases where very extreme parameters were used did the slope decline below a 4–5 dB difference between the amplitudes in the 30° and 330° directions of sound incidence. Therefore, the variations in the transmission gains

and directional patterns do not seem to have any important effects on the ability of the animals to locate singing crickets in the forward direction.

Observed directionality

The calculated directional patterns of driving force may be compared with the directional patterns for the tympanal vibration measured during the study of diffraction and time delays. The measured patterns at 4–5 kHz included nice “textbook-patterns” in which a deep null occurs at 270° sound direction (Fig. 12A), but other shapes also occurred. In the previous section it was described that the position of the minimum (of the force causing the tympanum to vibrate) tends to move backwards with decreasing frequency and forwards with increasing frequency. The same trend was observed in the measured patterns from single animals (Figs. 12 B & C are examples), but also the directional patterns observed at a given frequency varied considerably in different animals. For example, at 4.5 kHz some animals have the minimum at 300°, some at 270°, and some at 240°.

The measured directional patterns thus showed a considerable variation, but the slope of amplitude in the forward direction was as consistent as in the calculated patterns. The vibration amplitude at 30° sound direction was always approximately 2 dB above that at 0°. Around 4.5 kHz the amplitude at 330° was generally 5–6 dB below that at 0°, but larger differences were also observed. The slope of amplitude in the forward directions was less prominent at 4 and 5 kHz than at 4.5 kHz.

In summary, despite the large variations in the shapes of the measured and calculated directional patterns, the biologically important forward slope was very consistent. Furthermore, the same tendency for the position of the minimum to move with frequency was observed in both measured and calculated patterns. Although not enough animals were included in the experimental part of this study to allow us to detect systematic differences between experimental and calculated results, we conclude that the measured data on transmission, diffraction and time delays can account for the most prominent features of the directivity.

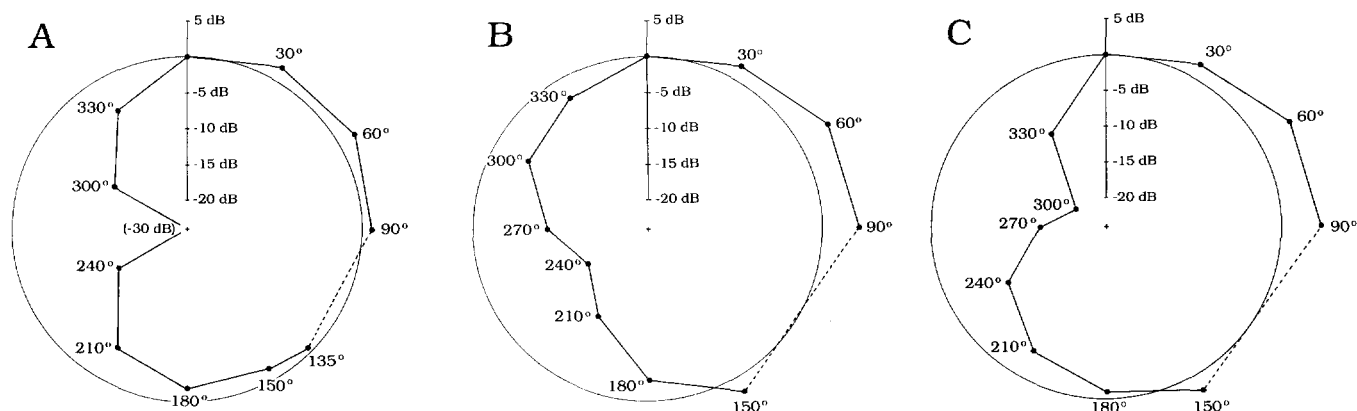


Fig. 12A–C Some observed directional patterns for tympanal vibration amplitude. **A** Directional pattern in which a deep (–30 dB) null is found at 4.5 kHz at the contralateral (270°) direction of sound incidence. **B,C** Directional patterns measured in another animal at 4.25 kHz and 4.75 kHz, respectively. Note how the position of the minimum moves with frequency. For all three patterns, note how stable the pattern is in the forward directions (330° to 30°)

Discussion

In 1940, H. Autrum proposed that the ears of small animals may derive their sensitivity to the angle of sound incidence (directionality) by working as pressure gradient (difference) receivers, that is, by sound propagating both to the external and internal surfaces of the tympanal membrane. The idea was not generally accepted by the scientific community before the 1960's, when several investigators started to search for possible anatomical pathways and for evidence of sound transmission to the inner surface of the tympanum. Unfortunately, not much theoretical work was done to specify the conditions that would lead to directionality.

The mere fact that sound waves can propagate both to the external and internal surfaces of a tympanal membrane does not automatically cause the system to become very sensitive to the direction of sound. Two conditions have to be fulfilled: the direction of sound must have a substantial effect on the amplitude and/or phase of (at least one of) the sounds reaching the tympanum, and the amplitude and phase relationships of the sounds have to be such that the directionality is still present when the sounds have been added at the tympanum.

In the cricket, these conditions are fulfilled around the frequency of the calling song, but not necessarily at other frequencies (a tuning of phonotaxis to frequencies around the calling song has been reported by Hill (1974), Popov et al. (1975), Boyd and Lewis (1983) and others). In other cases, the sound amplitude at the external and internal surface of the tympanum may not match. This is true in many birds where the amplitude of the sound arriving at the inner surface of the tympanum is too small to enhance binaural cues significantly (Klump and Larsen 1992). The opposite situation is found in many bushcrickets, where the directionality is determined al-

most entirely by the large internal sound pressure (Michelsen et al. 1994). An especially interesting situation is found in the cricket at frequencies where the amplitudes match, but the phase relationships are unfavourable (see the section Directionality, below).

A large number of investigators, including ourselves, have tried to obtain evidence for the magnitude of sound transmission to the inner surface of the tympanum by blocking possible sound inputs and observing the effects on the ear. This is a dubious strategy, since blocking may affect not only the sound transmission, but also the mechanics of the ear (by changing the radiation impedance of the tympanum, see Michelsen et al. 1994). A change of membrane impedance was in fact observed when we blocked the ipsilateral spiracle while measuring the tympanal vibrations caused by sound at the external surface of the tympanum. With the blocking approach the investigator is therefore trying to solve one equation with two variables. In the cricket, this popular approach would thus lead to quite misleading conclusions.

Diffraction

The data from our measurements confirm the findings of Kleindienst (1978, reproduced as Fig. 13): At 4–5 kHz the presence of the cricket in the sound field causes the amplitude of the sound at the tympana and thoracic spiracles to deviate by up to 1–2 dB from the values of the undistorted field. The change of phase is up to 10–20° at the tympana, and up to 20–30° at the thoracic spiracles. The amplitude tends to be enhanced and the phase advanced relative to the undistorted field at the side of the body facing the sound source, whereas the opposite trends are found at the other side of the body. The changes are close to a minimum for sounds arriving from the front and back of the cricket.

Kleindienst plotted his data as changes relative to the values in the undistorted sound field. Although scientifically correct, these plots are not useful for calculations of the directionality of the cricket ear. In the plots of our data (Figs. 3 and 4) we have chosen a reference that is more suited for our purpose: the amplitude and phase of the sound pressure at the external surface of the right (ipsilateral) tympanum when sound arrives from the frontal

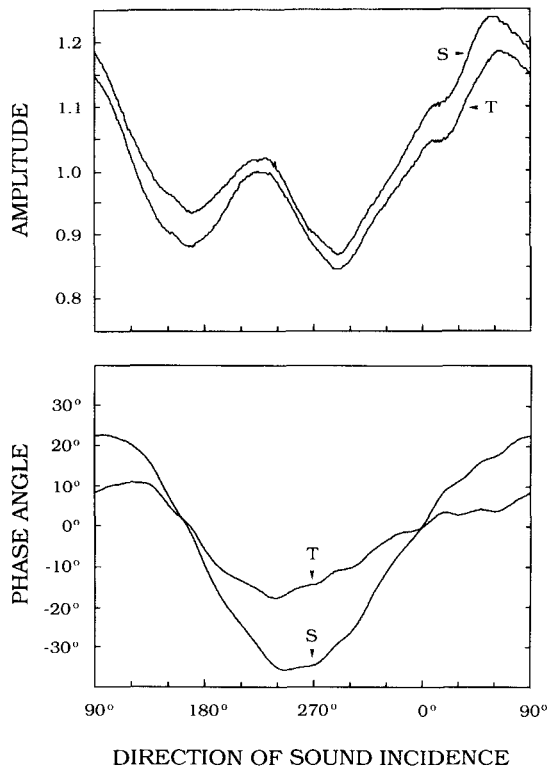


Fig. 13 Diffraction data obtained by Kleindienst (1978). The figure shows how much the amplitude (above, linear scale) and phase (below) at the ipsilateral tympanum (T) and spiracle (S) of a cricket on a flat, rigid substrate deviate at 5 kHz from the values in the undistorted sound field (i.e., without the cricket). The figure is a mirror image of the original, and the indication of direction has been changed to the system used in this paper

direction. The plot of amplitude (Fig. 3) is very close to that of Kleindienst (because the amplitude at the tympanum for frontal sound is almost the same as that in the undistorted field). In contrast, because of the different references our phase values (Fig. 4) deviate very much from those reported by Kleindienst. Our values represent the sum of two processes: the change of phase due to diffraction (cf. Fig. 13) and the change of phase due to the distance from the (ipsilateral) tympanum to the sound input in question (Fig. 1B). Only in the case of the ipsilateral tympanum itself does our plot correspond to that of Kleindienst.

Transmission gains

A brief look at the amplitude parts of the transmission gains for the sounds from the ipsilateral spiracle (IS) and the contralateral spiracle (CS) may provide an impression of similarity (Figs. 5 and 6). Both are at a maximum at 5–8 kHz and again at 18–20 kHz. A more detailed inspection reveals, however, that the low-frequency maximum for the sound from CS occurs at a lower frequency

(ca. 6 kHz) than that of the sound from IS (ca. 8 kHz). Furthermore, the amplitude of the sound from IS increases smoothly from a value of 1 at low frequencies, whereas that from CS increases abruptly from virtually zero. The rate of increase (ca. 48 dB/kHz) is surprising in a mechanical system.

The very different phase curves support the notion that these maxima are produced by widely different mechanisms. The phase curve for the sound from IS (Fig. 5) is not far from being a straight line, which is the phase curve expected in a transmission line where the propagation of sound takes a certain time. By assuming a sound propagation velocity of 344 m/s the length of the tracheal tube can be calculated. The result (15.6 mm) is significantly larger than the actual length (ca. 12 mm). This means that the sound propagates with a lower velocity inside the tube than in the air outside the animal. The propagation velocity estimated from our data is 264 m/s. This value is in excellent agreement with that determined by Larsen (1981) who found a value of 263 ± 29 m/s by measuring the delays of very short impulse sounds. He pointed out that the determined value is rather close to that expected for isothermal wave propagation in air (245 m/s), and he suggested that an exchange of heat may occur at the tracheal walls.

Above 10 kHz the change of phase of the sound from CS is not very different from that observed in the sound from IS and probably caused by the propagation in the tracheal tubes. In contrast, a transmission line with a length of no less than 58 mm (at a velocity of 264 m/s) would be required in order to account for the ca. 800° change of phase between 2 and 10 kHz. Most of this phase change must therefore be caused by the band-pass filter responsible for the changes in amplitude.

Preliminary observations suggest that at least two mechanisms may contribute to the high-pass part of the filter at 4–5 kHz. The slope decreases to approximately 18 dB/octave, if the ipsilateral spiracle is closed. A perforation of the central membrane at the middle of the trachea connecting the two acoustic tracheae then abolishes the high-pass filter (so that low frequency sounds are transmitted with a gain of 1). Further studies are needed in order to elucidate the physical mechanism(s) responsible for these observations.

The central membrane has been suspected to play a role in directional hearing (Hill and Boyan 1976) and to cause a delay of the sounds transmitted from the contralateral side (Larsen 1981). Recent observations by Wendler and Löhle (1993) have shown that the directional patterns of the ears change and the animal's sound localization becomes less precise when the central membrane is perforated. The change of the directional pattern involves a halving of both the ipsi-contra sensitivity difference (from 15 to 7–8 dB) and the sensitivity slope in the forward direction (from 6 dB to 3 dB difference between the sensitivities at 30° and 330°). Again, further studies on the biophysics involved would be interesting.

Directionality

The cues available for determining the direction of sound incidence can be illustrated by considering hypothetical animals, in which the ears have different properties. Let us begin with a cricket, in which the ears are simple pressure receivers, responding only to the pressure at the external surface of the tympanum. From Fig. 3 it is obvious that the amplitude of the sound pressure at the external surface of the tympanum changes only little with the direction of sound incidence. In the frontal directions (around 0°), which are of prime interest with respect to localization of a sound source, a change of 30° in sound direction would cause the forces driving the two ears to differ by only 1.3 dB (compare the values at 30° and 330°). This difference may be sufficient for a cricket locating a sound source in a very uniform sound field in the laboratory, but not in the field where the sound field is generally not very uniform.

A pressure difference receiver is obviously needed for providing more directionality, but from which input should the sound at the inner surface of the tympanum originate? Let us consider a cricket in which the sound at the inner surface comes exclusively from the ipsilateral spiracle (IS). Furthermore, let us make the favourable assumption that the sound amplitude at the two surfaces are almost equal in amplitude. From Fig. 3 we find that, although the amplitudes do change as a function of sound direction, the changes are in the same direction (compare the sound amplitudes at the tympanum and spiracle at 0° , 30° , and 330°). Obviously, the amplitude cue is even smaller than in the case of the two pressure receivers. The phase cue (Fig. 4) follows a similar pattern: the phase angles increase at both inputs when the sound direction changes from 0° to 30° and decrease from 0° to 330° . The difference in phase between the sounds at the inner and outer surfaces of the tympanum change by only 5° and 2° , respectively. Such small phase changes can cause a directional dependence of the tympanal vibration, but only if the phase is almost the same at the two sides. This is the case close to a null (like the contralateral minimum), but this is not the situation here. In conclusion, *pressure difference receivers, even when well balanced with respect to sound pressure, do not always provide a useful directionality!*

The sounds arriving from the two contralateral inputs are obviously much better potential contributors of directional cues. Both the amplitude (Fig. 3) and the phase (Fig. 4) of the contralateral sounds change in opposite directions to the values for the ipsilateral sounds when the sound source moves from one frontal direction to another. The change of phase is the largest contributor to the directionality of the ear. This study has confirmed the prominent role of the sound from the contralateral spiracle (CS) for determining the directionality of the ear in the forward directions. The sound from the ipsilateral spiracle (IS) is necessary, however, for producing the cardioid pattern. A pressure difference receiver with only

the external sound and the sound from CS would not provide any useful directionality in the forward directions.

The sound from the contralateral tympanum (CT) is also potentially useful, but at frequencies below 4.5 kHz its amplitude is generally too small to allow it to play an important role, except in the contralateral direction of sound incidence (270°) where the effects of the three other sounds tend to cancel. In this situation, the effect of the sound from CT may appear substantial. This is perhaps the reason for earlier reports of large effects on the sensitivity of the ear of blocking the contralateral tympanum (Hill and Boyan 1976). Above 4.5 kHz and in some (but not in all) animals the amplitude of the sound from CT increases to a level comparable with that of the external sound pressure (IT), and the sound from CT can no longer be ignored.

We have found that substantial differences between the transmission gains and tympanal vibrations measured at the left and right side of the body are quite common. Such asymmetries have also been observed in the nervous system (Boyan 1979) and in behavioural experiments (Hoy and Paul 1973).

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