

Chapter 19

Directional Hearing in Insects and Other Small Animals: The Physics of Pressure-Difference Receiving Ears

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19.1 Introduction

Animals may use several strategies for determining the direction to sound sources. Animals that are large relative to the wavelengths of the sounds of interest may base their directional hearing on variations of sound pressure at the ears caused by diffraction of sound by the body. Most mammals and birds can also exploit the differences in the time of arrival of the sounds at the ears. This is not so, however, for the majority of the hearing animals. Most insects live in dense vegetation, which filters away high-frequency sounds, and their bodies are often smaller than the wavelengths of the sounds of interest. In addition, the brains of insects cannot exploit the minute differences in the time of arrival of sound at their ears. For many years it has been suspected that their directional hearing could be based on a directional sensitivity of the ears, caused by sound reception at both the external and internal surfaces of the eardrums. We now know that this is actually so, and that pressure-difference reception also is common in several groups of vertebrates.

This chapter outlines the methods used in this branch of auditory research: Very accurate measurements of ears in animals situated in very homogeneous sounds fields and interpretation of the data by means of mathematical models of the physics of sound transmission from ear to ear. We have chosen a few examples from our own research (bushcrickets, grasshoppers, birds, and crickets) for illustrating the methods and some of the variations in the animals' strategies.

This research has been made possible by the contributions during 200 years from scientists and engineers in four different areas: anatomy, acoustics, instrumentation, and computing. During the 19th century, a few scientists such as Müller (1826) described the detailed anatomy of most of the insect ears that are known today. Some of these pioneers had an admirable capacity for hard work and published up to one printed page per day, year after year.

In the last part of the 19th century the field of acoustics was transformed into an exact science by Lord Rayleigh and others. However, the experimental biologists had to wait until the middle of the 20th century before they could exploit the methods of electrophysiology for measuring the output of ears. Simultaneously, a few scientists had speculated about the physics of hearing in insects. In 1940 two very different ideas were published by R. J. Pumphrey (1940) and by H. Autrum (1940), who wrote in English and German, respectively. The war and the following years witnessed a shift of the balance between English and German as the dominant language of science. It was therefore many years before the views of Autrum (that the directionality of insect ears could be accounted for if the ears worked like the pressure gradient receivers studied by Harry Olson in the 1930s) were accepted. Pumphrey's view (that the delicate insect ears follow the movements of the air particles) is now known to be correct only for the sensory hairs on the bodies of insects.

A major reason for the progress made in biological acoustics during the careers of the two of us is the technological development. In the beginning of the 1960s, nerve impulses were displayed on an oscilloscope screen and filmed. The film was developed, and the spikes were counted by the investigator. One of us (A. M.)

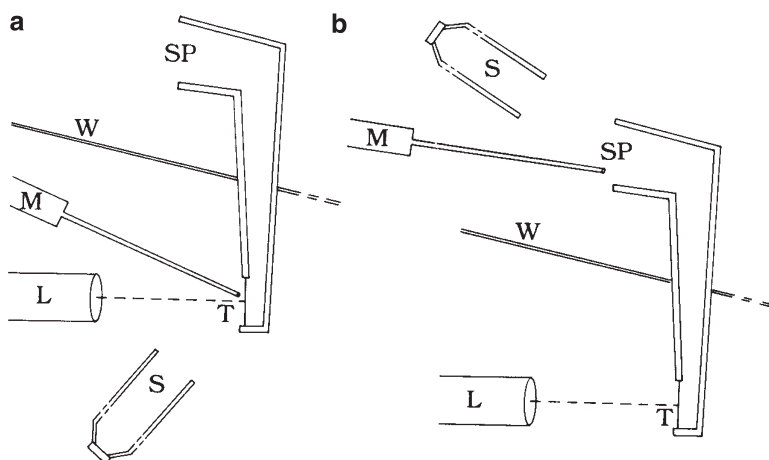


Fig. 19.1 Method for measuring the gain of a transmission path to the inner surface of an eardrum (tympanum T, here in a bushcricket). (a) The eardrum is calibrated with sound acting on its outer surface. (b) The calibrated eardrum is used for measuring the sound acting on the inner surface of the eardrum. Further explanations in the text. (From Michelsen et al., 1994a)

actually counted more than one million spikes when earning his doctorate! During the following decades, computers took over most of the trivial work and also made complex calculations like Fourier transformations a practical tool. Work on hearing and sound emission in small animals was eased by the invention of precision microphones with excellent long-term stability and diameters from 3 mm and up. An even higher spatial resolution of sound fields could now be obtained by means of probe microphones with probe diameters of only 1 mm and a long distance (e.g., 20 cm) from the tip to the bulky microphone.

Several very productive research groups took advantage of the new possibilities. In 1989, three leaders in the study of cricket biology published a book, in which the major themes of the behavior and neurobiology were covered by specialists. We contributed a chapter about sound reception (Larsen et al., 1989), in which the part about directional hearing was more descriptive than analytical. It was based on several attempts from 1978 to 1984 to understand the reasons for the directivity of the ears of crickets and bushcrickets. Such attempts showed, for instance, that the eardrum does indeed respond to the vectorial difference between external and internal sound pressures and that eardrum motion is a necessary part of the sensory transduction process and that it correlates strongly with ear directionality (Kleindienst et al., 1983; Larsen et al., 1984). However, we gave up further analysis when we realized that in order to arrive at a *real* understanding of the system, it was necessary for us to measure the sound pressure acting on the inner surface of the eardrum but no microphone could possibly do the job.

Approximately 10 years later during a shower early in the morning it suddenly occurred to A. M. what we should do. Figure 19.1 shows how one can measure the

gain of a horn-shaped trachea connecting the surface of the thorax with the inner surface of an eardrum in a foreleg of a bushcricket (*Poecilimon laevis*, Tettigoniidae). The gain of the horn-shaped trachea is the change of the amplitude and phase angle of the sound from the spiracular entrance of the tracheal system (SP) to the inner surface of the eardrum. The laser vibrometer (L) measures the vibrations of a small hollow, silver coated glass sphere (weight 0.5 ng, diameter 10 μm) placed on the eardrum (tympanum, T), which is set in motion by sound from a loudspeaker (S), while a probe microphone (M) records the local sound pressure at the outer surface of the eardrum (Fig. 19.1a). The next step is to measure the vibration spectrum when the eardrum is driven by sound reaching mainly its inner surface as a wall of beeswax (W) attenuates the sound between the two inputs (Fig. 19.1b). The ratio between the two recorded vibrations is then a measure of the gain of the horn-shaped spiracle and trachea guiding sound to the inner surface of the eardrum.

Why do the bushcrickets need a horn-shaped trachea to guide sound to their ears? Most ears seem to have evolved from existing sense organs, which were not always located at the most favorable position from an acoustical point of view. The ears of bushcrickets and crickets are located at the middle of their long and slender forelegs. This is not an ideal position for directional hearing, as the ears are located too far away to exploit the diffraction of sound by the main body. The “hearing trumpets” open at the lateral sides of the bushcricket body and guide the sounds to the inner surface of the eardrums in the legs. In many bushcrickets the hearing trumpets are horn-shaped and have a gain of 5–10 times. The sound acting on the outer surface of the eardrum therefore is much less intense than that acting on the inner surface and not a significant input to the ear. With respect to directional hearing, the ears are therefore in the same situation as if they had been located at the lateral surfaces of the body. One could say that the bushcrickets have built-in hearing aids!

19.2 Pressure-Difference Receivers

Most small animals cannot process the tiny differences in time, which are one of our cues for determining the direction to sound emitters. However, the ears may become sensitive to direction if the sound waves can reach both surfaces of the eardrums. Such sound transmitting pathways inside the heads or bodies are known in several insect groups and in frogs, reptiles, birds, and even some mammals, potentially coupling the two ears acting as reciprocal pressure-difference receivers (Köpl, 2009). In most cases, some experimental evidence supports the notion that the ears function as pressure-difference receivers and provide information about the direction of sound waves. Most studies in vertebrates have been performed with recordings of neural responses. A physical analysis has so far been carried out in some lizards (Christensen-Dalsgaard & Manley, 2008), bushcrickets, grasshoppers, crickets, budgerigars, and barn owls.

The existence of an anatomical air space leading to the inner surface of an eardrum from openings on the body surface or from the contralateral eardrum and

middle ear is a necessary prerequisite, but it does not automatically create a pressure-difference receiver with a useful directionality. The sound has to arrive at the inner surface of the eardrum with a proper amplitude and phase relative to that acting on the outer surface. In addition, the sound propagating through a sound guide inside the animal (an interaural canal) should be affected in a suitable manner by the direction from which the sound reaches the outer surface of the animal. The mere presence of an air-filled interaural pathway does not necessarily mean that the ear functions as a directional pressure-difference receiver in the relevant frequency range. This is seen, for instance in the barn owl, which possesses a substantial interaural canal and can locate sound emitting prey in total darkness with remarkable precision, yet the ears are functionally uncoupled in the frequency range relevant for prey localization (Moiseff & Konishi, 1981). One complicating factor in the analysis is that the sound arriving at the inner surface may have entered the body through several auditory inputs (e.g., through the other ear and through two spiracles in crickets; through the other ear and through the lungs in frogs).

The air-filled cavities leading to the inner surface of the eardrum are often a part of (or connected to) the respiratory pathways. This may have undesirable consequences since the large pressure fluctuations during respiration may affect the mechanics of the eardrums. In grasshoppers the eardrums (tympana) may be displaced outside their linear range (so that Hooke's law is no longer obeyed). This may affect the threshold for hearing and distort the frequency analysis (Michelsen et al., 1990). Large displacements coupled with the respiration can also be observed in frogs (in which the middle ear cavity and the mouth are connected through a wide Eustachian tube). Obviously, a reduction of such effects (at the expense of the directionality) may have been an important factor in the evolution of pressure-difference receivers. The air-filled spongy bone connecting the middle ears in birds and moles, and the middle-ear systems that are open to the buccal cavity in reptiles may be examples of this.

In the following, we present a few examples of pressure-difference receiving ears that we have analyzed. We start with two examples of ears with only two acoustical inputs (grasshoppers and budgerigars), and then consider the more complicated situation in crickets, where each ear receives sounds from four acoustical inputs.

19.2.1 Grasshoppers

Grasshoppers (Acrididae) have an ear at each side of the first abdominal segment. A sclerotized ring encircles an eardrum, to which 60–80 receptor cells attach in four groups, each having a different frequency preference. Between the ears are air-filled tracheal sacs, through which sound can propagate from one ear to the other. The physics of the pressure-difference receiver has been examined in locusts (*Schistocerca gregaria*) and in a three to four times smaller grasshopper (*Chorthippus biguttulus*) (Michelsen & Rohrseitz, 1995).

The locusts are 5–6 cm long and about 1 cm wide at the position of the ears. Above 8 kHz most of their directional hearing can be based on diffraction of sound

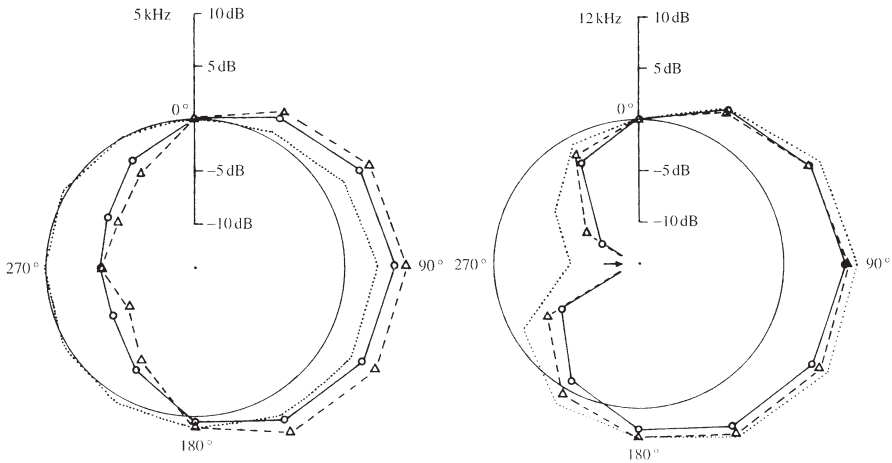


Fig. 19.2 Directional patterns at 5 kHz and 12 kHz for the right ear of the locust. Dotted lines: amplitude of sound pressure at the external surface of the eardrum. Solid lines with circles and dashed lines with triangles: Observed and calculated vibration velocity of the eardrum, respectively. (From Michelsen & Rohrseitz, 1995)

by the body, as the sound arriving from the other ear and acting on the inside of the eardrum is only 20–30% of the sound pressure acting at the outside of the eardrum. In contrast, below 8 kHz the amplitude of the sound from the other ear is about 50% of the sound acting on the outer surface of the eardrum. The duration of the sound propagation from one eardrum to the other can be estimated from the change of phase. The results suggest that the propagation velocity through the air sacs is less than in free space. A similar trend has also been found in other insects.

The directional diagrams for the locust at 5 and 12 kHz are shown in Fig. 19.2. The agreement between the calculated directional dependence and the actual values (measured with laser vibrometry) suggest that a two-input model is a valid description of the acoustics of the single ear, both at 5 kHz and at 12 kHz. There is therefore no reason to believe that sounds arriving at the internal surface of the eardrum through other routes should play a significant role.

From Fig. 19.2 it is obvious that the sound transmission from ear to ear is essential at 5 kHz, whereas at 12 kHz it only slightly improves the left–right gradient in the forward direction (when the animal turns so that the direction to the sound source changes from 330° to 30° or vice versa). The small grasshopper is much more dependent on the transmission of sound from ear to ear, and from 3 to 18 kHz the amplitude of the sound transmitted to the inner surface of the eardrum is 60–80% of the amplitude acting on the outer surface. In theory, the locust should be able to move directly toward targets singing either at low or high frequencies. In contrast, the small grasshopper has a clear gradient in eardrum vibration only at high frequencies. In ideal sound fields the directional hearing of small grasshoppers should thus improve with frequency. This prediction may not be true in natural habitats, where the presence of soil and vegetation may cause a substantial degradation of the directional cues.

Very careful studies of the strategies for grasshopper phonotaxis performed by the late Dagmar von Helversen (review 1997) demonstrated that the small grasshopper makes use of a very specific strategy for locating a conspecific sound source. Males searching for females sing at regular intervals, and the females respond, but it is up to the male to take the risk of approaching. When it hears a female, the male turns abruptly toward the side from which her signal arrives, moves forward, and sings again. The turning angle is usually larger than that needed to bring the female into the male's frontal auditory field, and the behavior thus results in a zigzag course. The female sings for about 1 s, and the male may therefore obtain closed-loop directional information during the turn. If the turn brings the female into his frontal auditory field, he is likely to jump forward. It is interesting that he will also jump forward, if the sound comes from behind, so he is probably not able to distinguish sounds from the front from sounds from the back (as suggested by the front-back symmetrical directional patterns (Fig. 19.2)).

19.2.2 *Birds*

The middle ears of birds are connected through an air-filled interaural canal located below the brain. So, it is reasonable to hypothesize that birds also take advantage of the pressure-difference receiver principle for directional hearing. Despite the superficial similarity to the situation in grasshoppers, however, it has been much more difficult to test this hypothesis in birds. For more than 50 years the role of the interaural canal in birds has therefore remained an open question. The main reason is that during ketamine–xylazine anesthesia (and perhaps also other types of anesthesia) birds do not regularly open their Eustachian tubes to equalize the intracranial air pressure with the ambient pressure. The resulting decrease in intracranial air pressure displaces the eardrums inward, increasing their tension. We can experience a similar situation when on board a passenger airplane descending to land. If we do not equalize the pressure in our middle ears, the low-frequency noise from the jet engines seems to disappear or at least reduce substantially but once we open our Eustachian tubes the enervating noise immediately returns!

This insight did not come easy to us. For a long time we just noticed that laser vibrometry recordings of vibrations in eardrums of birds were “unstable” and that recordings had to be performed very quickly to “keep stability” as the eardrum seemed to move (Klump & Larsen, 1992). It was only when one of us (O. N. L.) one day was very clumsy (probably too much coffee) when routinely trying to place a glass microsphere on the eardrum. The needle with the microsphere slipped and ripped a small hole in the eardrum, which responded by immediately moving much further out into the ear canal. Then he finally understood the obvious causation.

The increased tension in the eardrum during anesthesia substantially reduces the eardrum vibrations at frequencies below 3–4 kHz and hence the interaural coupling leading to a significant decrease in ear directionality in this frequency range (Larsen et al., 1996). We avoided this problem by ventilating the middle ears by means of a

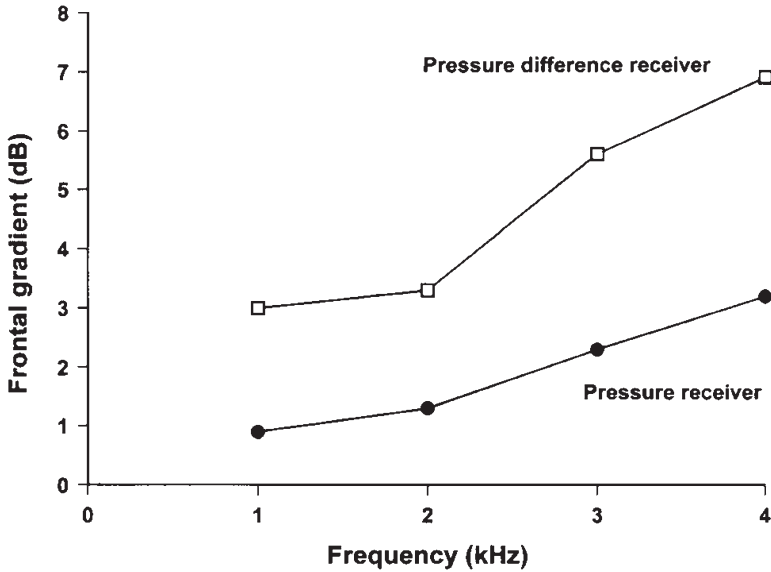


Fig. 19.3 Calculated effect of sound transmission through the interaural canal on the difference in the vibration velocities of the two eardrums of a budgerigar. The direction of sound incidence differs by 30° from the forward direction. In the lower curve (filled symbols), the eardrums are activated only by sound at their outer surfaces. In the upper curve (open symbols), the eardrums also receive sound at their inner surfaces through the interaural canal. (From Larsen et al., 2006)

thin injection needle when we studied the directional hearing of budgerigars (Larsen et al., 2006). We found that sound transmission through the interaural pathway considerably improves the directional hearing in the horizontal (azimuth) plane of the bird for two reasons: The frontal gradients of eardrum vibration become larger (Fig. 19.3) and the vibrations of the eardrums differ more in time. The latter effect is not relevant in grasshoppers, because the brains of insects cannot exploit so small time cues.

The methods were similar to those used with the grasshoppers, except that the anaesthetized bird had to be supported in such a manner that we kept a free sound field around the body of the bird. This was achieved with steel rods with a diameter, which was smaller than one tenths of the wavelength of the highest frequency investigated (4 kHz).

Although the bodies of most birds are larger than those of insects, bird skulls are often small relative to the body. One would therefore expect that the diffraction of sound by the head would be best suited for directional hearing at high frequencies, which unfortunately are easily absorbed by the vegetation. In the budgerigar, the skull has a diameter of about 16 mm at the position of the ears. At a point facing the sound source on the surface of a hard sphere with a diameter of 16 mm one expects a surplus pressure of 1.3 dB at 4 kHz. However, we found a surplus pressure of 3.3 dB, which is approximately the value expected for a sphere with a diameter of 28 mm. The reason for this difference is probably the presence of soft feathers on

the head, but the close proximity of the body may also play a role. This phenomenon deserves further study.

The physical theories for calculating the difference in time of arrival at opposite positions on a sphere reflect the complicated kinds of waves that a thought to exist at the surface. Contrary to intuitive expectation, the speed of sound close to the skull may be much lower than the ambient speed. In other words, the time difference depends on the frequency of sound (Kuhn, 1977). For a sound source facing one of two opposite positions on a sphere, the expected difference in the time of arrival of sound is $3a/c$ at low frequencies, but $2a/c$ at high frequencies (where a is the radius of the sphere, and c the ambient speed of sound). “Low” means that $2\pi a/\lambda \ll 1$ (where λ is the wavelength of sound), and “high” that $2\pi a/\lambda \gg 1$.

The measured values for the difference in the time of arrival (when one ear was facing the sound source) were 118 and 91 μs at 1 and 4 kHz, respectively. For a sphere of the size of the skull ($a=8$ mm) the expected differences are 70 μs at low frequencies and 47 μs at high frequencies, that is, much lower values than those observed. For $a=14$ mm (the size of the head determined from the surplus pressure), the expected time differences are 122 μs and 81 μs at low and high frequencies, respectively. The measured value at 1 kHz is thus close to the expected value at low frequencies, and the observed value at 4 kHz is a transition value toward the 81 μs expected at higher frequencies.

The presence of the air-filled interaural canal not only allows the eardrums to operate as coupled pressure-difference receivers, but also creates substantial interaural delays at low frequencies. These delays may be much larger than the delays caused by the path lengths around the head, and they increase with the amplitude of the sound transmitted through the interaural canal. However, the price for a large interaural transmission is a decrease of the sensitivity to sound in the forward direction. The actual amplitude of the sound in the interaural canal thus seems to be a compromise between sensitivity, forward gradients, and interaural time cues (Michelsen & Larsen, 2008).

The conclusions drawn from these biophysical studies have recently been supported and extended by behavioral experiments on budgerigars equipped with headphones, through which interaural time differences (ITD) and interaural level differences (ILD) were independently manipulated (Welch & Dent, 2011). These experiments confirmed that budgerigars can lateralize sounds behaviorally based on ITD and ILD cues with thresholds of 18–47 μs (0.5–4 kHz) and 2.3–3.4 dB, respectively, that is, well below the maximum interaural differences predicted from the biophysical analysis of the coupled pressure-difference receiving ears.

19.2.3 *The Tuned Cricket*

In contrast to many bushcrickets, the crickets (Gryllidae) generally communicate at sonic frequencies, and their calling song is often a pure tone. Like the bushcrickets, the crickets have their ears located in the thin front leg tibiae, where diffraction does

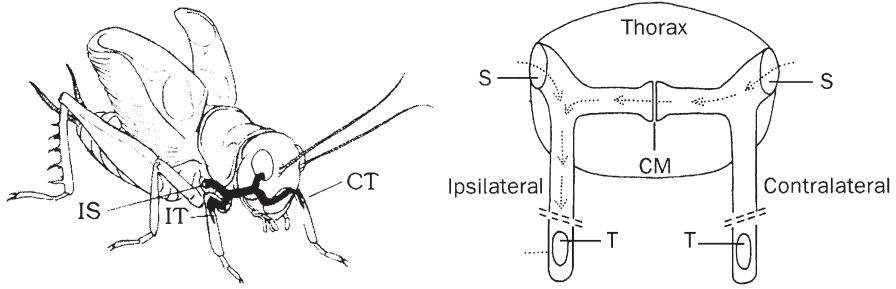


Fig. 19.4 (Left) The two ears in a cricket share four acoustic inputs: two eardrums (T, tympanum) and two spiracles (S). Each ear receives sound at the external surface of its eardrum (IT, ipsilateral tympanum), but also at the internal surface of its eardrum from the eardrum of the other ear (CT, contralateral tympanum), from the ipsilateral spiracle (IS), and from the contralateral spiracle (CS). Right: Sounds from the contralateral inputs pass the central membranes (CM), which act as a mechanical phase shifter. (From Michelsen et al., 1994b, and Michelsen & Löhle, 1995)

not provide useful directional cues. However, the crickets have solved the problem in a very different way. A pressure-difference receiver mechanism provides the ear with an excellent directionality within a narrow frequency band around the calling song.

A horn-shaped tracheal tube known as the acoustic trachea connects the inner surface of the eardrum with an ipsilateral acoustic spiracle (IS) on the thorax (Fig. 19.4). The acoustic trachea is also linked through a connecting trachea with the acoustic trachea on the other side of the body (Fig. 19.4, right). Sounds can therefore propagate from an ear and/or acoustic spiracle across the midline to the inner surface of the contralateral eardrum. The connecting trachea from the one side ends in a central membrane, which is a close neighbor to the central membrane from the other side.

For many years, very different opinions were held of the importance of the contralateral inputs to creating the directional characteristics of the ear (review: Weber & Thorson, 1989). It had been found that at 5 kHz, the frequency of the song, body screening effects could only account for a few dB of the directionality, but greater directionalities had been measured in receptor axons and thoracic neurons. Some investigators thought that the ear was mainly responding to sound from the contralateral ear, while others favored the sound from the contralateral spiracle. Finally, the observation that disrupting the central tracheal connection does not hinder sound localization in very homogeneous sound fields was regarded as evidence to “toll the death of cross-body-theories.” Obviously, in order to settle these disputes, it was necessary to determine the transmission gains of the three internal sound pathways. The transmission gain is the change of the amplitude and phase angle of the sound from the entrance of the tracheal system to the inner surface of the eardrum.

Such experiments were performed a few years later in the field cricket *Gryllus bimaculatus* (Michelsen et al., 1994b). The transmission gain from the ipsilateral spiracle to the inner surface of an ear was fairly simple and close to that expected for a delay line. In contrast, the transmission gains from the contralateral ear or spiracle, through the midline and to the ear were far from simple, both with respect

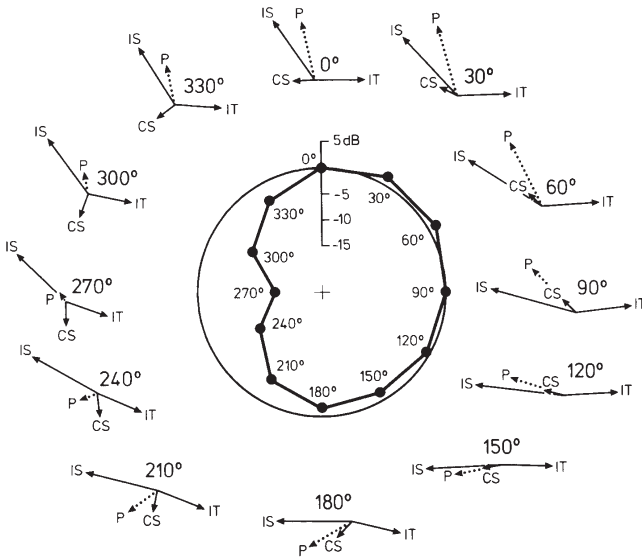


Fig. 19.5 Calculation of the directional hearing at 4.5 kHz in the right ear of the cricket, *Gryllus bimaculatus*. Three vectors (sounds from three sound inputs) add at each direction of sound incidence to produce the vector P, which is the net force acting on the eardrum. CS: sound from the contralateral spiracle. IS: sound from the ipsilateral spiracle. IT: sound acting directly on the eardrum. (From Michelsen et al., 1994b)

to amplitude and to phase. Apparently, the central membrane connection between the two acoustic tracheae behaves like an eight-pole filter. This finding was much more complicated than the ideas discussed during the previous decade, so the heated debate had no winners.

In addition to sound transmission, we measured the frequency spectra and time of arrival of sounds at the outer surface of the eardrum and from the 3 entrances at 12 directions of sound incidence. By combining these data we calculated how the total driving force at the eardrum depends on the direction of sound (Fig. 19.5). The results are in excellent agreement with the dependence on sound direction of the eardrum vibrations.

When measuring the amplitude and phase angle of the sounds from each of the four auditory inputs at various angles of sound incidence, our reference values were the amplitude and phase at the outer surface of the right eardrum when sound arrived from the frontal direction. In this manner we obtained values, which were not true values for the effects of diffraction, but those needed in the calculations of directionality. As we shall see, this is especially important for the phase angles of the sounds from the contralateral inputs.

From these data one can make some predictions about the mechanism of directional hearing. It is obvious that the amplitude of the sound pressure at the outer surface of the eardrum changes only little with the direction of sound incidence. In the frontal directions (around 0°), which are of prime interest with respect to how

a cricket localizes a sound source, a change in sound direction would cause the forces driving the two eardrums to differ by up to 1.3 dB. A pressure-difference receiver is obviously needed for providing more directionality, but from which input(s) should the sound at the inner surface of the eardrum originate? By testing all combinations of inputs, we found that more than two inputs were needed in order to account for the observed directionality, and that the two contralateral inputs are better potential contributors of directional cues than the ipsilateral spiracle. Both the amplitude and the phase 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 especially prominent and thus the most likely contributor to the directionality of the ear.

The transmission gains from the contralateral eardrum and the two thoracic spiracles were measured in the following manner. A small local sound source was used for delivering sound at one of the auditory inputs, while walls of beeswax between the auditory inputs ensured that the sound levels at the other inputs were at least 20 dB down (cf. Fig. 19.1). We first determined the transfer function of the eardrum by applying sound at its outer surface. The transfer function is the drum 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 eardrum, but this time the sound pressure was measured at the input in question. These transfer functions consist of the gain of the transmission path times the transfer function of the eardrum. The gains of the transmission paths could then be obtained by dividing these transfer functions with the transfer function of the eardrum.

For the transmission of sound from the ipsilateral spiracle (IS), the amplitude gain is close to 1 at low frequencies and increases to a maximum around 6–8 kHz and again at 17–19 kHz. At low frequencies, the phase at the inner surface of the eardrum is close to that at the outer surface. With increasing frequency the sound at the inner surface becomes progressively delayed, as one would expect in a transmission line where the propagation of sound takes a certain time. The phase changes approximately 360° between 1 and 22 kHz. At a temperature of 21 °C (and a sound propagation velocity in free space of 344 m/s), the length of the tracheal tube was calculated to be 15.6 mm, which is significantly larger than the anatomical length (about 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 an average value of 263 m/s by measuring the delays of very short impulse sounds. He pointed out that this value is 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.

The transmission of sound from the contralateral spiracle (CS) differs very much from this simple pattern. The amplitude is at a maximum at 5–7 kHz and again around 18 kHz (much like the sound from IS), but it is almost zero below 3.5 kHz. In the frequency range 4–5 kHz (around the frequency of the calling song, which is at 4.6–4.7 kHz in *G. bimaculatus*), the amplitude of the sound from CS varies

drastically with frequency. Between 4.0 and 4.6 kHz the amplitude increases by a factor of 4. The average increase between 4.6 kHz and 5.0 kHz is only 10%. The strong frequency dependence of the amplitude is accompanied by a large change of phase. From 4 to 10 kHz the phase angle of the sound from CS changes by approximately 560° (for comparison: the phase of the sound from the ipsilateral spiracle (IS) changes by only 100° from 4 to 10 kHz). From 10 to 20 kHz the changes of phase in the sounds from IS and CS have approximately the same magnitude. 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 ipsilateral eardrum is considerably smaller.

The measured diffraction, time delays, and transmission gains of the four sounds acting on the tympanum were now combined in an attempt to account for the dependence of the tympanal vibrations on the direction of sound incidence. We decided to use 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.

For frequencies up to 5 kHz, the amplitude gain of the transmission of sound from the contralateral tympanum (CT) is so small (below 0.1) that it does not have much effect on the directional pattern. In the following example at 4.5 kHz we ignore the sound from CT. The problem is then reduced to considering three vectors: the sound at the outer surface of the 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, the amplitude gain and the change of phase of the sounds transmitted from IS and CS are 1.5 and 154° and 0.44 and 208° , respectively. The first step in the calculation is to multiply the gain and the diffraction/time-of-arrival factor for each of the sound components and at each angle of sound incidence. In Fig. 19.5, the results are represented as three vectors, which are then added to produce a sound pressure (P), which is proportional to the force that causes the eardrum to vibrate. It should be noted that the phase angles for the transmission gains include a 180° phase shift, which means that in adding the three vectors, sound components acting on the inner surface (IS and CS) are subtracted from the sound component acting at the outer surface (IT).

The solid curve in Fig. 19.5 shows the pressure driving the eardrum. The polar plot is surrounded by the 12 vector diagrams. The calculated directional pattern has the most important of the features seen in the measured patterns: The driving force is at a maximum at the ipsilateral directions 30° and 60° ; the force decreases by approximately 6 dB from 30° , through 0° to 330° , and the force is at a minimum at 270° (the “contralateral null”).

When examining Fig. 19.5 one may start by looking at the vector diagram for the 270° direction. Obviously, the null is caused by the fact that the sum of CS and IT has approximately the same amplitude, but the opposite direction of IS. A deeper minimum (more perfect null) would require only a slight reduction in the amplitude of the sound from IS. In the vector diagrams for 300° , 330° , 0° , and 30° , the

amplitudes of the three vectors change only little, and only little variation is seen in the phase angles for IS and IT. The only major change is in the phase angle for CS. At 30° and 60°, CS has almost the same phase as IS, and the amplitude of P is now at a maximum. The slope of the driving force in the forward direction is therefore caused almost entirely by changes in the phase angle of the sound from CS.

Several directional diagrams have been calculated by selecting other values for IS and CS within the ranges observed during the measurements. The most conspicuous difference between the diagrams is in the magnitude and direction of the contralateral null, which is not always in the 270° direction. A closer examination of the data revealed that a change of sound frequency from 4.5 kHz toward 4 kHz causes the null to move backwards toward 240° or even 210°, whereas an increase of frequency from 4.5 toward 5 kHz causes the null to move forward toward 300°. This trend was, in fact, observed in directional diagrams of the tympanal vibrations measured with laser vibrometry during the collection of the data on diffraction and time-of-arrival.

In most of these crickets, the vibration velocity of the eardrum is a maximum at 4.6 kHz where the difference between the eardrum velocities for sound arriving from the 30° and 330° directions is about 10 dB (Michelsen & Løhe, 1995). The difference is lower than 5 dB below 4.3 kHz and above 4.8 kHz. The tuning to 4.6 kHz is destroyed if the central membranes are perforated by pushing a human hair through the spiracle. The difference between the eardrum velocities for sound arriving from the 30° and 330° directions is then only 1–2 dB.

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. We conclude that the measured data on transmission, diffraction, and time delays can account for the most prominent features of the directivity. It is obvious from Fig. 19.5 that the slope of sensitivity in the forward directions depends upon a change in the relative phase angles of the three vectors. The sound from the contralateral spiracle (CS) plays a prominent role in creating this directionality. The sound from the ipsilateral spiracle (IS) is necessary, however, for producing the cardioid pattern shown in Fig. 19.5.

Several investigators have studied the accuracy of the phonotactic steering in crickets. Some investigators have studied crickets walking on a closed-loop trackball system that compensated the animals' walking movements and found that the crickets meandered by 30°–60° around the frontal midline (e.g., Weber & Thorson, 1989). Others have studied directional orientation in a Y-maze and observed similar uncertainties. However, a recent study of *G. bimaculatus* females walking on an open-loop trackball system found that for angles of sound incidence between 1° and 6° the animals precisely walked towards the sound source (Schöneich & Hedwig, 2010). These results reveal hyperacute directional hearing and place the cricket at the same level of directional hearing as the fly *Ormia ochracea* (Mason et al., 2001), barn owls, and some mammals (humans, bats, elephants) and it is surpassed only by dolphins (Renaud & Popper, 1975).

19.3 Perspectives for Future Research

This chapter is focused on three examples of the physical mechanisms in pressure-difference receiving ears. Similar mechanisms probably occur in several other groups of insects and vertebrates, but the physical mechanisms have not been studied in detail. In some groups it is known that sound is entering the body, but that the sound inputs are too numerous and/or diffuse to allow a quantitative study. For example, large parts of the surface of cicadas are set in motion by sound, and cicadas may therefore behave as almost omnidirectional sound emitters and sound receivers. Although sound emitting tymbals and sound receiving eardrums are known anatomically, cicadas may radiate sound through their eardrums and receive sound partly through their tymbals. A similar confusing situation also seems to exist in some frogs.

In other animal groups, mainly lizards, there is evidence for pressure-difference reception (review: Christensen-Dalsgaard, 2011), but more comprehensive physical studies are needed in order to understand the exact mode of operation. The vital importance of the phase shifting filter for the directional hearing in crickets is one example of a discovery that was made possible by the quantitative physical approach.

From the findings described here one may guess about suitable strategies for behaviorally locating sound emitters in the three animals studied. The predictions were close to the actual strategies observed in grasshoppers and crickets, but not in small birds. We calculated the difference in eardrum vibration amplitude at 330° and 30° direction of sound incidence in birds with normal interaural sound transmission and facing sound sources. We guessed that exploiting this gradient in the forward direction would be a good strategy for a small bird to localize a sound source. Nevertheless, field experiments with small passerine birds (Nelson & Suthers, 2004) showed that prior to flying toward a sound source the birds (eastern towhees, *Pipilo erythrophthalmus*) turned their heads so that the angles between the beaks and the sound sources were 30° to 50°. This observation deserves further study in other species both in the field and in the laboratory. This example demonstrates the importance of confronting laboratory observations with field studies. In addition, comparative studies in a larger number of species and environments will give a more comprehensive picture than using just one species and one habitat as is usually seen.

We suggest that a major future theme is the study of pressure-difference receivers operating in natural habitats. In a study of sound localization of grasshoppers (Michelsen & Rohrseitz, 1997) we found that amplitude cues degrade much faster with distance than phase (time) cues. Animals exploiting phase cues may therefore maintain a reasonable directional hearing when the amplitude cues no longer make sense. The pressure-difference receiver type of ears responds to phase-differences, and these ears may be particularly suited to overcoming the degradation of directional cues. This suggests that the possession of such ears may be an adaptation not only to small body size relative to wavelength but also to the acoustic properties of the complicated natural habitat.

A number of authors still question the role of the avian interaural canal and find the pressure-difference receiver hypothesis controversial. We find it highly likely that many other small birds make use of this mechanism. The pressure-difference receiver properties of avian ears should therefore be studied in more species and with careful biophysical methods as those described here to arrive at a more comprehensive understanding of directional hearing in birds. We especially encourage careful measurements of the transmission through the interaural canal before designing experiments on awake and behaving birds. In addition, we urge experimenters to take into consideration the potential effects of anesthesia when designing physiological experiments on pressure-difference receivers.

Although we are very satisfied with the results of the investigations of the mechanisms for the directional hearing in crickets, there is a possible flaw. It is very difficult to see whether a tracheal spiracle is open or closed, because the opening is covered by a lid. During the preparations for the experiments the lid was fastened with beeswax, either in an open or a closed position. The actual state was then controlled by observing whether a local sound source had an effect on an eardrum. In theory, it is possible that the animals may control the degree of open/closed and thus be able to vary the properties of the directional receiver system. We will continue to think of a possible solution to this problem.

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