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Insect Bioacoustics

Despite being small, acoustical specializations allow insects to produce, detect, and localize sound for communication, predator detection, and host localization.

Introduction

Hearing and acoustic communication are widespread among vertebrate animals, but insects are the only invertebrate group in which sound production and hearing are widespread (sound is taken here to mean airborne sound; the sensing of substrate vibration is essentially ubiquitous among terrestrial invertebrates, and although some aquatic invertebrates produce or detect sound, they will not be considered here). Insects listen to, detect, and locate sound-producing predators, hosts, mates, and rivals, and they emit sound to attract, repel, or threaten members of their own species and to startle and evade predators.

Insects are small (**Figure 1**), and this constrains their use of acoustics (Michelsen, 1992; Bennet-Clark, 1998). For example, when an insect sings to attract a mate, it is advantageous for his song (and in most cases, it is the males that sing) to be heard over long distances, thereby maximizing the chance of its reaching a receptive partner. Sound production requires the transfer of energy from moving body parts to the air and is, fundamentally, powered by muscle contractions. Even large insects weigh only a few grams, limiting the available muscle power and resulting sound amplitude. Moreover, because of impedance-mismatch penalties, the efficient transfer of energy from insect to air is possible only if the wavelength of the sound is not too large relative to the size of the sound-radiating structure. Accordingly, most insect sounds have wavelengths of a few centimeters or less. But short wavelength sounds are readily reflected and/or absorbed by objects such as leaves and twigs, further limiting their effective range.

Hearing requires the reverse transfer of energy, from the environment to the receiver. The acoustical force exerted on the receiver, which is then available for transmission to and excitation of auditory nerve cells, is proportional to its surface area. The ability of small insect ears to detect very faint sounds is thus limited. Indeed, minimum auditory thresholds of insects are typically in the range of 30- to 50-dB sound pressure level (SPL), which is well above the minimum threshold of humans.

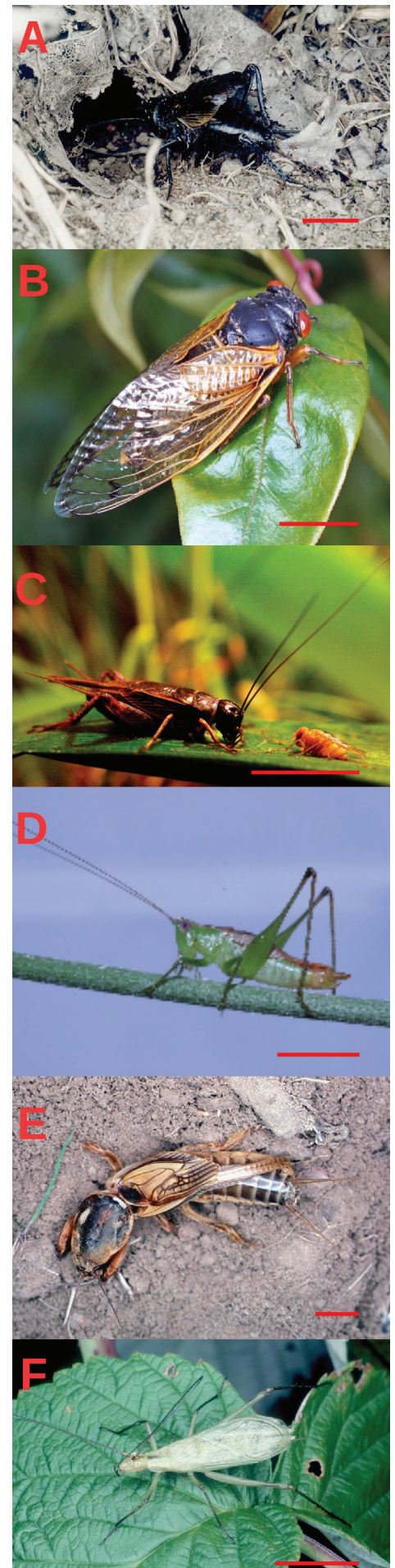
One way in which some insects rival other animals is in their ability to localize sound. Close to a sound source, air particles oscillate in the direction of wave propagation; thus particle velocity carries information about sound-source direction. Some insect ears, such as the antennae of mosquitoes or fruit flies, are sensitive to particle velocity and can extract information about the direction of the sound source directly. Other insects use eardrums to detect the sound pressure component, which is dominant at distances greater than a wavelength from the source. Sound pressure reflects local variation in the density of air and in itself carries no directional information; rather, that must be derived from the direction of sound propagation.

Determining the azimuth (direction in the horizontal plane) of a source is based on differences in the timing and/or intensity of sounds at the left and right ears, known respectively as interaural time difference (ITD) and interaural intensity difference (IID). Any sound that arises from off the midline will travel further to the offside ear than to the nearer one and thus will arrive later. The difference in path length depends on the direction of the sound source and the distance between the ears; the more lateral the sound and the larger the interaural distance, the greater the ITD.

For insects, maximum possible ITDs are small. For example, an interaural distance of 1 cm, which is possible only in relatively large insects such as crickets (Figure 1A) and cicadas (Figure 1B), would generate an ITD of only about 34 μ s for a sound source perpendicular to the midline. The sophisticated nervous systems of birds and mammals can process such miniscule time differences, but so far as is known, the simpler nervous systems of insects cannot.

IID depends both on source azimuth and on how effectively sound is blocked by whatever separates the two ears, which in turn depends on its size relative to the wavelength of the sound and on its sound-absorptive properties. Sound diffracts readily around objects that are small relative to its wavelength, as is the

Figure 1. A brief introduction to the insect groups discussed in this article. Scale bars indicate approximately 1 cm. Readers can hear sounds from each of these insects at <http://acousticstoday.org/gpollack>. **A:** Field crickets (order Orthoptera, family Gryllidae, subfamily Gryllinae). As the name suggests, most species live in relatively open areas, often in simple burrows or under rocks, logs, leaf litter, and the like. The figure shows a fall field cricket, *Gryllus pennsylvanicus*, singing outside its burrow. **B:** Cicadas (order Hemiptera, family Cicadidae). Cicadas spend most of their lives underground where, as larvae, they feed on tree roots. When nearly adult they emerge at the surface, climb a tree, and molt to adulthood. The periodic cicadas emerge in enormous numbers every 13 or 17 years when their loud songs result in many sleepless nights. The photograph shows a 17-year cicada, *Magicicada septendecim*. **C:** Parasitoid flies (order Diptera, families Tachinidae and Sarcophagidae). Larvae (maggots) of parasitoid flies burrow into their hosts that they devour from the inside. Mature larvae emerge from the host, killing it in the process, before forming pupae, the stage during which they transform from larva to adult. The photograph shows *Ormia ochracea* (right) alongside its host in Florida, the southeastern field cricket (*Gryllus rubens*). **D:** Katydid (Orthoptera, Tettigoniidae). Katydids live in vegetation. They vary considerably in size, shape, and color according to species. The photograph shows the short-winged meadow katydid, *Conocephalus allardi*. **E:** Mole crickets (Orthoptera, Gryllidae, Gryllotalpidae). With forelimbs specialized for digging, these large insects excavate elaborate burrows from which they sing. The photograph shows the prairie mole cricket, *Gryllotalpa major*. **F:** Tree crickets (Orthoptera, Gryllidae, Oecanthinae). These slender insects live in bushes and trees. Their songs are rather low in frequency (2-4 kHz), making them hauntingly attractive to at least this human listener. The photograph shows the black-horned tree cricket, *Oecanthus nigracornis*. Photos in A and F courtesy of J. E. Lloyd, used with permission from <http://entnemdept.ufl.edu/Walker/buzz/>; photo in B courtesy of John Cooley, used with permission from <http://magicicada.org/magicicada/>; Photo in C courtesy of N. Lee, used with permission; photos in D and E courtesy of T. J. Walker, used with permission from <http://entnemdept.ufl.edu/Walker/buzz/>.



case for many insects that thus experience very small IIDs. Despite these challenges, parasitoid flies (Mason et al., 2001; **Figure 1C**) and crickets (Schönich and Hedwig, 2010) can discriminate between sound sources positioned as little as 1° to the left or right of the midline, an acuity similar to that of humans.

In this article, I present a few examples in which clever acoustical engineering allows insects to overcome some of the constraints imposed by their small size. Note that by “engineering,” I mean adaptation effected through natural selection, not willful design. First, though, I briefly describe the roles that sound plays in insect lives. Readers should consult Gerhardt and Huber (2002), Balakrishnan (2016), and Pollack (2016) for more thorough reviews of how insects use sound signals.

Why Insects Listen

Predator Detection and Avoidance

Hearing has evolved independently in insects at least 24 times (Greenfield, 2016). Phylogenetic analysis shows that most insect ears evolved at around the time that echolocating bats appeared in the fossil record, about 65 million years ago, suggesting that hearing in these cases evolved in response to the selection pressure exerted by these predators. Hunting bats emit ultrasonic calls and detect their prey from the echoes that are returned from their bodies (Fenton et al., 2016). Moths, crickets, katydids, locusts, beetles, mantises, lacewings, flies, and perhaps others respond to bat-like ultrasound with behaviors that reduce the probability of capture, such as flying away from the sound source, diving into vegetation or, in some cases, jamming the bat’s echolocation system with their own ultrasound emissions. In many cases, antibat defense was the primitive (and still dominant) function of hearing, whereas in others, such as crickets and katydids, intraspecific communication, often using low-frequency sounds (<10 kHz), predated the evolution of echolocating bats by more than 100 million years. Extant insects in these groups hear bat-like frequencies in addition to those used for communication and respond to them defensively, suggesting that bat detection and avoidance evolved as “add-ons” to an already functioning auditory system.

Reproduction

The insect sounds most familiar to humans are produced by males to attract sexually receptive females. Crickets, cicadas, katydids (**Figure 1D**), and grasshoppers produce

loud acoustic signals, known as calling songs, that advertise their species identity, their location, and, in some cases, their “quality” as prospective mates. In many cases, females respond by walking or flying toward the sound source (see video at <http://acousticstoday.org/ptaxis>) of a Texas field cricket [*Gryllus texensis*] walking on a spherical treadmill toward a loudspeaker situated approximately 45° to her left). In other cases, females respond with their own songs that males then use as an acoustic guide to approach the female.

Host Localization

A third function of hearing in insects, host detection and localization, has so far been described only for parasitoid flies (**Figure 1C**), where it has evolved independently at least twice (Lakes-Harlan et al., 1999). The flies deposit larvae on or near their singing host (crickets, katydids, or cicadas, depending on the species of fly) that, like the singer’s intended audience, they locate by homing in on its song. The larvae then burrow into the host and consume it from the inside.

Being Small Yet Loud

As mentioned above, it is often advantageous for an advertising male’s signal to reach the largest possible number of receivers. Insects have evolved a number of mechanisms that boost their acoustic output.

Resonance

The loudest insect sounds are produced in one of two ways: stridulation, which involves rubbing of one body part against another, or tymbalation, which is a snapping or buckling of specialized regions of the exoskeleton known as tymbals. Crickets, katydids, and grasshoppers are stridulators, whereas cicadas are tymbalators. The radiation efficiency of sounds produced by both mechanisms is often enhanced through resonance (Bennet-Clark, 1999).

Stridulating crickets rub a plectrum, a hardened region on the edge of one front wing, against a row of “teeth,” hardened ridges on the underside of the opposite wing, in a manner similar to stroking the teeth of a comb with one’s thumbnail (**Figure 2**).

Each tooth strike produces a brief click that excites a resonance determined by the size, shape, and material properties of the wings. Sound is radiated mainly from a region of the wing called the harp, which resonates at a frequency close to that of the cricket’s song, which is typically 3–5 kHz depending on species (Montealegre-Z et al., 2011). The input of energy to the system through successive tooth strikes is coor-

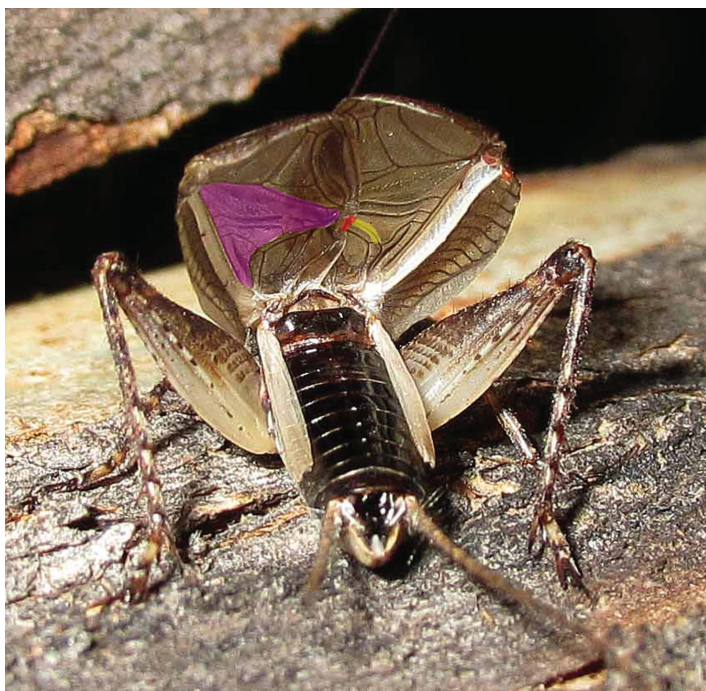


Figure 2. A stridulating cricket (*Eurepa* sp.) in a figure that has been modified to highlight the location of the harp (**magenta**), plectrum (**red**), and file (**yellow**). Courtesy of Vicki Powys.

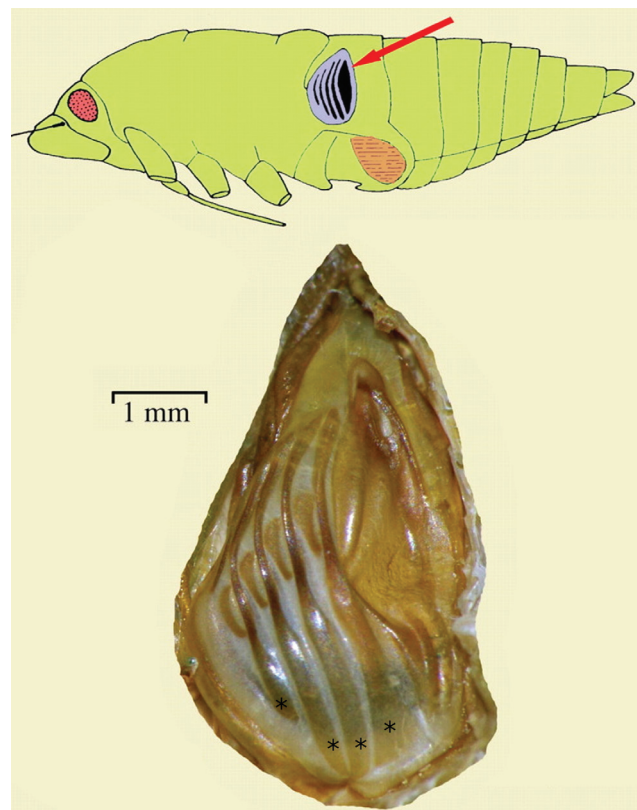


Figure 3. **Top:** location on a cicada's body (head is to the **left**) of the left tymbal (**arrow**); left eardrum is highlighted in **orange**. **Bottom:** cuticular ribs (**asterisks**). Modified from Bennet-Clark (2007).

dinated with the resonance of the wing by an escapement mechanism whereby each cycle of wing vibration disengages the plectrum from the tooth against which it is apposed, allowing it to strike the next tooth on the file (Eliot and Koch, 1985). As a result, input from each tooth strike is phased so that it adds constructively to the ongoing vibration of the wing. A slow-motion video of stridulation (courtesy of F. Montalgre-Z) can be seen here: <http://acousticstoday.org/toceanicus>.

The loudest known insect sounds are produced by cicadas. The sounds are generated by the distortion or buckling of a series of ribs that, together with the surrounding elastic material and an associated stiff plate, comprise each of the paired abdominal tymbals (**Figure 3**). Inward buckling of the tymbal is driven by the contraction of a powerful muscle that pulls the cuticular plate inward, and relaxation to the rest position is powered by the tymbal's elastic components.

As each rib buckles in turn, it undergoes a damped vibration with a resonant frequency near that of the male's song. Similar to the coherent phases of successive tooth strikes of crickets, the buckling of successive ribs occurs in phase with ongoing vibrations when the energetics are presumably most favorable, thereby generating an essentially continuous tone at the dominant frequency of the song.

The tymbals are coupled to another resonant structure formed by a large air sac that nearly fills the male's abdomen and the closely associated eardrums. Together, the air

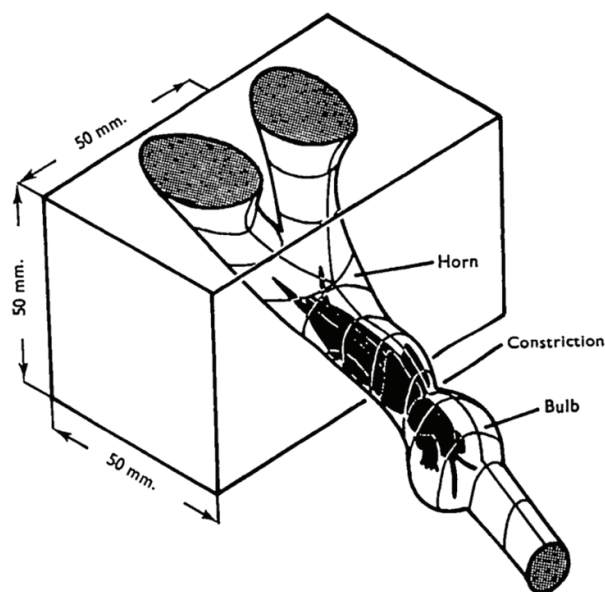


Figure 4. A mole cricket, *Gryllotalpa vinaea*, singing from his burrow. From Bennet-Clark (1970).

sac and eardrums function as a Helmholtz resonator that is tuned to the male's song frequency. Sound pressure within the air sac can reach the astonishing level of 158-dB SPL. The song, which is radiated through the large eardrums, can reach 100-dB SPL at 1 m.

Mole crickets (**Figure 1E**) lack an additional anatomical structure to boost their acoustic output. Rather, they construct and sing from burrows that are “designed” (by evolution) to enhance the radiation of the song. The burrows consist of two acoustically important components: a bulbous chamber linked by a short constriction to an approximately exponential horn (or in some cases, twin horns) that couples the chamber to the outside. The singing male positions himself near the constriction with his elevated wings a few millimeters into the throat of the horn (**Figure 4**).

The acoustical properties of this system were probed in model burrows of the species *Gryllotalpa australis* by replacing the male with a dipole sound source mimicking his vibrating wings (Daws et al., 2012). Both the bulbous chamber and the horn resonate at frequencies similar to the male’s song frequency (2.7 kHz). Measurements of sound pressure at various locations within the burrow showed that the structure supports a standing wave in which sound in the bulb and in the horn are out of phase with a null, where sound pressure is minimal, at the constriction. The opposite phases in bulb and horn reflect the dipole nature of the cricket’s elevated wings, whereby acoustic compression on one side of the vibrating wings is accompanied by rarefaction on the other side. The length of the bulb, about 26 mm, is close to one-quarter the wavelength of the song. As a result, sound that travels from its origin to the rear wall of the bulb and back again (which will thus have traveled half a wavelength) will arrive nearly in phase with sound in the horn, to which it can add constructively. This is not unlike the manner in which the notes produced by brass instruments are determined by their effective lengths (Moore, 2016).

A second acoustically important feature of the burrow is the nearly exponential increase in horn diameter from its narrow end, where sound is generated, to its opening at the surface. As mentioned earlier, the efficiency with which acoustic energy is transferred from its source to the air depends on the relationship between source size and sound wavelength. The increase in effective source area afforded by the horn helps the insect to overcome the impedance mismatch between its wings (ca. 1 cm) and the wavelength of its relatively low-frequency song (12.6 cm). In essence, the male is singing through a megaphone. Singing from a burrow results in a gain in sound pressure of up to 24 dB compared with singing in free air (Bennet-Clark, 1987).

Males construct their burrows incrementally while testing the results of their efforts along the way; they dig for a

few minutes, emit a few chirps, dig and shape some more, test again, etc., with the entire process taking up to an hour (Bennet-Clark, 1987). The performance of the burrow, as indicated by the power of the radiated sound, improves throughout this process, although how the male monitors this remains unclear (because he is inside the burrow, near the acoustic null, he cannot hear the radiated sound).

Baffles

Because cricket wings are dipole sound sources, their output is susceptible to acoustic “short-circuiting,” whereby compressed air on one side of the vibrating wings flows around the edge of the wing to the rarefied side rather than radiating away from the animal. Short-circuiting occurs when the diameter of the source (for crickets, 1 cm or so) is less than half the wavelength of the sound (typically 6–7 cm or greater for crickets); the smaller the source relative to wavelength, the more pronounced the effect (Beranek and Mellow, 2012). In mole crickets, the position of the wings at the constriction between bulb and horn helps to minimize short-circuiting. Field crickets often sing from the narrow entrance to a burrow, which can help to reduce short-circuiting in a manner analogous to the cabinet in which a loudspeaker might be mounted. Tree crickets (**Figure 1F**), a subfamily of insects distinct from the more familiar field crickets, use leaves as acoustic baffles to minimize short-circuiting. Males of some species sing from the edge of a leaf, from a notch in the leaf surface, or from the junction between two leaves, orienting their bodies so that their wings are coplanar with the leaf surfaces (Forrest, 1982). The leaves extend the effective size of the male’s wings, making it more difficult for the opposing sound pressures on the two sides to cancel one another. The use of baffles can increase radiated sound pressure by up to 10 dB. Go to <https://vimeo.com/120108754> for a video of a male singing from a leaf junction.

Males of some species actually construct baffles by chewing a hole in a leaf (Prozesky-Schulze et al., 1975). When singing, the male positions himself so that his raised wings fill the hole. The sizes of the leaf and hole and the position of the hole within the leaf determine the effectiveness of the baffle. In at least one species of tree cricket, *Oecanthus henryi*, the nervous system seems to be hardwired for optimizing these parameters. Modeling of the acoustics of the system shows that for maximal effectiveness males should build baffles in large leaves, the size of the hole they excavate should match the area of their wings, and the hole should be positioned centrally within the leaf rather than near its periphery. *O.*

henryi males indeed pick larger leaves when given a choice, make holes that match their wing area, and position the holes centrally. Unlike mole crickets, which fine-tune their burrows through trial and error, the tree crickets seem to get it right on the first try (N. Mhatre, personal communication).

Enhancing Sound Reception

As mentioned earlier, the small size of insect ears limits their ability to capture acoustical energy from the environment. As for sound production, insects have evolved adaptations that mitigate this problem.

Resonance

The eardrums of crickets are resonantly tuned to the dominant frequency of conspecific song (Paton et al., 1977). Similarly, the antennae of male mosquitoes resonate at a frequency near that of the flight tones of conspecific females, which serve as mate recognition signals (Göpfert et al., 1999). Frequency-matched resonance ensures efficient transfer of acoustic energy from air to ear, selectively increasing sensitivity to the sound frequency that matters.

Katydid Ear Trumpets

Unlike signals of mosquitoes and crickets, katydid songs are often rather broadband, spanning frequencies from a few kilohertz well into the ultrasonic range. Accordingly, katydid eardrums tend to be broadly tuned, limiting the utility of resonance as a means to enhance sensitivity. The eardrums receive acoustic input via two routes: directly from the sound source to the external surface of the eardrum and indirectly through a specialized portion of the respiratory system. Insects breathe through a network of tracheae, which are tubes that deliver air from external openings called spiracles directly to internal tissues. A specialized “acoustic trachea” extends from the exterior of the animal to the internal surface of the eardrum. In many species, the cross-sectional area of the trachea tapers exponentially from a relatively large spiracular opening, about 1-2 mm depending on species, to its smaller eardrum-associated end, about 0.1 mm, thereby concentrating acoustic energy. The acoustic trachea thus functions as an ear trumpet and is the dominant source of acoustical input to the eardrum. An infinitely long exponential horn transmits sound in a frequency-independent manner above a cutoff frequency determined by the rate of flare of the horn (Beranek and Mellow, 2012). The cutoff frequencies of katydid tracheal horns are low enough not to impede the transmission of songs. The horns are, of course, not infinite, and as a result, there are ripples in the transmission function amounting to a few decibels in magnitude. Nevertheless, both calculations

and measurements show a gain in acoustical power at the eardrum, amounting to some 10-20 dB over the rather broad spectra of katydid songs (Hoffman and Jatho, 1995).

Active Mechanics

The resonances of eardrums or antennae and the ear trumpets of katydids are passive mechanisms to enhance sound reception; they improve sensitivity but do not require energy to do so. A fundamentally different sort of mechanism, active amplification via input of mechanical energy to the receiver, has recently been found in three groups of insects: mosquitoes, fruit flies, and tree crickets (Mhatre, 2015). Active amplification has long been known in the ears of vertebrates (Hudspeth, 2008), where it is sometimes manifest as otoacoustic emissions, which are the emission of sound from the ear. Antennae of mosquitoes and fruit flies and eardrums of tree crickets exhibit an analogous phenomenon, spontaneous oscillations in the absence of acoustic stimulation.

Internally, insect ears, whether associated with eardrums as in tree crickets or antennae as in mosquitoes and flies, comprise groups of structures called scolopidia, each of which includes one or two auditory nerve cells together with several supporting elements (Yack, 2004). Motion of the external sound-capturing structure results in deformation of the nerve cells that, in turn, causes mechanosensory ion channels to open, thereby allowing the influx of ions that results in nerve action potentials. As in vertebrates, active amplification works by using metabolic energy to produce force that adds to that exerted by the sound stimulus, effectively amplifying the latter. In mosquitoes, fruit flies, and tree crickets, the combined forces of their many scolopidia (a few dozen in tree crickets, nearly 500 in fruit flies, and more than 1,000 in mosquitoes) are sufficient to cause vibration of the external structures, detectable as spontaneous vibrations in the absence of stimulation or as boosted vibration amplitude in response to sound stimuli. Studies on the fruit fly *Drosophila melanogaster*, where genetic manipulations allow modification or elimination of specific proteins, point to molecular motors as the source of the active force (Albert and Göpfert, 2015), although the precise details are still under investigation.

Active force production may be sharply tuned with respect to sound frequency, providing another mechanism, besides passive tuning, for selective sensitivity to species-specific signals. The frequency tuning of active mechanics is revealed by the spectra of spontaneous oscillations. Comparisons across seven different *Drosophila* species with different song

spectra show that the frequency of spontaneous oscillations matches the dominant frequency of the songs of the species (Riabinina et al., 2011). The passive mechanical properties of tree cricket wings are such that the song frequency varies considerably with temperature (Mhatre et al., 2012). Active mechanical processes in their ears result in a parallel shift in auditory tuning, allowing females to remain selectively sensitive to male songs over the wide temperature range that these insects experience (Mhatre et al., 2016).

Sound Localization

Most insects need to determine sound location in three dimensions: azimuth, elevation, and distance. It is generally assumed that distance estimation is based largely on the perceived stimulus amplitude, which decreases with distance from the source, although distance-dependent change in the signal spectrum caused by frequency-dependent attenuation is also a possibility (but only for those insects capable of fine spectral analysis, such as katydids). Although there is considerable behavioral evidence that at least some insects can determine the elevation of a sound source, little is known about the underlying mechanisms. In particular, insects lack the elaborate outer ear structures of mammals (pinnae) and birds (facial ruffs of owls) that generate elevation-dependent spectral cues (Roffler and Butler, 1968; and as noted above, only some insects could utilize these cues). One possibility is that they use behavioral strategies, such as twisting their bodies so as to generate left-right differences in orientation toward an elevated or depressed sound source. Another possibility for flying insects is that the flapping wings might differentially affect acoustic input to the ear for elevated versus depressed sound sources (Payne et al., 1966).

The mechanisms underlying determination of sound-source azimuth have received much more attention. As mentioned earlier, azimuth-dependent ITDs are likely to be too small to be resolved by insect nervous systems. In some cases, an insect's body may be sufficiently large relative to the sound wavelength to generate ITDs of at least a few decibels. Such is the case, for example, for the ultrasound (i.e., short wavelength) avoidance responses of large moths and similarly sized insects.

In other cases, the discrepancy between body size and wavelength is so large as to make sound localization based solely on diffraction unlikely. The two best studied examples of this are crickets and the parasitoid flies for which crickets are hosts. The cricket songs to which both insects orient have a wavelength of about 7 cm compared with an interaural distance in crickets of about 1 cm and of only 500 μm in the fly.

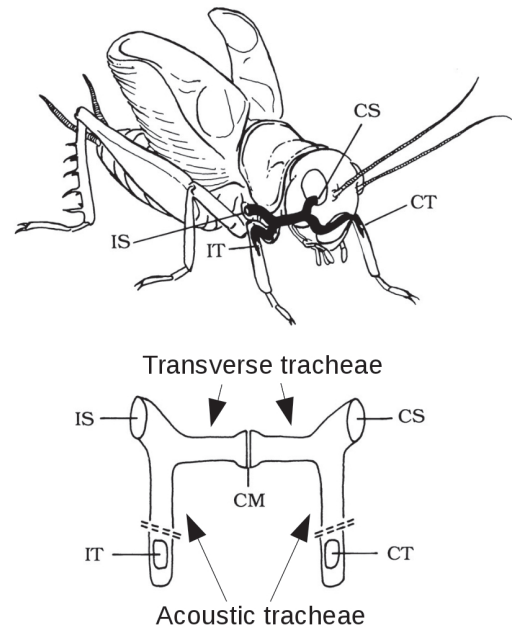


Figure 5. The cricket pressure-gradient system in situ (**top**) and schematically (**bottom**). Vibration of the ipsilateral tympanum (IT; the eardrum on the same side as the sound source) is affected by sound acting on its external surface and by sound reaching its internal surface via tracheal paths from the ipsilateral (IS) and contralateral (CS) spiracles. CT, contralateral tympanum; CM, septum that joins the left and right tracheal branches. **Dashed lines** indicate that the acoustic tracheae have been truncated. Modified from Michelsen (1998).

Nevertheless, both insect groups are capable of exquisitely fine determination of sound azimuth as a result of coupling between the left and right ears.

Pressure Gradient Ears of Crickets

As in katydids, the cricket respiratory system is adapted for auditory function where a specialized acoustic trachea links a spiracle to the inner surface of the eardrum. Here, however, the main result is improved directionality rather than increased sensitivity. Vibration of each eardrum is driven mainly by sound that reaches it along three routes: directly to its exterior surface, indirectly to its interior surface through the tracheal route on the same side, and via the acoustic spiracle and trachea on the opposite side. The latter route is possible because the left and right acoustic tracheae abut at the midline where they are separated by a thin septum (Figure 5).

The relative amplitudes and phases of the three inputs vary with the sound direction because of differences in arrival times at the three loci as well as the highly frequency-dependent transmission characteristics of the tracheal pathways (Michelsen, 1998). For cricket song frequency, which is about 5 kHz, summing the three inputs results in direction-dependent variation of vibration amplitude approaching 20 dB, far greater than the maximum of 1-2 dB possible from diffraction alone.

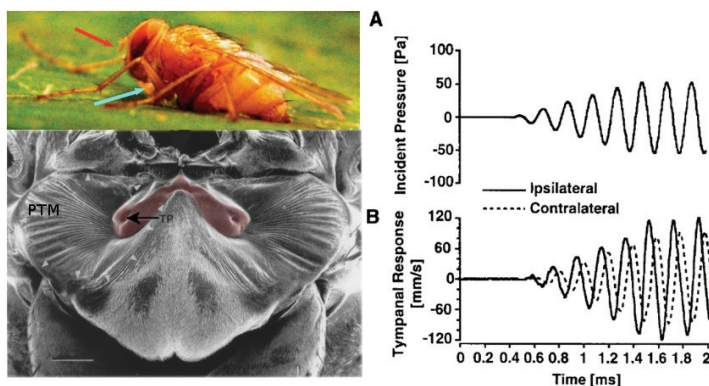


Figure 6. Mechanically coupled ears of the fly *Ormia ochracea*. **Top:** cyan arrow points to location of the eardrums, which are hidden by the head; **red arrow** shows approximate angle of view in the image below, after removal of the head. **Middle:** left and right eardrums (prosternal tympanal membrane [PTM]) are linked by a cuticular bridge, highlighted in **pink**. **Black arrow** points to tympanal pits (TP), the attachment sites of the inner ear neuronal components. Scale bar: 200 μm . Modified from Robert et al. (1994). **Right:** sound pressures at the two eardrums are indistinguishable (A), but vibration of the ipsilateral eardrum is earlier and larger (B). From Robert et al. (1996).

Mechanically Coupled Fly Ears

Not only are the eardrums of the parasitoid fly *Ormia ochracea* close together, they are nearly coplanar on the ventral surface of the fly's chest, so that there is essentially no "fly" between them. As a result, the IID is immeasurably small. The maximum ITD for a source located perpendicular to the intereardrum axis is only about 1.4 μs . The ability of this system to generate direction-dependent differences in eardrum vibration results from the linking of the two eardrums by a thin bridge of cuticle, the relatively stiff material that forms an insect's "shell" (Figure 6).

The left and right halves of the bridge are linked by a flexible joint that permits them to flex in one of two ways. Equal sound pressures on the two sides generate a tendency to oscillate inward and outward in synchrony, like the flapping wings of the butterfly. However the direction-dependent, albeit small, ITD gives the side nearest the sound source a slight head start, driving a rocking or seesaw-like motion. The overall mechanical response of the system is the sum of these two tendencies, resulting in a seesaw in which the two sides both pivot and flex about the midpoint. Remarkably, this complex motion pattern results in a difference in vibration amplitude for a cricket-like sound frequency of up to 12 dB, and the time shift between motion on the two sides is amplified to up to 50 μs (Miles et al., 1995). Moreover, because the response latencies of nerve cells is inversely related to stimulus strength (and thus to vibration amplitude), the ITD at the neuron level is even greater, up to 250 μs (Mason et al., 2001).

Conclusion

It is said that necessity is the mother of invention. This adage applies not only to human creativity but also when the "mother" in question is Mother Nature, whose method of invention is natural selection. Examples of remarkable biological adaptations that meet particular needs are abundant throughout the natural world but perhaps no more so than in the feats of "engineering" that allow insects to overcome the many constraints imposed by their diminutive size and exploit acoustics in their daily lives.

Acknowledgments

I thank Natasha Mhatre and Arthur Popper for helpful comments; John Cooley, Norman Lee, and Vicki Powys for generously contributing photographs; and Fernando Montealegre-Z for kindly supplying a video.

Biosketch



Gerald Pollack is professor emeritus of biology at McGill University, Montreal, QC, Canada. He has studied the neuroethology of insect sensory systems throughout his career, beginning with his graduate work on blowfly chemoreception and feeding behavior with Vincent Dethier. His interest in insect hearing and communication, which began with his postdoctoral work with Ron Hoy, persists in his "retirement" where, as a volunteer "postdoc" with Andrew Mason, University of Toronto Scarborough, Toronto, ON, Canada, he continues to work on the auditory neuroethology of tree crickets and parasitoid flies.

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