Invertebrate Ears and Hearing

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Synonyms

Acoustic Sensillum; Auditory Sensillum

Definition

A cuticular sense organ (sensillum) containing a specialized ►mechanoreceptor for transducing the particle velocity or pressure component of sound energy into electrochemical nerve impulses that are transmitted to the central nervous system (CNS) and which are used to mediate acoustically evoked behavior (e.g., detection and localization of mates, predators, prey or hosts).

Characteristics

Among invertebrates, a sense of hearing has been described only in arthropods. Except for a few species of Crustacea, members of the Insecta are the only invertebrates known to both produce and receive airborne sounds, and to use airborne acoustic signaling to mediate behavior. Some insect auditory organs, such as Trichoid Sensilla (Fig. 1a) or Johnston's Organs (Fig. 1b) are sensitive to the particle velocity component of sound, sometimes called near-field sounds. Particle displacement receivers are inherently directional because particle displacement occurs parallel to the direction of sound propagation and therefore the magnitude of the sensory response varies with the orientation of the receiver in the sound field. ►Tympanal Organs (Fig. 1d) detect sound pressure via the movement of a tympanal membrane (eardrum) that becomes deformed by fluctuations in the pressure component of sound. Pressure detector receivers are used to obtain directional information by comparing responses from receptors that are separated in space and time. Sound localization is thus achieved using ►interaural level difference (ILD) and ►interaural time difference (ITD) cues. The detection of substrate-borne vibrations is widespread in invertebrates, has many parallels with airborne sound reception, and has been widely studied in insects, spiders and other arthropods. Little is known of insect vibration receptor organs, but the best known is the Subgenual Organ (Fig. 1c).

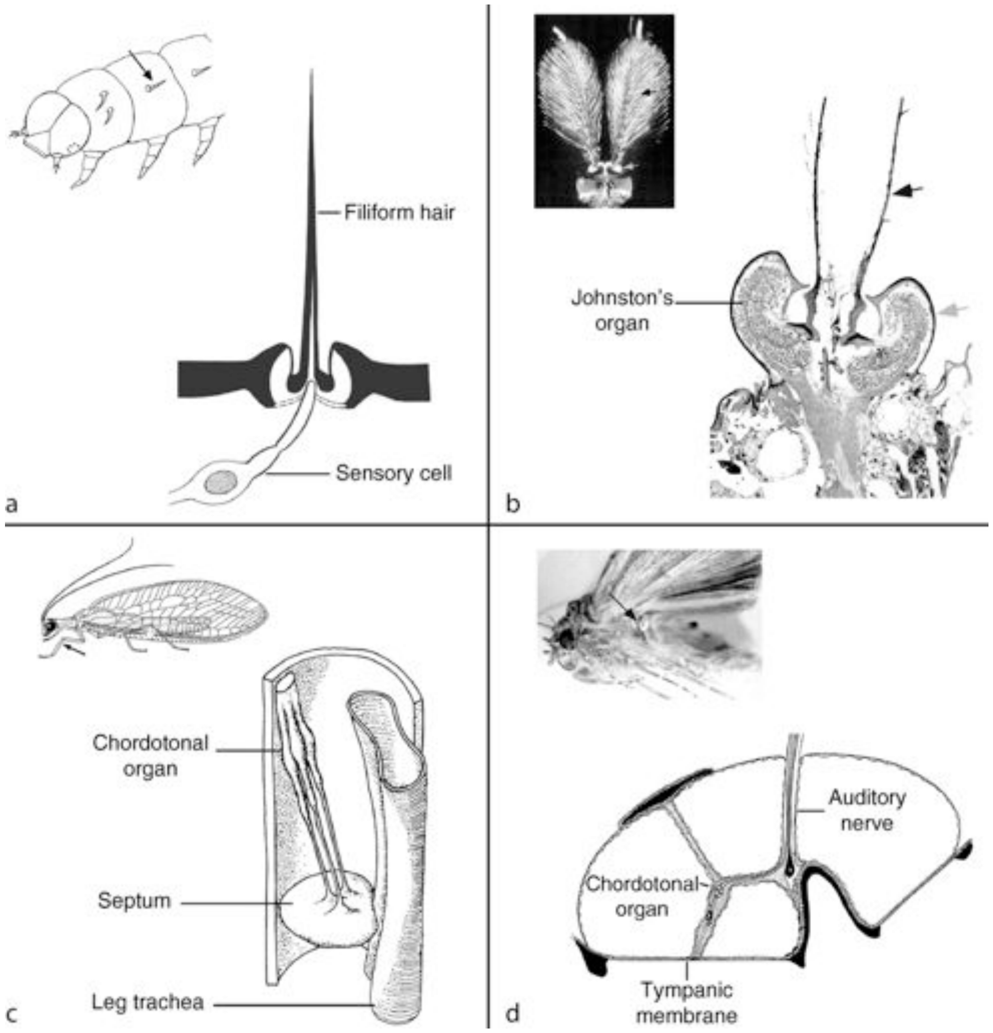
This essay will first discuss the ►chordotonal organ – the main type of acoustic sensillum innervating insect ears. We will then review the different types of acoustic receptors, with a concentration on tympanal organs but also including particle displacement and substrate vibration receptors.

Chordotonal Organs

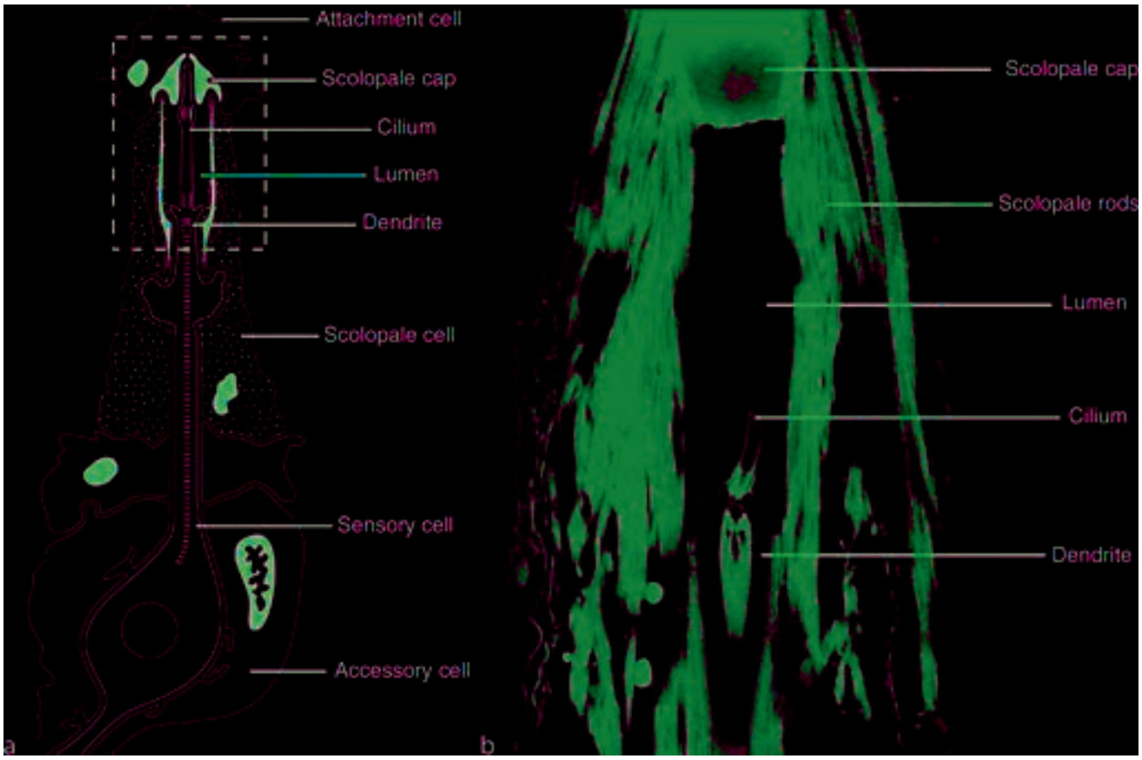
Insect auditory sensilla are derived from more generalized mechanosensory structures consisting of sensory cells, accessory cells, and cuticular structures [4]. The sensory cell is usually a ►bipolar neuron with a dendrite that becomes modified in its outer (distal) segment to contain a cilium constructed of microtubules – the ciliary dendrite that connects to the external cuticle. Accessory cells envelop and provide mechanical and nutritive support to the sensory neuron. Cuticular structures couple the point of mechanical stimulation, either directly or indirectly, to the sensory ciliary dendrite and aid in mechanoelectrical transduction.

The most common auditory sensillum is the chordotonal organ (Fig. 2). Chordotonal organs are proprioceptive stretch receptors in crustaceans and insects [1,3]. Individual mechanosensory units within chordotonal organs are called scolopidia. Scolopidia consist of a linear chain of four cell types. (i) One or more bipolar neurons, each with a dendrite containing a modified $9 \times 2 + 0$ cilium. At present, the function of the cilium is unknown; however, it may act to mechanically support the dendrite and/or it may aid in the transfer of vibrational energy to the stimulus transduction region of the sensory neuron. (ii) A scolopale cell that forms a lumen around the dendritic cilium, and inserts distally into the extracellular scolopale cap (Fig. 2).

Within the cytoplasm of the scolopale cell, adjacent to the lumen, are the scolopale rods, which are bands of electron dense material composed of longitudinally



Invertebrate Ears and Hearing. Figure 1 Insects possess a diverse array of acoustic sensilla that detect a broad range of sounds and vibrations. (a) Trichoid Sensilla. Some caterpillars use long hairs (*arrow*) to detect near-field acoustic signals produced by flying parasitoid wasps. A bipolar sensory cell responds to deflections of the hair shaft. [Caterpillar and sensillum redrawn with permission from Markl H, Tautz J (1975) The sensitivity of hair receptors in caterpillars of *Barathra barassicae* L. (Lepidoptera, Noctuidae) to particle movement in a sound field. *J Comp Physiol* 99:79–87, and [4], respectively.] (b). Johnston's Organ. Other insects, including many flies, detect near-field sounds of conspecifics with their antennae. Flight sounds cause the antennal flagellum (*black arrow*) to vibrate, stimulating chordotonal organs in the Johnston's organ located at the base of the antenna (*gray arrow*). A cross section of the antennal base shows that the Johnston's organ is comprised of thousands of scolopidia. [Photograph courtesy of D. Huber. Micrograph adapted from Göpfert MC, Robert D (2001) Active auditory mechanics in mosquitoes. *Proc R Soc Lond B* 268:333–339.] (c). Subgenual Organ. Many insects communicate using solid borne vibrations. The best-studied receptor of seismic signals in insects is the subgenual organ, illustrated here from the leg of a green lacewing (*arrow*). The chordotonal organ connects via attachment cells to a septum, and vibrations of the leg hemolymph result in stretching and stimulation of the constituent scolopidia. [Lacewing drawing courtesy C. Henry. Subgenual organ schematic redrawn with permission from Devetak D, Pabst MA (1994) Structure of the subgenual organ in the green lacewing, *Chrysoperla carnea*. *Tiss Cell* 26:249–257.] (d). Tympanal Organ. In noctuid moths, the ears are located on the posterior metathorax (*arrow*). Schematic drawing of the moth ear illustrates how the simple chordotonal organ, with only two sensory neurons, attaches to the tympanal membrane. [Redrawn with permission from Treat AE, Roeder KD (1959) A nervous element of unknown function in the tympanal organs of moths. *J Insect Physiol* 3:262–270.].



Invertebrate Ears and Hearing. Figure 2 Chordotonal Organ ultrastructure. Chordotonal organs are comprised of individual sensory units called scolopidia. (a). Diagrammatic representation of a monodynal, mononematic ►scolopidium illustrating the main cell types: attachment cell, scolopale cell, sensory cell, and accessory cell. [Drawing by M. Nelson modified with permission from Gray EG (1960) The fine structure of the insect ear. *Phil Trans R Soc Lond B* 243:75–94.] (b). Electron micrograph of a single scolopidium showing the principle components of the scolopale and sensory cell. The micrograph is at the location of the dashed box in panel A [Adapted from Yack JE, Roots BI (1992) The metathoracic wing-hinge chordotonal organ of an atympanate moth, *Actias luna* (Lepidoptera, Saturniidae): a light- and electron-microscopic study. *Cell Tissue Res* 267:455–471.].

oriented microtubules surrounded by actin filaments. The scolopale rods likely support and limit lateral movements of the dendritic cilium, thus providing a mechanism for restricting sensillum responses to specific locations or axes of mechanical stimulation. Scolopale cells are also thought to selectively transport ions into the space surrounding the dendrite, thus establishing an electrical potential difference between the lumen and the dendritic cytoplasm, which serves as the ionic basis for action potential generation during stimulus transduction. (iii) Attachment cells connect the scolopale cell to the external cuticle (or provide an internal anchor point for inverted scolopidia). In addition to providing mechanical support, they are likely important for transferring mechanical energy to the spike generation region of the neuron. (iv) Glial (accessory) cells envelop and provide nutritive and mechanical support to the sensory soma. Despite tremendous diversity in their form and function, all insect ears that respond to the pressure component of sound are innervated with chordotonal organs that have Type 1, monodynal, mononematic scolopidia (for definitions, see [1,9].

Acoustic Receptive Organs

Four main types of acoustic receptive organs have been described for insects: Trichoid Sensilla, Johnston's Organ, Subgenual Organs, and Tympanal Organs [8,9].

1. *Trichoid (filiform) sensilla* (Fig. 1a) are hair-like cuticular projections specialized for the detection of near-field, low frequency sounds at close distances. The hair rests loosely in an epithelial socket and is innervated at its base by one or more sensory afferents that are bathed in a receptor lymph of special ionic composition. The neurons become depolarized in response to lever-like deflections of the hair shaft. Some caterpillars use trichoid sensilla to detect faint air currents caused by the wing beats of hymenopteran predators and parasitoids. Filiform hairs on the cerci of many insects, such as crickets and cockroaches, are used to detect air particle oscillations that are generated by predatory strikes and/or the wing movements of singing conspecifics.
2. *Johnston's organs* (Fig. 1b) are chordotonal sensory organs associated with the second antennal segment

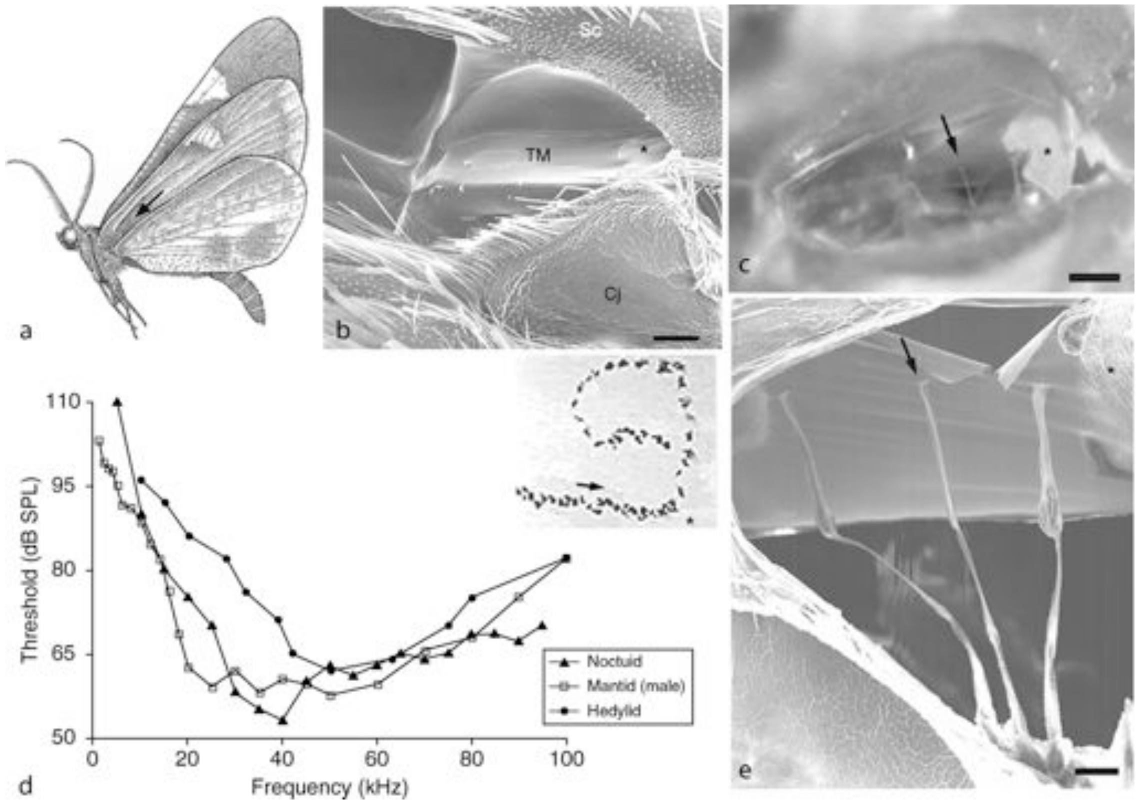
of insects. In some groups, including Diptera and Hymenoptera, the Johnston's organ is known to function in the detection of airborne sound [3]. The flagellar portion of the antenna oscillates in response to low frequency (near-field) sounds. The vibrations are then transmitted to mechanosensory scolopidia located at the base (pediculus) of the antenna. Many species of Diptera (e.g., mosquito) and Hymenoptera (e.g., honeybee) use the Johnston's organ to detect air currents produced by the wing beats of flying conspecifics, usually members of the opposite sex. The Johnston's organ is thought to be a diagnostic character for insects.

3. *Subgenual organs* (Fig. 1c) are chordotonal sensory organs located on the legs (proximal tibia) of most insects [1]. Substrate vibrations are thought to provide an adequate stimulus by setting into motion the fluid (hemolymph) within the leg, which in turn vibrates a septum to which the scolopidia are attached. Because subgenual organs are exquisitely sensitive to small-amplitude vibrations, they can effectively operate over long distances. Many terrestrial insects communicate with substrate vibrations, and the subgenual organ is thought to be the main vibrational receptor in adult insects. At present, little is known about how larval insects detect vibrations despite the widespread use of this modality by juvenile insects in a variety of taxa.
4. *Tympanal organs* (Figs. 1d, 3 and 4) are specialized for detecting the pressure (far-field) component of sound at relatively long distances and over a broad range of frequencies and amplitudes. Although anatomically and functionally diverse across taxa, insect tympanal organs are composed of three units: a tympanal membrane, a tracheal air space, and a chordotonal sensory organ. The tympanal membrane is a thinned region of cuticle that vibrates in response to changes in pressure between the external and internal sides of the membrane; the membrane vibrates most efficiently when the acoustic impedance of the sound medium is similar (matched) on the front and back sides. Insects obtain this impedance matching by modifying their internal, tubular tracheal (breathing) system to create an air space directly behind the membrane. The chordotonal organ is attached, either directly or indirectly, to the internal surface of the tympanal membrane. Oscillations of the membrane stretch the scolopidia. Longitudinal deformations of the sensory dendrite are thought to open membrane channels, resulting in a change of ion conductance, current flow, a change in receptor potential and the consequent generation of an action potential. The threshold of displacement for receptor activation can be as small as 1–10 nm [2]. Exact details of the spike generation mechanism are still unclear.

Most insects have a pair of tympanal membranes, and a few species have multiple paired membranes. Across taxa, the most common placement for the pair is on either side of the thorax or abdomen. This is typically the widest body region and is best suited for generating maximal interaural level difference (ILD) and interaural time difference (ITD) cues for sound localization [6,10]. ILD cues are generated by sound diffraction, which varies as a function of frequency (wavelength) relative to the size of the diffracting body. ITD cues vary with distance (arrival time or phase) between the two ears. Many insects show excellent directional hearing while flying or walking. Peripheral (tympanal organ) mechanisms of signal reception can be highly selective for sound direction.

Insect auditory afferents share many physiological characteristics with vertebrate receptors. For example, variation in the number, rate and timing of action potentials is the basis of information coding by the CNS [5]. Most auditory afferents fire tonically or phasitonically with an intensity-dependent change in spike rate and latency, and show spike adaptation to prolonged or repeated stimulus presentations. Receptor populations also vary in their absolute sensitivity to sound amplitude (range fractionation). In most cases where receptors are tuned to different frequencies, there is clear anatomical variation in scolopidia size and/or the mechanics of attachment to the point of stimulation, although the possibility that receptors with variable tuning also differ in their intrinsic cellular properties has not been eliminated. While both receptors and interneurons show a high degree of temporal pattern copying to the amplitude envelope of the stimulus, owing to the relatively high frequencies at which many species hear, insect auditory neurons typically do not phase lock to the fine waveform structure of the stimulus.

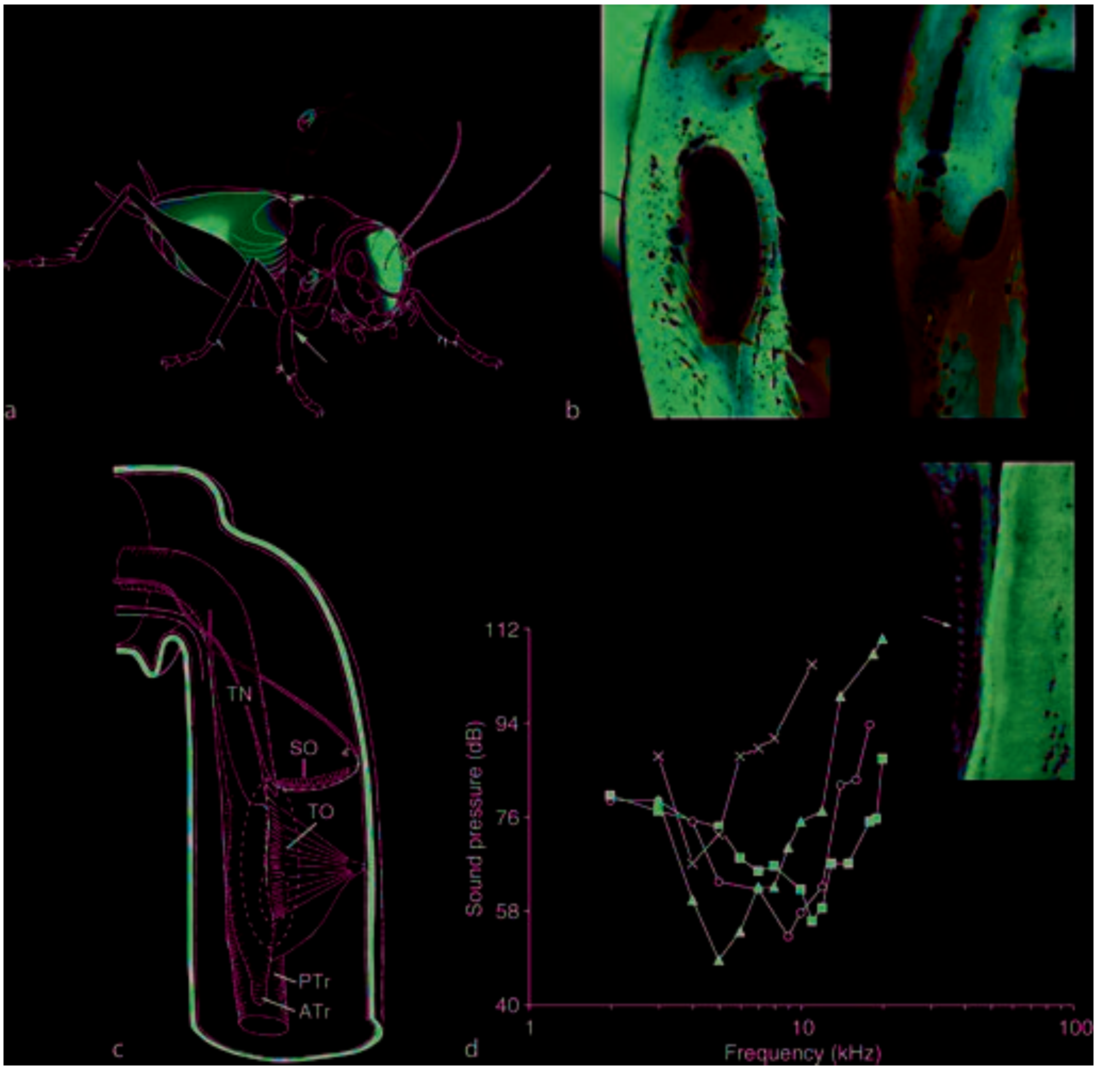
As in vertebrates, auditory behavior arises from serial and parallel central processing mechanisms [5]. Auditory afferents project to the ipsilateral auditory ►neuropile in the CNS where they synapse with interneurons (both intra- and interganglionic) that integrate with motoneurons. Central auditory neurons receive both excitatory (EPSP) and inhibitory post-synaptic potentials (IPSP) that vary in their strength, duration and latency. In some species a corollary discharge (efference copy) is used for processing self-generated sounds [7]. Central auditory neurons have responses that are tuned to stimulus frequency, amplitude, direction, or timing. Spectral tuning curves of interneurons are sharpened by frequency-dependent lateral inhibition. Extraction of directional information is achieved by integrating receptor spikes binaurally and is enhanced by reciprocal contralateral inhibition. A similar mechanism of mutual inhibition for contrast enhancement can also be used to extract stimulus amplitude or temporal pattern information.



Invertebrate Ears and Hearing. Figure 3 Tympanal ears used to detect the ultrasonic echolocation calls of predatory bats have evolved independently in several insect orders. (a). This nocturnal butterfly, belonging to the superfamily Hedyloidea, possesses a tympanal ear at the base of its forewing (*arrow*). (b). Scanning electron micrograph of the tympanal cavity, where the tympanal membrane (TM) resides. Modifications of the subcostal wing vein form a protective covering for the delicate tympanum and a canal that directs sound toward the ear. Also shown is the conjunctivum (Cj), also known as the countertympanal membrane. An asterisk marks a thickened region of the tympanal membrane. Scale bar: 100 μm. (c). Light micrograph of Hedylid ear. The *arrow* points to the middle of three chordotonal organs that attach to the inner surface of the transparent tympanal membrane. An asterisk marks the membrane thickening as shown in B and E. Scale bar: 100 μm. (d). Audiograms derived from extracellular recordings of auditory afferents in three groups of insects whose ears function primarily for bat detection: noctuid moth (*closed triangle*), praying mantis (*open square*), and hedylid butterfly (*closed circle*). *Inset*: consecutive video frames (33 ms interval) illustrating the evasive flight maneuver of a hedylid butterfly in response to stimulation with bat-like ultrasound. The direction of flight prior to stimulus onset (*asterisk*) is shown with a *black arrow*. (e). Scanning electron micrograph of the three hedylid chordotonal organs viewed from inside the tympanal chamber. The middle chordotonal organ is marked with an *arrow*. An asterisk marks the membrane thickening as shown in B and C. Scale bar: 20 μm. [(a–c), inset of (d), and (e) adapted from: Yack JE, Kalko EK, Surlykke A (2007) Neuroethology of ultrasonic hearing in nocturnal butterflies (Hedyloidea). *J Comp Physiol A* 193:577–590. Frequency tuning curves of (d) from Fullard JH, Yack JE (1993) The evolutionary biology of insect hearing. *TREE* 8: 248–252, and Yager DD (1996) Nymphal development of the auditory system in the praying mantis *Hierodula membranacea* Burmeister (Dictyoptera, Mantidae). *J Comp Neurol* 364:199–210.].

Diversity of Insect Ears

Tympanal hearing organs have arisen repeatedly in insects. To date, the count stands at 20 independent evolutions. Depending on the taxa, insect ears can be found all over the external body surface, including the thorax, abdomen, wings, legs, and mouthparts. The organs may be highly visible or cryptically located, and in some cases have become internalized. It is now commonly believed that the present diversity of insect auditory organs is a result of their evolving from pre-existing chordotonal sensilla that primarily served a proprioceptive or low-frequency vibratory detection function at that body location. The evolution of tympanal membranes, through a progressive thinning of appropriate regions of the exoskeleton, increased the organ's sensitivity to stimulus amplitude and frequency. The ubiquity of such mechanosensors near the exoskeleton surface provides many potential locations for the evolution of ears.



Invertebrate Ears and Hearing. Figure 4 Many insects use tympanal hearing organs for localizing and communicating with conspecifics. (a). Crickets use a pressure-difference receiver mechanism to localize sounds with wavelengths larger than the spatial separation of their ears, which are located on the proximal tibia of the forelegs (*arrow*). An H-shaped tracheal system (illustrated as floating above the cricket's body) internally connects sound inputs from both tympanal ears and from the acoustic spiracles located on opposite sides of the thorax. (b). Light micrographs of the large posterior (*left*) and small anterior (*right*) tympanal membranes. [(a–b) reproduced from: Yack J, Hoy R (2003) Hearing. In: Resh VH, Cardé RT (eds) Encyclopedia of insects. Academic Press, New York, pp. 498–505.] (c). Schematic internal view of the proximal tibia of a cricket, showing the tympanal nerve (TN), subgenual organ (SO), tympanal organ (TO) and the posterior and anterior trachea (PTr, ATr) that back their respective tympanal membranes. The approximate locations of the anterior (*small dashed oval*) and posterior (*large dashed oval*) tympanal membranes are shown. [Redrawn from Michel K (1974) Das Tympanalorgan von *Gryllus bimaculatus* Degeer (Saltatoria, Gryllidae). Z Morph Tiere 77:285–315.] (d). Threshold tuning curves of four primary auditory neurons showing a range of characteristic frequencies. The *inset* shows the linear, tonotopic arrangement of the tympanal organ scolopidia. A *black arrow* points to the cell body of an individual sensory cell. [Data extracted from Oldfield BP, Kleindienst HU, Huber F (1986) Physiology and tonotopic organization of auditory receptors in the cricket *Gryllus bimaculatus* DeGeer. J Comp Physiol A 159:457–464.].

The number of scolopidia, and thus sensory neurons per hearing organ, varies widely across taxa, ranging from 1–4 in moths, 2 in water boatman, 3–8 in beetles, 5–20 in lacewings, 20–75 in crickets and katydids, 60–100 in locusts, 100+ in flies, 600–2,000 in cicadas, and 2,000+ in some primitive grasshoppers. No clear relationship exists between the number of sensory afferents and the sensitivity of the tympanal organ to stimulus amplitude, frequency or phase (timing). Ears tend to be simplest in those groups that use hearing primarily for predator detection, and more complex in those groups that use sound for intraspecific communication.

Many of the simplest tympanal organs are the broadband pressure detecting ears found in moths and butterflies (Lepidoptera), lacewings (Neuroptera), beetles (Coleoptera) and mantids (Dictyoptera). Hearing in these groups has evolved primarily in the context of predator detection. More specifically, their ears function mainly to detect the ultrasonic echolocation signals of aerial insectivorous bats, and hearing in many species has been shown to mediate evasive flight maneuvers (Fig. 3).

Lepidopteran ears are often found on the thorax or abdomen, although a few species have evolved ears on their wings and mouthparts. The ears of lacewings are located in the radial vein at the base of each forewing. In beetles, ears have recently been described on both the abdomen and on the prothorax just behind the neck region. The ears of mantids are hidden within a groove along the ventral midline between the metathoracic legs. In many mantids, hearing is sexually dimorphic because the females are flightless and therefore are not subject to predation by aerial insectivorous bats; male mantids fly and thus their ears are better developed anatomically and have a higher sensitivity. A minority of lepidopterans use sound production and hearing for intraspecific communication. There is no behavioral or physiological evidence for frequency discrimination or well-developed directional hearing in these insect groups.

In two groups of Hemiptera the sense of hearing primarily serves intraspecific communication. In both groups the ears are normally sharply tuned to the sounds of calling conspecifics. With only two sensory cells, the mesothoracic ears of water boatman (Heteroptera) may appear to be simple, but are functionally complex. Each tympanal membrane connects to a clubbed cuticular process that alters the membrane resonance frequency and imposes a left–right hearing asymmetry. The membrane can vibrate effectively underwater because it contacts an air bubble that becomes trapped by the waxy integument when the bug submerges; the bubble oscillates in response to the stridulatory calls of conspecifics. During a dive, the volume of air depletes due to respiration, and this increases its resonance frequency. The ears of terrestrial cicadas (Homoptera) are also structurally complex. The tympanal membranes are located ventrally in a recess on the second abdominal segment; the chordotonal organ is contained in a rigid capsule connected to the membrane. Depending on the species, the organs may have thousands of scolopidia. The sense of hearing is often sexually dimorphic (commonly more sensitive in males). Male cicadas emit very loud songs to attract females from far distances. To avoid self-deafening while singing, the males fold (relax) their tympanal membranes and this dampens the dynamic range of their auditory sensitivity by >20 dB.

Invertebrate hearing is probably best understood in the Orthoptera, where hearing serves the functions of mate attraction, courtship, display, territorial spacing, aggression, prey detection, and defense from predators and parasitoids. Within this group there is ample behavioral and physiological evidence for frequency discrimination and directional hearing [6]. Locusts (Caelifera) possess a tympanal ear on either side of the first abdominal segment, and the modes of vibration of the tympanum systematically vary with sound frequency. Frequency discrimination is achieved by having four groups of scolopidia attached to the membrane at different positions that correspond to locations of vibrational maxima at different frequencies. Crickets and katydids (Ensifera) have a pair of tympanal membranes (anterior and posterior) on the proximal tibia of each foreleg (Fig. 4a, b), although the anterior membrane is not sensitive in crickets. A tracheal chamber apposed to the interior tympanal surface forms an air space behind each membrane, thus providing impedance matching (Fig. 4c). The tracheal chamber is continuous with a complex system of acoustic tracheae that influence hearing sensitivity, frequency tuning and directionality (Fig. 4a). As in vertebrates, frequency discrimination is achieved by having receptors that are tuned to different frequencies (tonotopy). The chordotonal organ consists of a linear array of scolopidia that attach indirectly to the tympanal membrane. Although the mechanism of receptor tuning is unresolved, a mechanical basis is likely because scolopidia gradually taper in size within the organ; proximal cells are tuned to lower frequencies whereas distal cells are tuned to higher frequencies (Fig. 4c, d). In katydids, the peripheral tonotopy is maintained with the CNS by the differential projection of receptors to interneurons within the auditory neuropile.

Some parasitoid flies (Diptera) have evolved tympanal hearing organs on the thorax just behind the head. Hearing is also sexually dimorphic in this group – poorly developed in males, whereas females use their ears to localize the songs of acoustic Orthoptera or Homoptera, and then deposit larvae on the host. Directional hearing in some female Diptera is among the most accurate in the animal kingdom. Although each ear has a single chordotonal organ connected to the inner surface of the tympanal membrane via an apodeme, the two membranes share a common tracheal air space and are also mechanically coupled. This has resulted in a completely novel and remarkably accurate sense of directional hearing [5].

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