Hearing in Insects

Martin C. Göpfert[1,*] and R. Matthias Hennig[2]

[1]Department of Cellular Neurobiology, University of Göttingen, D-37077 Göttingen, Germany; email: mgoepfe@gwdg.de

[2]Department of Biology, Behavioral Physiology, Humboldt-Universität zu Berlin, D-10115 Berlin, Germany; email: matthias.hennig@biologie.hu-berlin.de

*Corresponding author

Keywords

Abstract

Insect hearing has independently evolved multiple times in the context of intraspecific communication and predator detection by transforming proprioceptive organs into ears. Research over the past decade, ranging from the biophysics of sound reception to molecular aspects of auditory transduction to the neuronal mechanisms of auditory signal processing, has greatly advanced our understanding of how insects hear. Apart from evolutionary innovations that seem unique to insect hearing, parallels between insect and vertebrate auditory systems have been uncovered, and the auditory sensory cells of insects and vertebrates turned out to be evolutionarily related. This review summarizes our current understanding of insect hearing. It also discusses recent advances in insect auditory research, which have put forward insect auditory systems for studying biological aspects that extend beyond hearing, such as cilium function, neuronal signal computation, and sensory system evolution.

THE EVOLUTIONARY EMERGENCE OF INSECT HEARING

The first insects that took to land some 400 million years ago (89) were presumably deaf. From the initial perception of substrate vibrations (14), hearing evolved during the subsequent diversification of insects, which led to 30 orders and more than 900,000 species (45). During this diversification, the ability to hear airborne sounds evolved independently multiple times within at least nine insect orders: Orthoptera, Mantodea, Blattodea, Hemiptera, Hymenoptera, Coleoptera, Neuroptera, Lepidoptera, and Diptera (31, 60, 98, 154). Two major driving factors promoted the evolution of hearing in insects: acoustic communication, which can operate over large distances in cluttered environments (123), and acoustic detection of predators, most prominently echolocating bats (15). Within Orthoptera, for example, hearing presumably evolved primarily to facilitate intraspecific communication: Judging from fossils, bushcrickets already produced sounds (46)—and might have communicated acoustically (46, 107, 127)—some 165 million years ago in the era of dinosaurs. Predation by bats, which appeared 65 million years ago (139), then seems to have triggered the independent evolution of hearing in mantids and some coleopteran, neopteran, and lepidopteran taxa (15, 60, 100, 136). Although hearing was independently invented multiple times over the course of insect diversification, most insect species have remained deaf. Of the approximately 350,000 beetle species, for example, only some scarab and tiger beetles have ears and respond to airborne sound (26, 155), and although various beetles communicate via substrate vibrations (14), most beetle species seem devoid of hearing. Some hearing insects also eventually abandoned hearing, for example, when they gave up flight and thus were released from predation by bats (134).

THE MAKING OF INSECT EARS

Hearing relies on auditory sensory organs that convert sound-induced mechanical vibrations into electrical signals. With the exception of sound-sensitive filiform hairs, all the known insect auditory organs are derived from chordotonal organs—internal stretch receptors that are serially arranged along the insect body (21, 25, 152). Monitoring relative movements between adjacent body segments, chordotonal organs seem to primarily serve proprioception in the context of locomotion (25). Chordotonal organs often respond to substrate vibrations (21, 25), apparently predestining them for attaining auditory functions.

When evolving hearing, insects typically utilized a pair of chordotonal organs in one segment of their body and transformed them into a pair of auditory organs. Because different insects independently modified chordotonal organs in different segments, auditory organs can occur on various parts of the insect body (60). Mosquitoes, midges, honey bees, and some drosophilid flies, for example, hear with the Johnston's organ—a chordotonal organ in the second segment of the insect antenna (98). Crickets and grasshoppers, in contrast, bear auditory organs in their forelegs and the first abdominal segment, respectively, demonstrating that hearing must have independently evolved within these two orthopteran taxa (136). Occasionally, related insect taxa converged on the same chordotonal organs when independently evolving hearing. One example for such convergent evolution of auditory organs is provided by two distantly related taxa of parasitoid sarcophagid and tachinid flies, the Emblemasomatini and Ormiini. Species of both taxa independently transformed the same pair of chordotonal organs in their neck into auditory organs to acoustically locate their larval hosts, singing bushcrickets and crickets (75). Some insects use chordotonal organs even in more than one segment for hearing, such as mantids of the genus *Creobroter*, which detect sounds at different frequencies with meso- and metathoracic auditory organs (153). Even more spectacular in this respect is the bladder grasshopper *Bullacris membracioides*, whose abdomen bears six serially arranged auditory organ pairs (142).

To attain auditory functions, chordotonal organs had to be associated with accessory auditory structures that vibrate in response to sound and couple these vibrations to the organs. With respect to the sound-receiving structures, insect ears can be classified into antennal and tympanal ears. Like filiform hairs, antennal ears respond to the particle velocity component of sound, which sets the antenna into vibration (98). Tympanal ears, by contrast, bear a sound-receiving eardrum, a tympanum, that vibrates in response to the sound pressure component (60). Eardrums typically arose through a stepwise thinning of the cuticle and are backed with air sacs (60). Entering through the tracheal system, sound impinges on some insect eardrums from both the exterior and interior sides, turning these eardrums into pressure-difference receivers (87). Because the eardrums are backed with air sacs, impedance-matching middle-ear structures are unnecessary, allowing the auditory organ to pick up the vibrations directly from the eardrum. A striking exception is the endolymph-filled tympanal ears of the katydid *Copiphora gorgonensis*, which bear levers that match the impedance between air and the inner-ear fluid, analogous to human middle ears (92) (**Figure 1a**).

The sound-receiving cuticular region in some tympanal ears is not conspicuously thinned into a tympanal membrane. Anatomically, such ears might be classified as atympanal, although the cuticle might nonetheless vibrate in response to sound and function as an eardrum (142). For some sphingid moths, true atympanal pressure-sensitive ears are found on the mouthparts, which receive sounds with a plate-like structure on the inner side of their labial palps that is formed by overlapping scales (42, 44). Other sphingids independently thinned the cuticular region that carries the scales into the tympanum (42, 118, 119), indicating a parallel evolution of tympanal and atympanal hearing organs (42).

AUDITORY FREQUENCY CHARACTERISTICS AND MECHANICAL SOUND PROCESSING

Pressure-sensitive tympanal and atympanal ears operate at frequencies of up to some 300 kHz (91) and detect communication sounds and bat echolocation signals over large distances (60). Particle-velocity-sensitive antennal ears, in contrast, are advantageous for intimate communication at close distances and usually operate at frequencies below 1 kHz (9, 98, 145). In all three ear types, frequency filtering is provided by the mechanics of the sound-receiving and sound-transmitting structures, which, in some tympanal ears, tonotopically map sound frequencies to auditory sensory cells by means of traveling waves (**Figure 1b**). Such mechanical frequency decomposition, which is akin to that in the mammalian cochlea (117), has been documented for the tympanal ears of some orthopterans (103, 149) and the cicada *Cicadatra atra* (137). In tympanal ears, traveling waves are propagated either by the eardrum proper or by membranous inner-ear structures, whereby the waves seem to arise from a spatial grading of the mechanical properties of the wave-propagating structures and, in the case of the fluid-filled ears of some katydids, through interactions with the inner-ear fluids (92, 93) (**Figure 1a**). Insect antennal ears lack such mechanical frequency decomposition: The antennal mechanics provide a single resonant filter, and the vibration frequencies that pass through this filter are sufficiently low to phase lock the ensuing neuronal response (98). Intriguingly, the auditory sensory cells of antennal ears can differ in their frequency characteristics, even though they experience the same mechanical frequency filtering by the antenna (66). These differences in tuning point to additional, cell-intrinsic mechanisms of frequency tuning (35), such as the electrical tuning that is realized in some vertebrate hair cells (24). The hallmark of such electrical tuning is a depolarization-induced oscillation of the cell membrane potential (24), which has hitherto not been tested for in insect ears.

Some insects have interconnected the tympana of their two ears, making them rock up and down like a seesaw about their medial connection. This unusual tympanal arrangement is found

in the parasitoid sarcophagid and tachinid flies, where it facilitates directional hearing (115, 116, 122): Because the two ears of these flies sit side by side on the neck, the two tympana usually would always vibrate in unison, independent of the direction of sound incidence. Due to the coupling, however, the tympanum that is first hit down by sound makes the other tympanum swing up (115). This seesaw-like movement introduces a binaural time difference that, enabling highly accurate
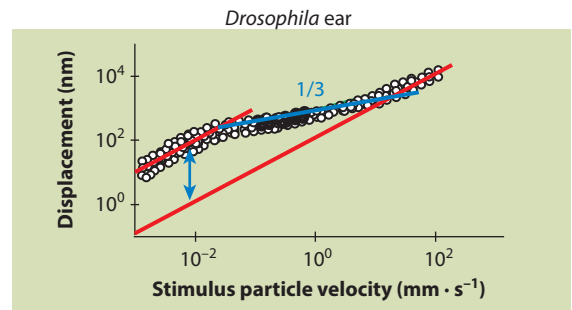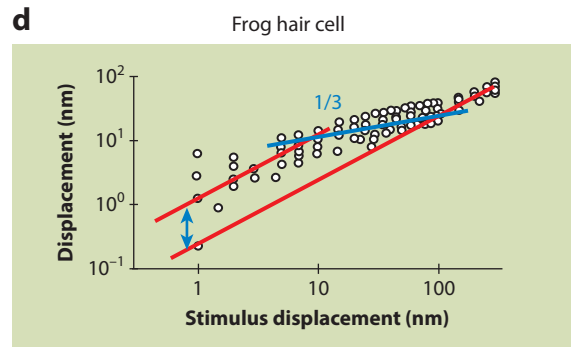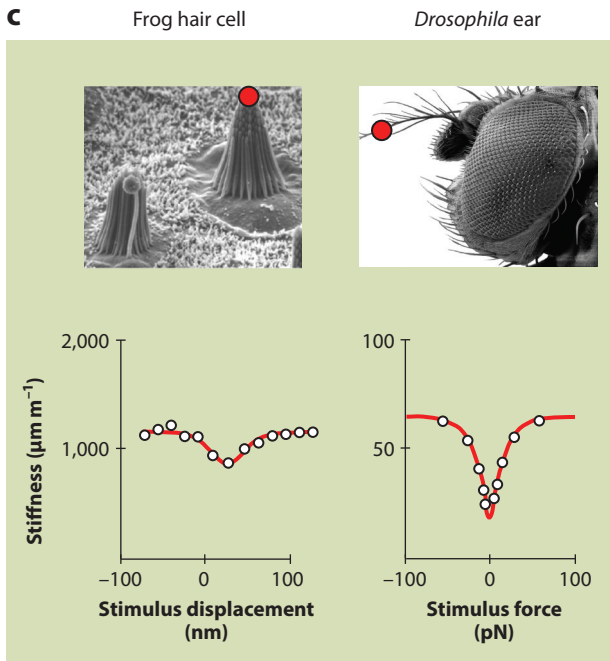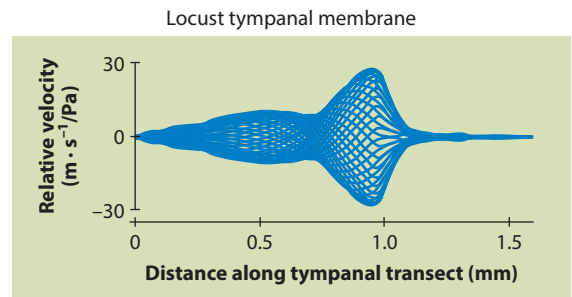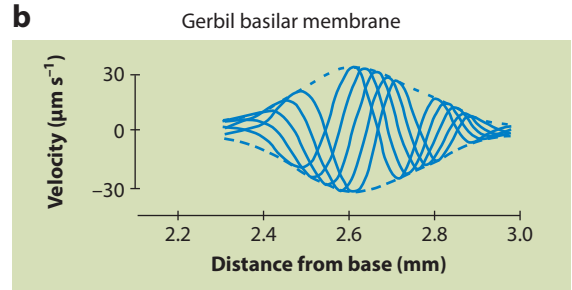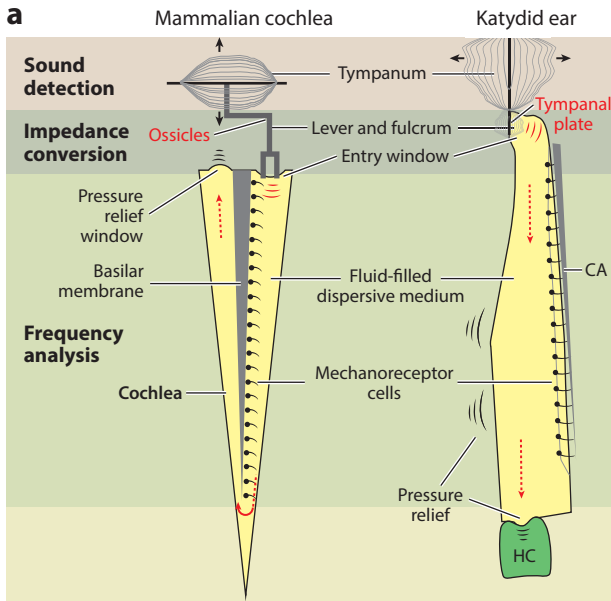
directional hearing (84), allows the flies to localize the singing insects on which they parasitize (96).

AUDITORY SENSILLA AND SENSORY NEURONS

Like chordotonal organs in general, insect auditory organs are composed of multicellular units, the scolopidia or chordotonal sensilla. Each chordotonal sensillum harbors one (tympanal ears) or two to three (antennal ears) mechanosensory neurons and several supporting cells (25, 98, 152). The sensory neurons are bipolar and monodendritic, bearing one single distal dendrite and a proximal axon. The outer dendritic segment represents a primary cilium with a 9+0 microtubule axoneme [nine peripheral microtubule doublets (9) and no central microtubule pair (+0)] (25). Supporting attachment and ligament cells stretch the neurons across different cuticular regions. A supporting scolopale cell forms an endolymphatic scolopale space around the cilia. Its endolymph seems to resemble that in the scala media of the mammalian cochlea in that it is potassium rich (25). The scolopale cell also supports the cilia through a barrel-shaped sleeve of intracellular rods, and supporting cells also secrete extracellular tubes or caps that surround the cilium tips (25, 152).

The numbers of auditory sensilla and sensory neurons vary greatly among insect hearing organs. Whereas one single auditory neuron per ear suffices to trigger bat avoidance maneuvers in notodontid and sphingid moths (43, 138), a cicada ear can house up to 2,200 sensory neurons (20). Triumphs in complexity are the antennal hearing organs of male mosquitoes, whose sensory neuron number (ca. 15,000; 6) comes close to the number of sensory hair cells in the human cochlea (ca. 16,000; 61).

Hair cells and chordotonal sensory neurons vastly differ in their anatomies, yet genetic evidence suggests that they might be evolutionarily related: Chordotonal sensilla are developmentally derived through mitotic divisions from single sensory organ precursors that are selected and specified by the basic-helix-loop-helix transcription factor Atonal (63). Atonal homologs are required for hair cell development (4), and it seems that chordotonal organs and hair cells might have diversified from ancestral *atonal*-expressing cells that were already present some 550 million years ago, before the protostome and deuterostome lineages split (27, 47, 64). Such an evolutionary scenario seems supported by the highly conserved microRNA miRNA-183, which occurs in both hair cells and chordotonal organs (106) and whose association with mechanosensory cell development might have evolved with bilaterian triploblasts or even diploblasts (28) prior to the protostome/deuterostome split.

Figure 1

Parallels between vertebrate and insect ears. (*a*) Schematics of the mammalian cochlea and the tympanal ear of the katydid *Copiphora gorgonensis*, documenting parallels in impedance matching (middle-ear ossicles and tympanal plate, respectively), fluid filling of inner ears, tonotopic arrangement of sensory cells along the auditory sensory organ, the crista acoustica (CA), and pressure relief [round window and hemolymph channel (HC), respectively]. Reproduced with permission from Reference 92. (*b*) Traveling waves, as measured at subsequent phase intervals along a section of the basilar membrane in the gerbil (*Meriones unguiculatus*) cochlea and across the locust (*Locusta migratoria*) tympanal membrane. Modified from References 113 and 149. (*c*) Nonlinear gating compliance betrayed by the hair bundle mechanics of a hair cell from the bullfrog (*Rana catesbeiana*) sacculus and the antennal sound receiver of *Drosophila melanogaster*. Red circles in upper panels indicate measurement sites. Red lines in lower panels represent the fitted gating spring models. Modified from References 1 and 59. (*d*) Compressive nonlinearity introduced by active amplification in the mechanics of actively oscillating hair bundles of bullfrog hair cells and actively oscillating *D. melanogaster* antennal sound receivers. Both systems display linear regimes (*red lines*) at high and low stimulus intensities and a nonlinear regime at an intermediate stimulus intensity (*blue lines*). In the nonlinear regime, the response amplitude increases with one-third the power of the stimulus amplitude, as characteristic of active oscillators operating at a Hopf bifurcation. Blue arrows indicate amplification gains. Modified from References 36 and 83.

AUDITORY TRANSDUCTION

Insect auditory neurons rival hair cells in terms of sensitivity, responding to sound-induced vibrations with amplitudes of less than 1 nm (116, 148). Insect auditory neurons also detect vibrations with an exquisite speed, transducing them into electrical signals within less than 1 ms (1). These short latencies signal that the mechanical stimuli activate ion channels directly, without intermittent second messenger cascades (1, 157). The strongest evidence for such direct gating is nonlinear gating compliance, in other words, a drop in the stiffness of the sound-receiving structures that is caused by the direct ion channel gating (59). Nonlinear gating compliance can be seen in the mechanics of the stereociliar hair bundles of vertebrate hair cells (59, 69) and the antennal sound receivers of the yellow fever mosquito, *Aedes aegypti* (98), and the fruit fly, *Drosophila melanogaster* (1, 97) (**Figure 1c**). In all these cases, the gating compliance quantitatively conforms to the gating spring model of mechanotransduction, which posits that mechanical stimuli directly gate ion channels that occur in series with elastic elements, the gating springs (3, 99). In *D. melanogaster*, these gating springs contribute significantly to the auditory mechanics, with their combined stiffness accounting for almost half of the stiffness of the antennal sound receiver (97).

The fly's antennal mechanics report the direct gating of at least two types of ion channels that differ in their mechanosensitivities (22). Whereas the less sensitive channel remains unidentified molecularly, the gating of the more sensitive channel type requires the transient receptor potential (TRP) family member No Mechanoreceptor Potential C (NOMPC = TRPN1) (22). NOMPC localizes to the tips of chordotonal sensory neurons (78) and forms a mechanogated ion channel (156). In the *Drosophila* ear, NOMPC is specifically required for sensitive hearing (23), yet whether it mediates or facilitates sound transduction remains controversial (158): In addition to NOMPC, two members of the TRPV (vanilloid receptor–related TRP) subfamily, Nanchung (Nan) and Inactive (Iav), were surmised to mediate insect sound transduction (79). Nan and Iav are essential for chordotonal neuron function and localize downstream of NOMPC to the proximal region of auditory neuron cilia (34, 70), where they form Nan-Iav heteromers (34, 101). Neither Nan-Iav heteromers nor their single subunits can be gated mechanically (101); future investigations are required to determine how these channels are activated.

In addition to being a mechanogated channel, NOMPC bears an exceptionally large number of N-terminal ankyrin repeats that, forming a coil with one turn, might act as a gating spring that promotes and admits gating movements of the channel (58). Consistent with such gating spring function, the NOMPC ankyrin domain binds to microtubules (10), confers NOMPC mechanogating (159), and, in some insect mechanosensory neurons, extends into fine filaments that span between the cell membrane and the microtubule cytoskeleton (80). Whether such membrane-microtubule connectors also occur in chordotonal neurons remains to be tested, and the same applies to the putative function of the NOMPC ankyrin domain as a gating spring (157).

Mammals and birds lack NOMPC orthologs, and it seems unlikely that hair cells use TRP channels for mechanotransduction (158). One accessory subunit of the hair cell transduction channel that might also be implicated in insect hearing (16) is a conserved tetraspan family protein (151), and candidates for the pore-forming subunits are transmembrane channel-like (TMC) proteins (57). TMC proteins also occur in insects, and although their involvement in insect hearing has not been examined, it seems likely that insect and vertebrate auditory transduction employ equivalent mechanisms but different proteins.

MECHANICAL AMPLIFICATION

In addition to using hair cell–like transduction mechanisms, insect auditory neurons share the ability of hair cells to actively amplify the sound-induced vibrations they transduce (40, 85).

This mechanical amplification modulates the auditory mechanics, introducing salient features in the macroscopic performance of the ear. These features include (*a*) a compressive nonlinearity that condenses a wide range of sound intensities into a narrow range of vibration amplitudes, (*b*) frequency-specific amplification that enhances the ear's mechanical susceptibility and frequency selectivity, (*c*) self-sustained oscillations in the absence of sound, and (*d*) power gain, reflecting active energy contributions that assist the vibrations inside the ear (40, 62). Physically, all these features are generic properties of a self-tuned critical oscillator that operates near the verge of an oscillatory instability, a Hopf bifurcation (62). Most of these features have been observed in various vertebrate ears and in the hair bundle mechanics of individual hair cells (62). The hair bundle mechanics of individual hair cells are largely mimicked by the antennal sound receiver of *Drosophila*, which likewise is actively tuned (39), shows power gain (37, 97), can oscillate spontaneously (36, 37, 39), and displays a compressive nonlinearity and frequency-dependent amplification with a gain of approximately 10 (36) (**Figure 1d**). Self-sustained oscillations, compressive nonlinearities, and frequency-dependent amplification have also been documented for the antennal ears of mosquitoes (38) and the tympanal ear of two tree cricket species, *Oecanthus henryi* (86) and *O. nigricornis* (95). Harmonic distortion products, which in vertebrates arise from active amplification, were detected in the form of otoacoustic emissions (i.e., sounds generated by the tympanal ears of locusts and moths) (72) and were also observed in the mechanics of mosquito antennae (145) and of insect tympanal membranes (86, 90).

Active amplification makes soft sounds audible, sharpens the ear's mechanical frequency tuning, and matches vibration amplitudes to the mechanosensitivities of auditory transduction channels (40, 62, 85). In mosquitoes, active amplification might also enable high-frequency hearing (9, 145), and in *Drosophila*, it matches the ear's mechanical tuning to conspecific songs (39, 114). Mechanistically, active amplification in insect ears seems driven by auditory sensory neurons (32). Analogous to hair cells, these neurons can be motile and exert positive feedback on the mechanical input of the ear (39, 97). Hair cells display two different forms of motilities: a somatic electromotility that manifests itself in voltage-driven length changes of the hair cell somata, and a hair bundle motility in which their stereociliar hair bundles twitch (62). The somatic electromotility arises from Prestin—a member of the SLC family of anion transporters that no longer transports ions but converts changes of the cell membrane potential to movements, much like a piezo crystal (62). The active hair bundle motility, by contrast, is driven by the direct mechanical gating of transduction channels and associated movements of myosin motors that also seem to promote transduction channel adaptation (62). Prestin-based motility reportedly occurs in mammals and birds, whereas hair bundle motility might be a conserved property shared by all hair cells (62). Prestin orthologs are expressed in the auditory neurons of mosquitoes and *Drosophila* (147), yet mutant analysis revealed that, at least in the *Drosophila* ear, mechanical amplification is independent of Prestin (67). Instead, an active version of the gating spring model that explains active hair bundle motility was found to also describe active amplification in *Drosophila* hearing (97), indicating that mechanogated channels and associated motors promote amplification in the fruit fly's ear. The channels seem to be formed by NOMPC, which is essential for amplification (23, 36), and the mere presence of dynein-like arms in the auditory neuron cilia suggests that the motors might be axonemal dyneins. Indeed, several evolutionarily conserved proteins implicated in the assembly of dynein arms are required for mechanical amplification in *Drosophila* hearing, including, for example, the leucine-rich repeat domain protein TILB (68), the zinc-finger protein ZMYND10 (94, 131), and the coiled-coil domain protein Hmw (133). Also, axonemal dynein genes seem to be expressed in insect auditory sensory neurons (131), yet whether they contribute to active mechanical amplification remains to be seen (35).

Only about half the sensory neurons in the *Drosophila* ear contribute to amplification (23), demonstrating that not all chordotonal neurons amplify mechanical stimuli. In tree cricket ears,

amplification appears and disappears sporadically (86), pointing to regulatory mechanisms that control the amplification gain (32). The proteins calmodulin (131) and the Nan and Iav TRPV channels (36) have been implicated to control amplification gain. Amplification in vertebrate ears is controlled by auditory efferent fibers that synapse onto the hair cells (111), yet chordotonal organs have hitherto not been reported to receive efferent innervation (25), and in *Drosophila*, mechanical amplification persists when synaptic transmission is blocked pan-neurally (65).

GENETICS OF SENSORY NEURON ASSEMBLY AND FUNCTION

In addition to TRP channels and proteins implicated in dynein arm assembly, various other proteins are required for insect auditory sensory neurons to function, including several components of the intraflagellar transport machinery that moves proteins along the ciliary axonemes. One component of this machinery, reduced mechanoreceptor potential A (REMPA), is required for compartmentalizing chordotonal neuron cilia into distal and proximal regions and for targeting the Nan-Iav channels to the latter proximal zone (77). The proper ciliary localization of TRP channels also involves Tubby (104), which is implicated in cochlear function, and a chordotonal neuron-specific forkhead transcription factor, Fd3F (102). Regulating various genes that encode mechanosensory-relevant cilium proteins, Fd3F seems to control a genetic program that renders chordotonal neuron cilia mechanosensitive. Another transcription factor, Engrailed, was implicated in the central wiring of auditory neurons to their downstream axonal targets (105), and auditory-relevant ion pumps and extracellular matrix proteins in insect ears have been defined (11, 126). Genetic screens have identified various additional insect auditory organ genes, including ciliary proteins (2) and, rather unexpectedly, phototransducer components: Almost the entire phototransduction machinery was found in the auditory organ of *Drosophila*, and visual rhodopsins were discovered to facilitate mechanotransduction and amplification by the auditory sensory neurons of the fly (131).

Despite the progress in the genetic dissection of insect hearing, we still do not know whether the functional transition of chordotonal organs into auditory organs was accompanied by modifications to the sensory cells: All the auditory organ genes whose cellular expression patterns have been analyzed seem to also occur in nonauditory chordotonal organs. Likewise, the genetic programs that direct the formation of accessory auditory structures such as tympanal membranes have hitherto remained elusive. Hints that the formation of auditory organs and accessory auditory structures might be genetically linked come from *Drosophila* mutants lacking Atonal and Spalt transcription factors: These mutants lack the Johnston's organ as well as the antennal joints that transform their antennae into sound receivers (19, 41).

CENTRAL SOUND PROCESSING

Insect auditory neurons are primary sensory neurons whose axons propagate action potentials to the central nervous system (25). Here, behaviorally relevant auditory information is extracted to trigger sound-evoked behavioral responses (50, 109). In the context of bat avoidance these responses include freezing or evasive flight maneuvers, whereas in the context of intraspecific communication they may entail the production of acoustic replies or positive phonotaxis movements toward the signaling animal. The latencies of these behavioral responses can be minute: In some katydids, the females reply to male songs within 25 ms (18), leaving time for just a handful of neurons to drive the female's decision to reply. Indeed, whereas mammals allocate six separate nuclei in their brains to auditory signal processing (128), moths, mantids, and crickets already extract information about approaching bats at the first auditory synapse (110), and crickets employ just four to six interneurons to compute sparse representations of conspecific songs (74). Rather
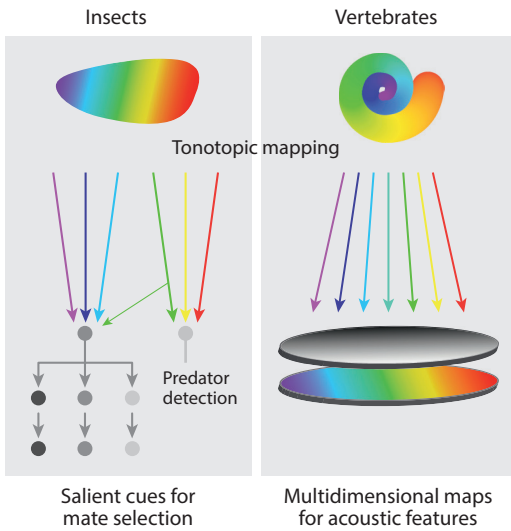
than allow for general-purpose operations, this computational sparseness restrains auditory processing to the selective recognition and localization of salient acoustic signals (i.e., intraspecific communication signals and the echolocation calls of hunting bats).

When co-opting chordotonal organs for hearing, insects seem to have taken over the central mechanosensory tracts downstream of these organs for auditory signal processing (7). Although auditory organs can feed into these longitudinal tracts in different parts of the body, the neural substrates for central auditory processing, including even homologous interneurons (8), seem surprisingly similar across taxa. These auditory interneurons process information about the sound frequency, intensity, and direction that is conveyed to them by auditory sensory neurons.
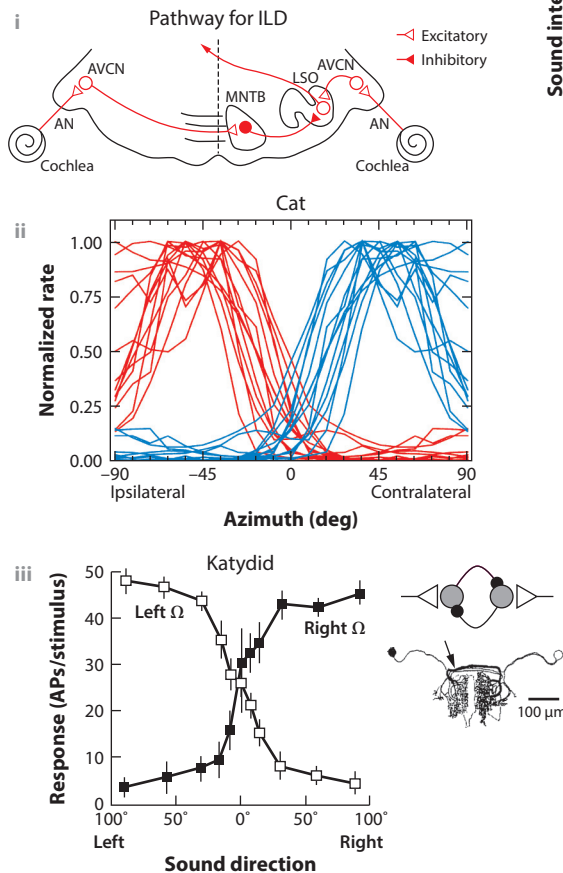
Within the central nervous system, auditory sensory cells with different frequency characteristics can converge onto different interneurons and thus feed into separate frequency channels (121), whereas other interneurons integrate over the whole available frequency range. Several insects that fly at night hold two semantic frequency channels, allowing for a categorical perception of communication signals and ultrasonic bat echolocation calls (136, 150) (**Figure 2a**). Insect auditory sensory neurons can tonotopically map sound frequencies to central neuropiles (121), yet unlike in vertebrates, these frequency maps are not conserved at the level of downstream interneurons (53) (**Figure 2a**). Some computational principles of frequency and intensity processing, however, are shared by vertebrates and insects. One example is lateral inhibition, which sharpens neuronal frequency selectivity and can selectively tune neurons to sex-specific mating signals (50). Another example is dynamic range fractionation, which affords hearing across a wide intensity range (50) (**Figure 2b**). Even the two auditory sensory cells comprised by some moth ears show such dynamic range fractionation: The more sensitive neuron informs the moth about the presence of bats, while the less sensitive neuron may trigger last-chance escape maneuvers once a bat has come close (30). Although commonalities exist between insect and vertebrate central sound processing, there are aspects of vertebrate auditory systems that have not been observed in insects. Although insects hold records in high-frequency hearing (91), neuronal phase locking (i.e., the spiking activity coupled to the phase of a sine wave) at kilohertz frequencies, as known from barn owls (*Tyto alba*) (71), has not been documented for insect auditory systems. The same applies to the reduction of noise across frequency channels by a mechanism known as comodulation masking release, by which the signal-to-noise-ratio is improved because correlated noise across spectral bands is suppressed (128). Maplike representations in insect auditory systems seem restricted to carrier frequencies at early stages of neuronal processing (53), and tonotopic representations of higher-order cues such as location, pitch, timbre, and frequency-modulated sweeps (128) have not been observed.

Despite their small size, insects can pinpoint the direction of sound sources with exquisite accuracy, even though interaural time differences are virtually nonexistent and interaural intensity differences are small (122). By mechanically coupling their tympana, parasitoid flies introduce microsecond-range interaural time differences in their tympanal mechanics. These differences are enhanced neurally by intensity-dependent latencies, precise spike timing, and the averaging of the responses of many sensory neurons, allowing the flies to locate their singing insect hosts with an angular accuracy of 2° (84, 116). As in flies, high accuracy in the frontal plane is observed in crickets and katydids (124, 129); beyond 5°–10° sound localization quickly changes over to a simple lateralization. Grasshopper ears are extreme in this respect, as these insects neurally collapse the accuracy of localization into two simple left-right hemispheres (144). Notwithstanding this apparent waste of information, this left-right distinction allows the animals to localize singing conspecifics with an utmost precision by approaching them in a zigzag course. The interaural intensity differences that drive the direction of these body turns are minute, hardly exceeding 1 decibel (144). Whereas vertebrates employ large numbers of interneurons to compute interaural time and intensity differences, insects perform these computations with single cells. A prominent example is

a Convergent vs. distributed representations

Insects | Vertebrates

Tonotopic mapping

Predator detection

Salient cues for mate selection | Multidimensional maps for acoustic features

b Lateral inhibition and range fractionation

Katydid

Mouse

Moth

Vertebrate

c Directional hearing and contralateral inhibition

i Pathway for ILD

◁ Excitatory
◀ Inhibitory

AVCN · AVCN · LSO · MNTB · AN · AN · Cochlea · Cochlea

ii Cat

iii Katydid

Left Ω · Right Ω

100 µm

d Band-pass filters

Cat

Crickets

Toce
Gbim
G14
Grub
Gtex
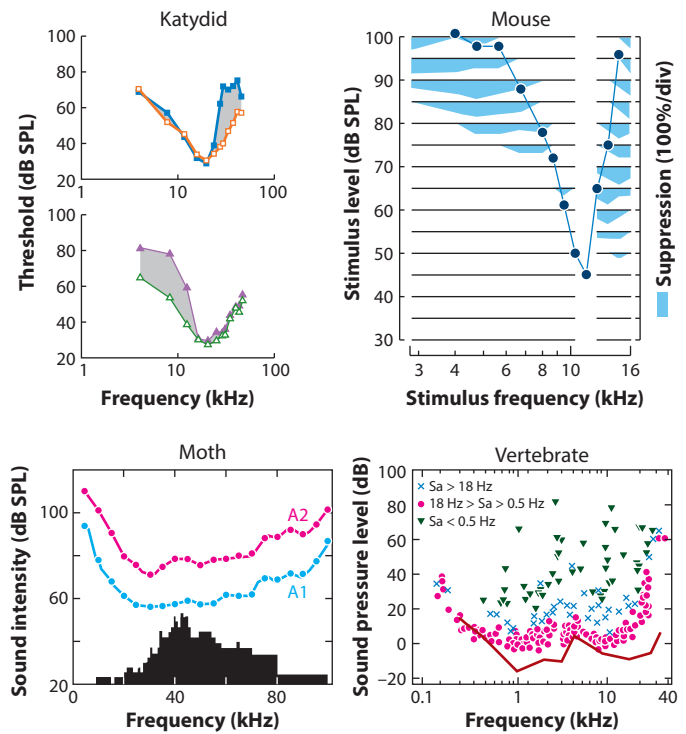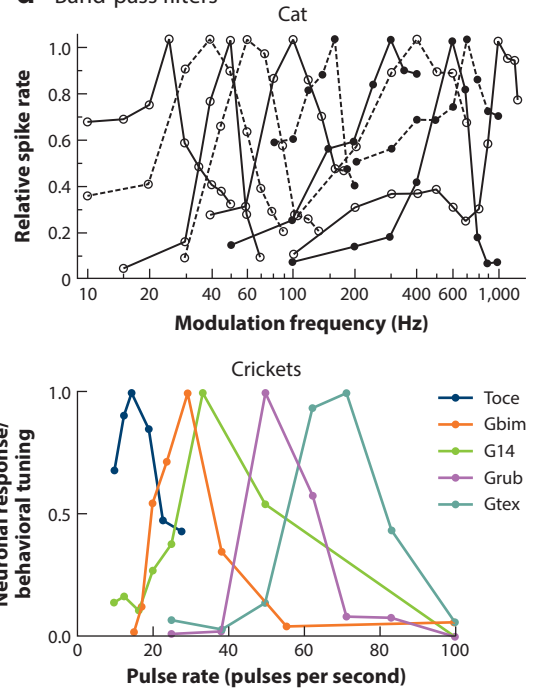
the omega-shaped first-order auditory interneuron of katydids and crickets, which receives input from both ears and, analogous to mammalian directional auditory interneurons, reduces noise by averaging across carrier frequencies and employs contrast enhancement by contralateral inhibition (**Figure 2c**). Activation of this neuron by the contralateral ear is selectively inhibited when sound at the ipsilateral ear is only 2 to 5 decibels louder, rendering the neuron highly direction selective (108, 124).

For the auditory system to recognize acoustic objects such as mating or bat calls, neuronal signals are first conditioned to contrast sound sources of varying intensities at different background levels. Already at the first synapse, spike frequency adaptation exerts gain control (55). As in vertebrate auditory systems, this adaptation covers several timescales and arises from cell-intrinsic properties and local or network feedback loops (54). Directional information and information about temporal patterns can be extracted from adapting spike trains via a time window separation, whereby directional information is read-out from the unadapted onset of the spike trains, whereas their ensuing adapted part is used to process pattern information (56). Along the auditory pathway, spike rates quickly decline, demonstrating a transformation of neuronal coding. Initially, spike rates are high and spike timing is important (56), and the neurons can accommodate high information rates (82). Within two to four synapses, however, spike rates rapidly decline, along with an increase in spike train variability. Two types of representations can now occur along with each other: a population code, which carries information about several signal characteristics (13), and individually firing cells that respond selectively to one salient auditory feature, for example, the pulse rate of a mating call or its pulse/pause ratio (17, 74).

Pulse rates are important features of both insect communication songs and bat echolocation signals (**Figure 2d**). Individual auditory neurons can selectively extract certain pulse rates, for example, by a resonant mechanism, if the sound pulse first triggers a subthreshold membrane potential oscillation. Only if a subsequent pulse falls into an oscillation maximum will the ensuing depolarization reach threshold and the neuron fire (146). A post-inhibitory rebound and a coincidence detector neuron were demonstrated to account for pulse rate selectivity in the auditory pathway of the cricket *Gryllus bimaculatus* (130). Auditory interneurons can also extract salient information about signals from the duty cycle, that is, the relative amount of sound energy over a given time window of sound-producing activity (17), or they may employ simple high-pass filtering through postsynaptic integration depending on the membrane time constants (110). Short gaps between sound pulses may be detected by a repeatedly triggered inhibition that affects the balance of excitation, as was documented for the grasshopper auditory interneuron AN4 (125). Salient cues as described above were extracted over short timescales (73), and respective computational

---

Figure 2

Comparison of processing schemes in vertebrate and insect auditory pathways. (*a*) Peripheral tonotopic frequency mapping is followed by high convergence in insects, but distributed representations in vertebrates (modified with permission from Reference 53). (*b*) Lateral frequency inhibition in auditory nerve fibers by cochlear mechanics in a mouse and inhibition in interneurons in katydids (gray shading indicates suppression). Range fractionation by auditory sensory cells in a moth and a vertebrate, a cat (A1, A2, individual sensory neurons; Sa, spontaneous activity) (modified with permission, from left to right, from References 29, 81, 132, 135). (*c*) Enhancement of directional hearing by contralateral inhibition in a cat and a katydid. The insets depict wiring schemes (AN, auditory nerve; AVCN, anteroventral cochlear nucleus; ILD, interaural level difference; LSO, lateral superior olive; MNTB, medial nucleus of the trapezoid body; Omega symbol, Omega cells depicted to the right) (modified with permission from References 124, 140, 141). (*d*) Band-pass tuning for modulation frequencies in the colliculus inferior of the cat and for pulse rates in an individual brain neuron of a cricket (*red*). Band-pass-like preference functions of related cricket species are given in other colors [Toce, *Teleogryllus oceanicus*; Gbim, *Gryllus bimaculatus*; G14, *Gryllus* species (undescribed); Grub, *G. rubens*; Gtex, *G. texensis*] (modified with permission, top to bottom, from References 5, 52, 74, 76).

models have been devised (12). LN-models with a short, linear filter (L) and nonlinearity (N), equivalent to a sigmoidal response function, reproduced many aspects of the preference profiles the females show when acoustically selecting their mates (51). The linear filter part of LN-models can be well approximated by Gabor functions (a sine modulated by a Gaussian), which also describe many aspects of vertebrate auditory and visual signal processing (143). In terms of computations, temporal auditory processing in insects can be described by a comparison (i.e., in the simplest case a cross-correlation) of the incoming signal with an innate template, whose output is integrated over a certain time window. An example of the cellular substrate of such a template is the rebound property of an interneuron in the cricket brain (130). Accordingly, temporal processing involves a differentiation for salient cues followed by temporal integration, conforming to general schemes in decision making (33).

Auditory pathways of insects are commonly described as layered feedforward networks (12, 56), which is in stark contrast to the massive top-down modulation reported for vertebrates and mammals (128). Yet auditory processing in insects exhibits numerous feedback loops at the local level, implemented by presynaptic inhibition, several timescales of adaptation, and inhibitory network connections (56). There seems to be only few exceptions to the general feedforward structure of auditory processing in insects. In crickets and some katydids, feedback from the brain gates an acoustic reflex and response, respectively, in a top-down manner (18, 49). Local feedback evidently occurs in insect auditory pathways; however, large-scale top-down modulations from higher processing stages have not been described so far.

Given the small numbers of auditory interneurons, one may wonder whether insect central auditory pathways operate smartly on a low budget or whether they represent a bag of computational gadgets. At the peripheral level of the auditory sensory organs, the sensory world of insects might be rich. Along the auditory pathways, however, they quickly proceed to extract very specific information. At the very periphery, insects often use computational gadgets, for example, to obtain directional cues, as found in the auditory pathways of small vertebrates. More centrally, individual auditory interneurons can be highly selective for certain aspects of sound signals (17, 73, 125) and their activity can trigger specific motor outputs. Such extreme convergence of information is also seen in the decision-making command neurons that trigger complex behaviors by integrating sensory information (48, 49). In terms of general computational motifs, insects employ numerous standard tools of sensory processing, including, for example, lateral and contralateral inhibition and sparse representations. Insects therefore seem to take a rather practical approach to make sense of sound information, collapsing operations into single neurons and sacrificing available resolutions by approximate solutions. As witnessed by the astonishing accuracy of ensuing behavioral responses, this reductionist approach works very well.

CONCLUSION

Research over the past decade has put forward insect auditory systems for studying fundamental auditory processes and evolutionary innovations in hearing. Some insect ears are multifunctional, combining auditory and vestibular functions (66). Along with other chordotonal neurons, insect auditory neurons were implicated in the entrainment of circadian clocks and in temperature sensing (35). Whether and, if so, how the neurons encode thermal stimuli, however, remain to be tested; a study on grasshoppers revealed that auditory sensory neuron responses are surprisingly invariant to temperature changes, reflecting mechanisms of temperature compensation that reside inside the cells (120).

Having evolved independently multiple times, insect auditory systems are prime paradigms for studying sensory organ evolution. Expressing photo- and chemotransducer components, insect

auditory sensory cells might also provide insights into the evolution of sensory modalities and sensory signaling cascades (131). Insect hearing research can be technically relevant in that it can inspire sensor fabrication (88) and robotic applications (112). Insect hearing research can be medically relevant in that can help define causes of human ciliopathies (94) and hearing disorders (16, 131) and in that it might offer strategies to control insects that transmit human diseases (143). Above all, insect auditory systems remain fascinating; they still hold many secrets, and deciphering their function, development, and evolution remains a scientific challenge.

SUMMARY POINTS

1. Hearing in insects serves primarily intraspecific acoustic communication and the detection of bat echolocation calls.

2. Within insects, hearing has independently evolved multiple times by converting existing mechanosensory systems to auditory systems. With the exception of particle-velocity-sensitive hairs, all insect ears derive from chordotonal sensory organs and can be categorized into particle-velocity-sensitive antennal and pressure-sensitive tympanal or atympanal ears.

3. Insect auditory sensory neurons and vertebrate hair cells share genetic programs for mechanosensory cell development and seem evolutionarily related.

4. Many key aspects of peripheral sound processing in vertebrates, including impedance-matching middle-ear structures, a mechanical decomposition of sound frequencies by means of traveling waves, active mechanical amplification, and the use of mechanogated ion channels for sound transduction, can be observed in insects.

5. Auditory-relevant proteins of insect auditory sensory neurons include auditory transduction channel candidates, ion pumps, and many cilium proteins, as well as transcription factors that transform auditory neuron cilia into mechanosensory organelles and organize axonal wiring.

6. The axonal projections of insect auditory sensory neurons can create central frequency maps from which one to two semantic frequency channels are formed. The directionality of tympanal ears, along with the subsequent neuronal processing, allows for the highly accurate localization of sound sources in the frontal plane.

7. Central sound processing uses numerous standard computations, from lateral and contralateral inhibition to sparse representations. Highly specific information about salient auditory cues is extracted within a few synapses along the central auditory pathways.

8. Insect hearing research can have technical and medical implications, for example, by inspiring technical sensor design or sound-based strategies for disease vector control.

FUTURE ISSUES

1. Was the evolutionary transition of chordotonal organs into auditory organs associated with changes in gene expression, and how is the formation of accessory auditory structures such as tympanal membranes (tympanal ears) or joints (antennal ears) genetically controlled?

2. Do insect auditory sensory neurons employ electrical tuning mechanisms and efferent control mechanisms known from vertebrate hearing, and which motor proteins drive mechanical amplification by these neurons?

3. Which ion channels mediate transduction in insect auditory neurons? How do Nan and Iav channels contribute to auditory transduction? Is NOMPC the primary transduction channel that enables sensitive hearing, and does its ankyrin domain act as a gating spring? And, more generally, do vertebrate and insect auditory transduction complexes share homologous genes?

4. What are the roles of phototransduction genes in insect auditory neurons? Which stimuli activate rhodopsins in these cells and how do rhodopsins facilitate auditory transduction channel gating? Can insect auditory organs encode thermal stimuli, and what are the roles of thermosensory-relevant proteins in insect ears?

5. How do insects solve the task of integrating auditory information over timescales of up to several hundred milliseconds, not unlike humans do when processing syllables and words?

6. How do insect auditory pathways process complex acoustic signals and courtship displays? And how does the sensory-motor interface operate given the extreme convergence in auditory signal processing?

7. Given that insects that independently evolved hearing can share homologous auditory interneurons, what are the functional properties and the behavioral relevance of these neurons in insects that cannot hear?

8. How can hearing be exploited to control pathogen-transmitting insects, and what can insect ears tell us about technical sensor design?

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

LITERATURE CITED

1. Albert JT, Nadrowski B, Göpfert MC. 2007. Mechanical signatures of transducer gating in the *Drosophila* ear. *Curr. Biol.* 17:1000–6

2. Bechstedt S, Albert JT, Kreil DP, Müller-Reichert T, Göpfert MC, Howard J. 2010. A doublecortin containing microtubule-associated protein is implicated in mechanotransduction in *Drosophila* sensory cilia. *Nat. Commun.* 1:11

3. Bechstedt S, Howard J. 2007. Models of hair cell mechanotransduction. *Curr. Top. Membr.* 59:399–424

4. Bermingham NA, Hassan BA, Price SD, Vollrath MA, Ben-Arie N, et al. 1999. *Math1*: an essential gene for the generation of inner ear hair cells. *Science* 284:1837–41

5. Blankers T, Hennig RM, Gray DA. 2015. Conservation of multivariate female preference functions and preference mechanisms in three species of trilling field crickets. *J. Evol. Biol.* 28:630–41

6. Boo KS, Richards AG. 1975. Fine structure of the scolopidia in the Johnston's organ of male *Aedes aegypti* (L.) (Diptera: Culicidae). *Int. J. Insect Morphol. Embryol.* 4:549–66

7. Boyan GS. 1993. Another look at insect audition: the tympanic receptors as an evolutionary specialization of the chordotonal system. *J. Insect Physiol.* 39:187–200

8. Boyan GS, Ball EE. 1993. The grasshopper, *Drosophila* and neuronal homology (advantages of the insect nervous system for the neuroscientist). *Prog. Neurobiol.* 41:657–82

9. Cator LJ, Arthur BJ, Harrington LC, Hoy RR. 2009. Harmonic convergence in the love songs of the dengue vector mosquito. *Science* 323:1077–79

10. Cheng LE, Song W, Looger LL, Jan LY, Jan YN. 2010. The role of the TRP channel *NompC* in *Drosophila* larval and adult locomotion. *Neuron* 67:373–80

11. Chung YD, Zhu J, Han Y, Kernan MJ. *nompA* encodes a PNS-specific ZP domain protein required to connect mechanosensory dendrites. *Neuron* 29:415–28

12. Clemens J, Hennig RM. 2013. Computational principles underlying the recognition of acoustic signals in insects. *J. Comp. Neurosci.* 35:75–85

13. Clemens J, Kutzki O, Ronacher B, Schreiber S, Wohlgemuth S. 2011. Efficient transformation of an auditory population code in a "small" sensory system. *PNAS* 108:13812–17

14. Cocroft RB. 2011. The public world of insect vibrational communication. *Mol. Ecol.* 20:2041–43

15. Conner WE, Corcoran AJ. 2012. Sound strategies: the 65-million-year-old battle between bats and insects. *Annu. Rev. Entomol.* 57:21–39

16. Cosetti M, Kulang D, Kotla S, O'Brien P, Eberl DF, Hannan F. 2008. Unique transgenic animal model for hereditary hearing loss. *Ann. Otol. Rhinol. Laryngol.* 117:827–33

17. Creutzig F, Wohlgemuth S, Stumpner A, Benda J, Ronacher B, Herz AV. 2009. Timescale-invariant representation of acoustic communication signals by a bursting neuron. *J. Neurosci.* 29:2575–80

18. Dobler S, Heller K-G, von Helversen O. 1994. Song pattern recognition and an auditory time window in the female bush-cricket *Ancistrura nigrovittata* (Orthoptera: Phaneropteridae). *J. Comp. Physiol. A* 175:67–74

19. Dong PD, Todi SV, Eberl DF, Boekhoff-Falk G. 2003. *Drosophila spalt/spalt-related* mutants exhibit Townes–Brocks' syndrome phenotypes. *PNAS* 100:10293–98

20. Doolan JM, Young D. 1981. The organization of the auditory organ of the bladder cicada, *Cystosoma saundersii*. *Philos. Trans. R. Soc. B* 291:525–40

21. Eberl DF. 1999. Feeling the vibes: chordotonal mechanisms in insect hearing. *Curr. Opin. Neurobiol.* 9:389–93

22. Effertz T, Nadrowski B, Piepenbrock D, Albert JT, Göpfert MC. 2012. Direct gating and mechanical integrity of *Drosophila* auditory transducers require TRPN1. *Nat. Neurosci.* 15:1198–200

23. Effertz T, Wiek R, Göpfert MC. 2011. NOMPC TRP channel is essential for *Drosophila* sound receptor function. *Curr. Biol.* 21:592–97

24. Fettiplace R, Fuchs PA. 1999. Mechanisms of hair cell tuning. *Annu. Rev. Physiol.* 61:809–34

25. Field LH, Matheson T. 1998. Chordotonal organs of insects. *Adv. Insect Physiol.* 27:1–228

26. Forrest TG, Read MP, Farris HE, Hoy RR. 1997. A tympanal hearing organ in scarab beetles. *J. Exp. Biol.* 200:601–6

27. Fritzsch B, Eberl DF, Beisel KW. 2010. The role of bHLH genes in ear development and evolution: revisiting a 10-year-old hypothesis. *Cell. Mol. Life Sci.* 67:3089–99

28. Fritzsch B, Straka H. 2014. Evolution of vertebrate mechanosensory hair cells and inner ears: toward identifying stimuli that select mutation driven altered morphologies. *J. Comp. Physiol. A* 200:5–18

29. Fullard JH. 2006. Evolution of hearing in moths: the ears of *Oenosandra boisduvalii* (Noctuoidea: Oenosandridae). *Aust. J. Zool.* 54:51–56

30. Fullard JH, Dawson JW, Jacobs DS. 2003. Auditory encoding during the last moment of a moth's life. *J. Exp. Biol.* 206:281–94

31. Fullard JH, Yack JE. 1993. The evolutionary biology of insect hearing. *Trends Ecol. Evol.* 8:248–52

32. Geurten BR, Spalthof C, Göpfert MC. 2013. Insect hearing: active amplification in tympanal ears. *Curr. Biol.* 23:R950–52

33. Gold JI, Shadlen MN. 2007. The neural basis of decision making. *Annu. Rev. Neurosci.* 30:535–47

34. Gong Z, Son W, Chung YD, Kim J, Shin DW, et al. 2004. Two interdependent TRPV channel subunits, Inactive and Nanchung, mediate hearing in *Drosophila*. *J. Neurosci.* 24:9059–66

35. Göpfert MC, Albert JT. 2015. Hearing in *Drosophila*. *Curr. Opin. Neurobiol.* 34:79–85

36. Göpfert MC, Albert JT, Nadrowski B, Kamikouchi A. 2006. Specification of auditory sensitivity by *Drosophila* TRP channels. *Nat. Neurosci.* 9:999–1000

37. Göpfert MC, Humphris AD, Albert JT, Robert D, Hendrich O. 2005. Power gain exhibited by motile mechanosensory neurons in *Drosophila* ears. *PNAS* 102:325–30

38. Göpfert MC, Robert D. 2001. Active auditory mechanics in mosquitoes. *Proc. R. Soc. B* 258:333–39

39. Göpfert MC, Robert D. 2002. Motion generation by *Drosophila* mechanosensory neurons. *PNAS* 100:5514–19

40. Göpfert MC, Robert D. 2008. Active processes in insect hearing. In *Springer Handbook of Auditory Research*, Vol. 30: *Active Processes and Otoacoustic Emissions in Hearing*, ed. GA Manley, RR Fay, AN Popper, pp. 191–201. New York: Springer

41. Göpfert MC, Stocker H, Robert D. 2002. *atonal* is required for exoskeletal joint formation in the *Drosophila* auditory system. *Dev. Dyn.* 225:106–9

42. Göpfert MC, Surlykke A, Wasserthal LT. 2002. Tympanal and atympanal 'mouth-ears' in hawkmoths (Sphingidae). *Proc. R. Soc. B* 259:89–95

43. Göpfert MC, Wasserthal LT. 1999. Auditory sensory cells in hawkmoths: identification, physiology and structure. *J. Exp. Biol.* 202:1579–87

44. Göpfert MC, Wasserthal LT. 1999. Hearing with the mouthparts: behavioural responses and the structural basis of ultrasound perception in acherontiine hawkmoths. *J. Exp. Biol.* 202:909–18

45. Grimaldi D, Engel MS. 2005. *Evolution of the Insects*. Cambridge, UK: Cambridge Univ. Press

46. Gu JJ, Montealegre-Z F, Robert D, Engel MS, Qiao GX, Ren D. 2012. Wing stridulation in a Jurassic katydid (Insecta, Orthoptera) produced low-pitched musical calls to attract females. *PNAS* 109:3868–73

47. Hassan BA, Bellen HJ. 2000. Doing the MATH: Is the mouse a good model for fly development? *Genes Dev.* 14:1852–65

48. Hedwig B. 1994. A cephalothoracic command system controls stridulation in the acridid grasshopper *Omocestus viridulus* L. *J. Neurophysiol.* 72:2015–25

49. Hedwig B, Poulet JF. 2004. Complex auditory behaviour emerges from simple reactive steering. *Nature* 430:781–85

50. Hennig RM, Franz A, Stumpner A. 2004. Processing of auditory information in insects. *Microsc. Res. Tech.* 63:351–74

51. Hennig RM, Heller KG, Clemens J. 2014. Time and timing in the acoustic recognition system of crickets. *Front. Physiol.* 5:286

52. Hennig RM, Weber T. 1997. Filtering of temporal parameters of the calling song by cricket females of two closely related species: a behavioral analysis. *J. Comp. Physiol. A* 180:621–30

53. Hildebrandt KJ. 2014. Neural maps in insect versus vertebrate auditory systems. *Curr. Opin. Neurobiol.* 24:82–87

54. Hildebrandt KJ, Benda J, Hennig RM. 2009. The origin of adaptation in the auditory pathway of locusts is specific to cell type and function. *J. Neurosci.* 29:2626–36

55. Hildebrandt KJ, Benda J, Hennig RM. 2011. Multiple arithmetic operations in a single neuron: the recruitment of adaptation processes in the cricket auditory pathway depends on sensory context. *J. Neurosci.* 31:14142–50

56. Hildebrandt KJ, Benda J, Hennig RM. 2015. Computational themes of peripheral processing in the auditory pathway of insects. *J. Comp. Physiol. A* 201:39–50

57. Holt JR, Pan B, Koussa MA, Asai Y. 2014. TMC function in hair cell transduction. *Hear. Res.* 311:17–24

58. Howard J, Bechstedt S. 2004. Hypothesis: A helix of ankyrin repeats of the NOMPC-TRP ion channel is the gating spring of mechanoreceptors. *Curr. Biol.* 14:R224–26

59. Howard J, Hudspeth AJ. 1988. Compliance of the hair bundle associated with gating of mechanoelectrical transduction channels in the bullfrog's saccular hair cells. *Neuron* 1:189–99

60. Hoy RR, Robert D. 1996. Tympanal hearing in insects. *Annu. Rev. Entomol.* 41:433–50

61. Hudspeth AJ. 1985. The cellular basis of hearing: the biophysics of hair cells. *Science* 230:745–52

62. Hudspeth AJ. 2014. Integrating the active process of hair cells with cochlear function. *Nat. Rev. Neurosci.* 15:600–14

63. Jarman AP, Grau Y, Jan LY, Jan YN. 1993. *atonal* is a proneural gene that directs chordotonal organ formation in the *Drosophila* peripheral nervous system. *Cell* 73:1307–21

64. Jarman AP, Groves AK. 2013. The role of *Atonal* transcription factors in the development of mechanosensitive cells. *Semin. Cell Dev. Biol.* 24:438–47

65. Kamikouchi A, Albert JT, Göpfert MC. 2010. Mechanical feedback amplification in *Drosophila* hearing is independent of synaptic transmission. *Eur. J. Neurosci.* 31:697–703

66. Kamikouchi A, Inagaki HK, Effertz T, Hendrich O, Fiala A, et al. 2009. The neural basis of *Drosophila* gravity-sensing and hearing. *Nature* 458:165–71

67. Kavlie RG, Fritz JL, Nies F, Göpfert MC, Oliver D, et al. 2015. Prestin is an anion transporter dispensable for mechanical feedback amplification in *Drosophila* hearing. *J. Comp. Physiol. A* 201:51–60

68. Kavlie RG, Kernan MJ, Eberl DF. 2010. Hearing in *Drosophila* requires TilB, a conserved protein associated with ciliary motility. *Genetics* 185:177–88

69. Kennedy HJ, Crawford AC, Fettiplace R. 2005. Force generation by mammalian hair bundles supports a role in cochlear amplification. *Nature* 433:880–83

70. Kim J, Chung YD, Park DY, Choi S, Shin DW, et al. 2003. A TRPV family ion channel required for hearing in *Drosophila*. *Nature* 424:81–84

71. Köppl C. 1997. Phase locking to high frequencies in the auditory nerve and cochlear nucleus magnocellularis of the barn owl, *Tyto alba*. *J. Neurosci.* 17:3312–21

72. Kössl M, Möckel D, Weber M, Seyfarth EA. 2008. Otoacoustic emissions from insect ears: evidence of active hearing? *J. Comp. Physiol. A* 194:597–609

73. Kostarakos K, Hedwig B. 2012. Calling song recognition in female crickets: Temporal tuning of identified brain neurons matches behavior. *J. Neurosci.* 32:9601–12

74. Kostarakos K, Hedwig B. 2014. Pattern recognition in field crickets: concepts and neural evidence. *J. Comp. Physiol. A* 201:73–85

75. Lakes-Harlan R, Lehmann GU. 2015. Parasitoid flies exploiting acoustic communication of insects—comparative aspects of independent functional adaptations. *J. Comp. Physiol. A* 201:123–32

76. Langner G, Schreiner CE. 1988. Periodicity coding in the inferior colliculus of the cat. I. Neuronal mechanisms. *J. Neurophysiol.* 60:1799–822

77. Lee E, Sivan-Loukianova E, Eberl DF, Kernan MJ. 2008. An IFT-A protein is required to delimit functionally distinct zones in mechanosensory cilia. *Curr. Biol.* 18:1899–906

78. Lee J, Moon S, Cha Y, Chung YD. 2010. *Drosophila* TRPN(= NOMPC) channel localizes to the distal end of mechanosensory cilia. *PLOS ONE* 5:e11012

79. Lehnert BP, Baker AE, Gaudry Q, Chiang AS, Wilson RI. 2013. Distinct roles of TRP channels in auditory transduction and amplification in *Drosophila*. *Neuron* 77:115–28

80. Liang X, Madrid J, Gärtner R, Verbavatz JM, Schiklenk C, et al. 2013. A NOMPC-dependent membrane-microtubule connector is a candidate for the gating spring in fly mechanoreceptors. *Curr. Biol.* 23:755–63

81. Liberman MC. 1978. Auditory-nerve response from cats raised in a low-noise chamber. *J. Acoust. Soc. Am.* 63:442–45

82. Machens CK, Schütze H, Franz A, Kolesnikova O, Stemmler MB, et al. 2003. Single auditory neurons rapidly discriminate conspecific communication signals. *Nat. Neurosci.* 6:341–42

83. Martin P, Hudspeth AJ. 2001. Compressive nonlinearity in the hair bundle's active response to mechanical stimulation. *PNAS* 98:14386–91

84. Mason AC, Oshinsky ML, Hoy RR. 2001. Hyperacute directional hearing in a microscale auditory system. *Nature* 410:686–90

85. Mhatre N. 2015. Active amplification in insect ears: mechanics, models and molecules. *J. Comp. Physiol. A* 201:19–37

86. Mhatre N, Robert D. 2013. A tympanal insect ear exploits a critical oscillator for active amplification and tuning. *Curr. Biol.* 23:1952–57

87. Michelsen A, Larsen ON. 2008. Pressure difference receiving ears. *Bioinspir. Biomim.* 3:011001

88. Miles RN, Su Q, Cui W, Shetye M, Degertekin FL, et al. 2009. A low-noise differential microphone inspired by the ears of the parasitoid fly *Ormia ochracea*. *J. Acoust. Soc. Am.* 125:2013–26

89. Misof B, Liu S, Meusemann K, Peters RS, Donath A, et al. 2004. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346:763–67

90. Möckel D, Nowotny M, Kössl M. 2014. Mechanical basis of otoacoustic emissions in tympanal hearing organs. *J. Comp. Physiol. A* 200:681–91

91. Moir HM, Jackson JC, Windmill JF. 2013. Extremely high frequency sensitivity in a 'simple' ear. *Biol. Lett.* 9:20130241

92. Montealegre-Z F, Jonsson T, Robson-Brown KA, Postles M, Robert D. 2012. Convergent evolution between insect and mammalian audition. *Science* 338:968–71

93. Montealegre-Z F, Robert D. 2015. Biomechanics of hearing in katydids. *J. Comp. Physiol. A* 201:5–18

94. Moore DJ, Onoufriadis A, Shoemark A, Simpson MA, zur Lage PI, et al. 2013. Mutations in *ZMYND10*, a gene essential for proper axonemal assembly of inner and outer dynein arms in humans and flies, cause primary ciliary dyskinesia. *Am. J. Hum. Genet.* 93:346–56

95. Morley EL, Mason AC. 2015. Active auditory mechanics in female black-horned tree crickets (*Oecanthus nigricornis*). *J. Comp. Physiol. A* 201:1147–55

96. Müller P, Robert D. 2001. A shot in the dark: the silent quest of a free-flying phonotactic fly. *J. Exp. Biol.* 204:1039–52

97. Nadrowski B, Albert JT, Göpfert MC. 2008. Transducer-based force generation explains active process in *Drosophila* hearing. *Curr. Biol.* 18:1365–72

98. Nadrowski B, Effertz T, Senthilan PR, Göpfert MC. 2011. Antennal hearing in insects: new findings, new questions. *Hear. Res.* 273:7–13

99. Nadrowski B, Göpfert MC. 2009. Modeling auditory transducer dynamics. *Curr. Opin. Otolaryngol. Head Neck Surg.* 17:400–6

100. Nakano R, Takanashi T, Surlykke A. 2015. Moth hearing and sound communication. *J. Comp. Physiol. A* 201:111–21

101. Nesterov A, Spalthoff C, Kandasamy R, Katana R, Rankl NB, et al. 2015. TRP channels in insect stretch receptors as insecticide targets. *Neuron* 86:665–71

102. Newton FG, zur Lage PI, Karak S, Moore DJ, Göpfert MC, Jarman AP. 2012. Forkhead transcription factor Fd3F cooperates with Rfx to regulate a gene expression program for mechanosensory cilia specialization. *Dev. Cell.* 22:1221–33

103. Palghat Udayashankar A, Kössl M, Nowotny M. 2012. Tonotopically arranged traveling waves in the miniature hearing organ of bushcrickets. *PLOS ONE* 7:e31008

104. Park J, Lee J, Shim J, Han W, Lee J, et al. 2013. dTULP, the *Drosophila melanogaster* homolog of *tubby*, regulates transient receptor potential channel localization in cilia. *PLOS Genet.* 9:e1003814

105. Pézier A, Jezzini SH, Marie B, Blagburn JM. 2014. Engrailed alters the specificity of synaptic connections of *Drosophila* auditory neurons with the giant fiber. *J. Neurosci.* 34:11691–704

106. Pierce ML, Weston MD, Fritzsch B, Gabel HW, Ruvkun G, Soukup GA. 2008. MicroRNA-183 family conservation and ciliated neurosensory organ expression. *Evol. Dev.* 10:106–13

107. Plotnick RE, Smith DM. 2012. Exceptionally preserved fossil insect ears from the Eocene Green River Formation of Colorado. *J. Palaeontol.* 86:19–24

108. Pollack GS. 1988. Selective attention in an insect auditory neuron. *J. Neurosci.* 8:2635–39

109. Pollack GS. 1997. Neural processing of acoustic signals. In *Springer Handbook of Auditory Research*, Vol. 10: *Comparative Hearing: Insects*, ed. RR Hoy, AN Popper, RR Fay, pp. 138–96. New York: Springer

110. Pollack GS. 2015. Neurobiology of acoustically mediated predator detection. *J. Comp. Physiol. A* 201:99–109

111. Rabbitt RD, Brownell WE. 2011. Efferent modulation of hair cell function. *Curr. Opin. Otolaryngol. Head Neck Surg.* 19:376–81

112. Reeve R, van Schaik A, Jin C, Hamilton T, Torben-Nielsen B, Webb B. 2007. Directional hearing in a silicon cricket. *Biosystems* 87:307–13

113. Ren T. 2002. Longitudinal pattern of basilar membrane vibration in the sensitive cochlea. *PNAS* 99:17101–6

114. Riabinina O, Dai M, Duke T, Albert JT. 2011. Active process mediates species-specific tuning of *Drosophila* ears. *Curr. Biol.* 21:658–64

115. Robert D. 2001. Innovative biomechanics for directional hearing in small flies. *Biol. Bull.* 200:190–94

116. Robert D, Göpfert MC. 2002. Novel schemes for hearing and orientation in insects. *Curr. Opin. Neurobiol.* 12:715–20

117. Robles L, Ruggero MA. 2001. Mechanics of the mammalian cochlea. *Physiol. Rev.* 81:1305–52

118. Roeder KD, Treat AE, Vandeberg JS. 1968. Auditory sense in certain sphingid moths. *Science* 159:331–33

119. Roeder KD, Treat AE, Vande Berg JS. 1970. Distal lobe of the pilifer: an ultrasonic receptor in choerocampine hawkmoths. *Science* 170:1098–99

120. Roemschied FA, Eberhard MJ, Schleimer JH, Ronacher B, Schreiber S, et al. 2014. Cell-intrinsic mechanisms of temperature compensation in a grasshopper sensory receptor neuron. *eLife* 8:e02078

121. Römer H. 1983. Tonotopic organization of the auditory neuropile in the bushcricket *Tettigonia viridissima*. *Nature* 306:60–62

122. Römer H. 2015. Directional hearing: from biophysical binaural cues to directional hearing outdoors. *J. Comp. Physiol. A* 201:87–97

123. Römer H, Bailey W. 1996. Ecological constraints for the evolution of hearing and sound communication in insects. In *The Evolutionary Biology of Hearing*, ed. DB Webster, RR Fay, AN Popper, pp. 79–93. New York: Springer

124. Römer H, Krusch M. 2000. A gain-control mechanism for processing of chorus sounds in the afferent auditory pathway of the bushcricket *Tettigonia viridissima* (Orthoptera, Tettigoniidae). *J. Comp. Physiol. A* 186:181–91

125. Ronacher B, Stumpner A. 1988. Filtering of behaviourally relevant temporal parameters of a grasshopper's song by an auditory interneuron. *J. Comp. Physiol. A* 163:517–23

126. Roy M, Sivan-Loukianova E, Eberl DF. 2013. Cell-type-specific roles of Na$^+$/K$^+$ ATPase subunits in *Drosophila* auditory mechanosensation. *PNAS* 110:181–86

127. Rust J, Stumpner A, Gottwald J. 1999. Singing and hearing in a Tertiary bushcricket. *Nature* 399:650

128. Schnupp JWH, Nelken I, King AJ. 2011. *Auditory Neuroscience—Making Sense of Sound*. Cambridge, MA: MIT Press

129. Schöneich S, Hedwig B. 2010. Hyperacute directional hearing and phonotactic steering in the cricket (*Gryllus bimaculatus* deGeer). *PLOS ONE* 5:e15141

130. Schöneich S, Kostarakos K, Hedwig B. 2015. An auditory feature detection circuit for sound pattern recognition. *Sci. Adv.* 1:e1500325

131. Senthilan PR, Piepenbrock D, Ovezmyradov G, Nadrowski B, Bechstedt S, et al. 2012. *Drosophila* auditory organ genes and genetic hearing defects. *Cell* 150:1042–54

132. Song L, McGee JA, Walsh EJ. 2008. Development of cochlear amplification, frequency tuning, and two-tone suppression in the mouse. *J. Neurophysiol.* 99:344–55

133. Soulavie F, Piepenbrock D, Thomas J, Vieillard J, Duteyrat JL, et al. 2014. *hemingway* is required for sperm flagella assembly and ciliary motility in *Drosophila*. *Mol. Biol. Cell* 25:1276–86

134. Strauß J, Stumpner A. 2015. Selective forces on origin, adaptation and reduction of tympanal ears in insects. *J. Comp. Physiol. A* 201:155–69

135. Stumpner A. 1998. Picrotoxin eliminates frequency selectivity of an auditory interneuron in a bushcricket. *J. Neurophysiol.* 79:2408–15

136. Stumpner A, von Helversen D. 2001. Evolution and function of auditory systems in insects. *Naturwissenschaften* 88:159–70

137. Sueur J, Windmill JF, Robert D. 2006. Tuning the drum: the mechanical basis for frequency discrimination in a Mediterranean cicada. *J. Exp. Biol.* 209:4115–28

138. Surlykke A. 1984. Hearing in notodontid moths: a tympanic organ with a single auditory neuron. *J. Exp. Biol.* 113:323–35

139. Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* 307:580–84

140. Tollin DJ. 2003. The lateral superior olive: a functional role in sound source localization. *Neuroscientist* 9:127–43

141. Tollin DJ, Yin TCT. 2002. The coding of spatial location by single units in the lateral superior olive of the cat. II. The determinants of spatial receptive fields in azimuth. *J. Neurosci.* 15:1468–79

142. van Staaden MJ, Römer H. 1989. Evolutionary transition from stretch to hearing organs in ancient grasshoppers. *Nature* 394:773–76

143. Vigoder FDM, Ritchie MG, Gibson G, Peixoto AA. 2013. Acoustic communication in insect disease vectors. *Mem. Inst. Oswaldo Cruz* 108(Suppl. 1):26–33

144. von Helversen D. 1997. Acoustic communication and orientation in grasshoppers. In *Orientation and Communication in Arthropods*, ed. M Lehrer, pp. 301–41. Basel, Switz.: Birkhäuser

145. Warren B, Gibson G, Russell IJ. 2009. Sex recognition through midflight mating duets in *Culex* mosquitoes is mediated by acoustic distortion. *Curr. Biol.* 19:485–91

146. Webb B, Wessnitzer J, Bush S, Schul J, Buchli J, Ijspeert A. 2007. Resonant neurons and bushcricket behaviour. *J. Comp. Physiol. A* 193:285–88

147. Weber T, Göpfert MC, Winter H, Zimmermann U, Kohler H, et al. 2003. Expression of prestin-homologous solute carrier (SLC26) in auditory organs of nonmammalian vertebrates and insects. *PNAS* 100:7690–95

148. Windmill JF, Fullard JH, Robert D. 2007. Mechanics of a 'simple' ear: tympanal vibrations in noctuid moths. *J. Exp. Biol.* 210:2637–48

149. Windmill JF, Göpfert MC, Robert D. 2005. Tympanal travelling waves in migratory locusts. *J. Exp. Biol.* 208:157–68

150. Wyttenbach RA, May ML, Hoy RR. 1996. Categorical perception of sound frequency by crickets. *Science* 273:1542–44

151. Xiong W, Grillet N, Elledge HM, Wagner TF, Zhao B, et al. 2012. TMHS is an integral component of the mechanotransduction machinery of cochlear hair cells. *Cell* 151:1283–95

152. Yack JE. 2004. The structure and function of auditory chordotonal organs in insects. *Microsc. Res. Tech.* 63:315–37

153. Yager DD. 1996. Serially homologous ears perform frequency range fractionation in the praying mantis, *Creobroter* (Mantodea, Hymenopodidae). *J. Comp. Physiol. A* 178:463–75

154. Yager DD. 1999. Structure, development, and evolution of insect auditory systems. *Microsc. Res. Tech.* 47:380–400

155. Yager DD, Spangler HG. 1997. Behavioral response to ultrasound by the tiger beetle *Cicindela marutha* Dow combines aerodynamic changes and sound production. *J. Exp. Biol.* 200:649–59

156. Yan Z, Zhang W, He Y, Gorczyca D, Xiang Y, et al. 2013. *Drosophila* NOMPC is a mechanotransduction channel subunit for gentle-touch sensation. *Nature* 493:221–25

157. Zanini D, Göpfert MC. 2013. Mechanosensation: tethered ion channels. *Curr. Biol.* 23:R349–51

158. Zanini D, Göpfert MC. 2014. TRPs in hearing. *Handb. Exp. Pharmacol.* 223:899–916

159. Zhang W, Cheng LE, Kittelmann M, Li J, Petkovic M, et al. 2015. Ankyrin repeats act as a tether for conveying force to gate the NOMPC mechanotransduction channel. *Cell* 162:1391–403