

Chapter 2

Insect Hearing: Selected Historical Vignettes



Ronald R. Hoy

2.1 Introduction

Insects are common, numerous, and specific. Most are also miniscule in size as compared to vertebrates. Yet some insects can make audible, often startlingly loud, sounds when signaling to one another.

Insects have been around for hundreds of millions of years. When the first humans arose in Africa, a mere one or two million years ago, the calls of insects pierced their emerging consciousness—serenaded by cicadas by day and crickets and katydids by night. Sonic insects have shared ecological habitats with humans since humans evolved and their presence has been noted in the cultural artifacts and practices of ancient civilizations that persist today, as will be seen in this chapter.

The sounds that insects make are signals that serve the same adaptive function as do language and music in humans. They are communication signals for survival that mediate reproductive behavior. The sense of hearing serves as a key surveillance channel for monitoring the external world, especially for the countless nocturnally active insects and it serves the same adaptive purpose as it does for birds and frogs. However, the evolutionary origins of hearing organs in insects took multiple and diverse phylogenetic pathways, as opposed to simpler route in the vertebrates, which has been described as closer to one “big bang” event (e.g., Clack et al. 2016). This multiple origin led to a diversity of hearing organs that have novel anatomic, biomechanical, and neurophysiological “design features” that enable insects to hear a wide variety of sonic signals of salience.

This volume in the Springer Handbook of Auditory Research (SHAR) series is devoted to “A History of Discoveries on Hearing,” and this chapter on insects will tackle sonic/acoustic activity from two viewpoints. First, is a reflection on how

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D. R. Ketten et al. (eds.), *A History of Discoveries on Hearing*, Springer Handbook of Auditory Research 77,

https://doi.org/10.1007/978-3-031-41320-9_2

human observers/listeners have interpreted the phenomenon of insect hearing anthropomorphically. Second, only when these anthropocentric suppositions were squared with the ground-truth of what and how the insects, themselves, hear did we realize the remarkable diversity of hearing organs in form and function that evolved in insects. Our understanding of how insects hear is still very much a work in progress. While certain fundamental issues were recognized by Greek philosophers, critical studies on insect hearing awaited scientific inquiry until the nineteenth century. Indeed, most issues were not clarified until the twentieth century, and many new discoveries continue to be made, aided by twenty-first-century technical tools.

This historical survey is purposely highly selective—it will be presented as a series of case histories focused on the most recognizable of sonic insects that will be familiar to a naturalist or curious layperson. The editorial guideline for the time-frame unifying these chapters is from antiquity to around 1970–1980, when the SHAR volumes picked up the story of comparative hearing, over the course of its 77 volumes. I have tried to respect this historical interval, but break from it when necessary to maintain the integrity of narrative flow, especially when referring to review articles on salient and timely issues.

At the same time, considering the extraordinary diversity of insects, it is impossible to cover all species and all the ways in which these species have “reinvented” hearing in any single chapter. Thus, rather than attempt to tackle the extreme breadth, this chapter will focus on a select species and groups that give the greatest representation of the diversity of insect hearing and the extraordinary range of “ears” they use for sound detection.

2.1.1 Three Cautionary Notes in Comparing Hearing in Terrestrial Vertebrates with Insects

The reader should keep in mind three issues when comparing insects to terrestrial vertebrates in terms of bioacoustics and auditory behavior. (1) Insects are really small—in addressing the sense of hearing, size matters; (2) biologists tend to make implicit anthropocentrically based expectation that auditory sensitivity is largely a matter of detecting differences in acoustic pressure of an impinging sound wave; and (3) the *evolutionary origins* of insect hearing organs differ markedly, yielding great diversity in structure as well as function.

2.1.1.1 Body Size Constrains Structure and Function of Hearing Organs in Insects

First and most obvious, the body size of an insect can be 4–6 orders of magnitude smaller, both in surface area and volume, than the typical vertebrate. Naturally, insect ears are even smaller and on the micro or even nanoscale. This difference imposes important constraints on the physics of both sound production and sensory

detection (Bennet-Clark 1971, 1991). The constraints of small size on the production of acoustic signals in both intensity level and spectral frequency or timbre of the sound emitted. Size also imposes limits for sensing sound, especially sensing air pressure with a tympanum, as was noted by Bennet-Clark in a series of important studies (1991, 1999). Despite these constraints, many sonic insects can hear as well as make sounds that can be distractingly loud to the human ear. Insects deploy a remarkable number of morphological adaptations for amplifying sound level (Bennet-Clark 1999; Yack 2004).

2.1.1.2 Insect Hearing Organs Can Detect Pressure Differences in Acoustic Airflow as Well as Particle Velocity Depending on Species and Body Size

It is not surprising that the eighteenth-century natural history approach, as well as the twentieth-century scientific study of insect bioacoustics, was biased toward species whose sonic emissions or calls are clearly audible to human observers. Insects, like humans, are terrestrial creatures meaning that their sense of hearing is a matter of detecting acoustic signals that propagate through air. Not until the mid-twentieth century did instruments become available to reveal the infra- and ultrasonic sensitivities of the insect ear and Doppler laser vibrometry to measure mechanical responses to airflow.

The acoustics of insect hearing has historically been studied in larger species like crickets, grasshoppers, moths, and cicadas whose hearing organs feature externally visible tympanic membranes. This reinforces the expectation that such ears are pressure or pressure-difference detectors (Roeder 1967; Larsen and Michelsen 1978), by obvious analogy to vertebrate eardrums. It is not surprising that hearing in insects has been interpreted as the detection of changes in air pressure, as in vertebrate hearing, which is valid for larger, tympanate insects. However, as will be discussed below, many minutely small insects can also hear—but by detecting velocity in propagating airflow, not pressure (Menda et al. 2019).

2.1.1.3 Evolutionary Origins

Finally, there is the vitally important matter of evolutionary origins. The ear of all vertebrates appears to have evolved from a common origin (Webster et al. 1992; Clack et al. 2016) and whether or not the term “monophyletic” is invoked to describe the origin of the vertebrate ear it is true that essentially all vertebrate ears are found on opposite sides of the head (Manley 1973; Allin 1975). However, in the late nineteenth and twentieth centuries, when naturalists and entomologists had better tools to investigate insect hearing, it was discovered that insect hearing organs could be located just about anywhere on the body including on appendages, thorax, abdomen, as well as on the head, clearly orthogonal to the monophyletic pattern of vertebrates (Yack 2004). What accounts for these differences?

In terrestrial vertebrates, the organization of outer-to-middle-to-inner ear is obligatory because of the need for acoustic impedance matching in transferring acoustic energy of sound waves to the outer ear of animal and thence into ponderable vibrations in the fluid that bathes the cochlea of the mammalian inner ear. Impedance matching is solved by the middle ear bone(s) that are interposed between an air-facing eardrum and the fluid-filled cochlea. However, in sonic insects, like cicadas, crickets, and grasshoppers, that possess an external tympanal membrane (outer ear), this thin cuticular membrane is directly apposed internally to an air-filled tracheal chamber which means that the external and internal face of the tympanal membrane is air-to-air, obviating the necessity for a middle ear (Fullard and Yack 1993).

The insect's auditory sensory organ is a type of mechanoreceptive chordotonal organ, specialized for hearing. It is where auditory transduction occurs and is analogous to the vertebrate "inner ear." This kind of ear is directly attached to the air-filled tracheal tube, if not directly to the tympanal membrane itself (Yack 2004). This air-to-air coupling of external to inner ear obviates the need for a middle ear in insects that possess tympanal membranes for hearing.

Similarly, where the external acoustic biosensor is a simple cuticular hair that protrudes into the air and is internally innervated by bipolar sensory neuron(s), the transfer of acoustic energy (air particle movements) is direct from air-to-hair-to-neuron and no intervening structure is needed. This simplicity of functional mechanics removes a severe constraint in the task of hearing, even for tympanate insects, by comparison with terrestrial vertebrates.

Lacking the biomechanical constraints of hearing in the vertebrate ear, the evolution of hearing organs in insects has resulted in a multitude of locations where insect ears can be found, to nearly anywhere on the body. The insect ear has evolved multiple times in the Class Insecta and independent evolution has occurred even within Orders and Suborders, especially in the Orthoptera (crickets, katydids, grasshoppers) and the Lepidoptera (moths and butterflies) (Song et al. 2020). These twentieth and twenty-first century papers underscore that the structure-function understanding of insect hearing is still very much a work in progress and should be kept in mind when reading the rest of this chapter. My account will focus on selected examples of sonic insects, which have historical interest.

2.2 The Bioacoustics, Evolution, and Neuroethology of Calling Song in Crickets

Crickets and their songs have been the focus of attention not only by biologists but have figured in popular culture for centuries. Charles Dicken's (1846) "Cricket on the Hearth™" and Walt Disney's Jiminy Cricket in "Pinocchio™" are but two of many testaments from literature and film.

Crickets have co-existed/cohabited with humans from prehistory onward because humans built their villages and towns in what were once open fields and forests, natural habitats for crickets, so that crickets are always within “earshot” since the beginning of humankind. These mostly nocturnal insects and their loud, incessant calling are conspicuously present during the warm seasons in temperate climates and even longer in the tropics. They are large enough to capture by hand and easily kept in captivity where some societies and cultures treasure their calls and cage them for their songs, just like canaries and finches are household companions.

Thus, it is not surprising that when naturalists and biologists selected animals for auditory studies, crickets were among the first chosen—in season, they are always “at hand.” As it turned out, studying crickets was not only convenient but a strategically fortuitous choice of insect for comparative studies in bioacoustics and hearing science.

Regrettably, space limits the discussion in this chapter to the field crickets (Family Gryllidae, Genus *Gryllus*) and tree crickets (Family Oecanthidae, Genus *Oecanthus*) to the exclusion of grasshoppers (Family Acrididae) and katydids (Family Tettigoniidae), thus neglecting at least two-thirds of the ubiquitous, species-rich, singing Orthoptera. Historically, however, the sheer breadth of studies of cricket bioacoustics including evolution, taxonomy, behavior genetics, and neuroethology of calling behavior have been conducted over multiple levels of analysis, ranging from molecular and cellular to phylogenetics to neural circuits, and ultimately, to behavior and sensory ecology, warranting their focus in this brief review. Entire books have been devoted to cricket bioacoustics, behavior, and neuroethology (Huber et al. 1989; Gerhardt and Huber 2002) and were reviewed in the SHAR series (Hoy et al. 1998; Pollack et al. 2016). Hence, this section will cover the topic very selectively because, arguably, acoustic behavior in crickets is the ideal model system for the study of hearing in insects.

2.2.1 The Scientific Study of Acoustic Behavior in Crickets: The First Model System in Insect Bioacoustics

The nineteenth century was the golden age of comparative anatomy enabled by advances in microscopy and development of histological techniques and staining reagents, including vital dyes and silver staining methods that permitted studies of hearing organs at cellular level resolution. The first careful histological study of the cricket tympanal hearing organ, the “crista acustica,” was performed by Schwabe (1906; also replicated by Michel 1974). The spindly auditory sensory cells, scolopidia, are anatomically arranged as a linear proximal to distal array along the long axis of the tibial segment of the leg itself. Much later, when it became possible to make neurophysiological recordings from single cells was it shown that the scolopidial cells of the crista acustica of crickets and katydids were tonotopically organized, similar to the inner hair cells of the mammalian cochlea (Oldfield 1982).

Schwabe's work was known to the late nineteenth-century Slovenian entomologist, Johannes Regen, who was studying the behavior of the field crickets that sang in the capacious, verdant fields surrounding his laboratory.

2.2.2 *Regen and Playback Experiments*

While it may have seemed obvious to naturalists that male crickets “sing” as part of their mating behavior (Darwin 1871, no experimental approaches to confirm this presumption. But it was to come a few decades later. In 1876, Alexander Graham Bell had invented the telephone and within a few decades, telephone installations became common in Europe. Regen's (1913) experiments demonstrated that he was an ingenious early adapter of the telephone for scientific exploration. His experiment involved capturing sexually mature, singing males and female field crickets, *Gryllus campestris*, from nearby fields, and bringing them into his laboratory.

Regan maintained his male and female crickets in separate rooms of his lab building. When Regen heard a male commencing to sing its calling song, he telephoned his assistant who was patiently waiting in another room, distantly located and acoustically isolated, tending his collection of female crickets. Regen then placed the speaker mouthpiece of his phone next to the calling male cricket. When the assistant took the call, he placed his phone's earpiece receiver a short distance away from a female cricket contained within a large, sand-filled arena in which it could walk freely.

The assistant observed the female crickets invariably responded by walking directly to the phone's earpiece and crawling around and over it, presumably in search of the calling male. This clever experiment demonstrated that sound, and sound alone, was sufficient to bring both sexes together around the calling male. In a single stroke, other sensory cues such as odors, tactile touch, and vision as possible cues for attraction were eliminated as necessary. Just as Alexander Graham Bell rang his assistant Thomas Watson with his famous message, “Mr. Watson, come here, I want to see you,” so too did Regen's male cricket send a compelling message to a remotely located female cricket to come to the phone, perhaps ironically with a similar urgency! Both Bell and Regen had completed a remote auditory communication loop.

Furthermore, when Regen amputated the tibial joints of the female cricket's forelegs it no longer responded to calls, even though the insect's ability to walk was unimpaired. Tibial amputation acoustically deafferents the insect by removing its hearing organ (crista Acustica) which is contained within its foreleg tibial segment. Regen's experiments were pioneering in his use of an electronic loudspeaker (the telephone's) to broadcast acoustic signals to assess their behavioral relevance and potency to change the behavior of the animal hearing the signal.

Regan's experiments were the forerunner of the playback paradigm to measure phonotaxis—the orientation or tracking movements made by the receiver animal in response to an acoustic playback. Whereas Regen had to use live, calling male

crickets to provide the acoustic stimulus, experimentalists, from the 1950s onward, could substitute tape recordings of real animals or electroacoustically generated analogs for playback. By the 1970s, acoustic signals could easily be generated from electronic waveform generators controlled by computers. Phonotaxis trials remain a robust and powerful methodology in bioacoustic research.

Indeed, Regen's experiments in Slovenia inspired, after the two World Wars, historically important "schools" of cricket and orthopteran neurobiology and behavior in Europe, especially Germany because Franz Huber single-handedly founded the electrophysiological study of the song generating networks of field crickets and whose work influenced the careers of hundreds of subsequent cricketeers, including myself. Huber's pioneering work (Huber 1962; Huber et al. 1989; Gerhardt and Huber 2002) established the cricket song system as a model system for investigating the inherently innate temporal pattern or rhythm of species-specific mating calls of males and how conspecific females hear and perceive mating calls. The sheer diversity of species-specific temporal pattern (pulse rhythm) in cricket mating calls combined with the tonal simplicity of song pulses, themselves, provoked the possibility that not only was the motor production of the call rhythm under innate, genetic control, but so too was the perception (recognition) of temporal pattern also innate, presumably under genetic control. His lab and others to follow contributed to the important question of the central auditory processing of songs by tackling how the female cricket's audio-motor neural system discriminates her own species-specific temporal patterns from those of other species, which leads her to localize and "steer" her to the male (Gerhardt and Huber 2002; Hedwig et al. 2018; Schoeneich and Hedwig 2019).

2.2.3 More Playback Experiments

These neuroethological studies that eventually led to the key understanding that a neural network within the male cricket's central nervous system (CNS) generated the species-specific temporal pattern of sound pulses (Alexander 1962; Huber 1962). The Central Pattern Generator "revolution" of the 1960s (Wilson 1961; Bentley 1969) that led to Bentley, Hoy's genetic analysis. In fact, I was drawn to study the auditory behavior of crickets having been inspired by two of the founders of insect neuroethology, the aforementioned Franz Huber and Kenneth Roeder, whose pioneering work on auditory behavior in moths will be described in detail in the following pages.

My laboratory at Cornell University (Ithaca, NY) deployed an auditory playback paradigm to measure the phonotactic steering response of tethered crickets, suspended in mid-air and induced to fly in a laminar wind flow (Moiseff et al. 1978). In this experiment, crickets (both males and females) could sustain wing-flapping (fictive flight) for minutes at a time and respond to directional sounds played from loudspeakers placed to the right or left of the suspended insect. In brief, we confirmed that fictively flying female crickets responded to playback of both

tape-recorded calling songs from conspecific males as well as live song, by making asymmetrical movements with their appendages and wings toward the speaker that would steer them toward the song.

This confirms the behavior of walking crickets to playback experiments that are to Regan's time as well as more systematic studies (Walker 1957, 1962). However, when the acoustic stimulus was switched from cricket-like carrier frequency (ca. 5 kHz) to ultrasonic frequencies (25–100 kHz) the fictively flying crickets abruptly responded with reflexively fast steering movements of its appendages that would steer the cricket away from the ultrasound source (Moiseff et al. 1978). This action is an auditory startle (ASR), in this case escape, response that is characteristic of many animals with a sense of hearing, from invertebrates to humans (Eaton 1984). In crickets and moths (see Sect. 2.3), acoustic startle occurs only during flight behavior and reflects evasive behavior in response to the ultrasonic echolocation calls of insectivorous bats (Roeder 1967; Moiseff et al. 1978). Subsequent work by talented students at my Cornell lab showed that many genera and species of nocturnally active, flying insects have evolved ultrasound-sensitive hearing organs for detecting bats that relentlessly hunt insects on the wing, by echolocation (Hoy 1992).

2.2.4 *The Cricket's Tympanal Hearing Organ*

The cricket's hearing organ and auditory system are typical for insects commonly known to possess a sense of hearing (Hoy 1998; Yack 2004). Such hearing organs are characterized by three traits: (1) a pair of external tympanal membranes, which in crickets and katydids are located in the tibial segment of their prothoracic forelegs and visible by eye or under a magnifier; (2) the internal wall of the tympanal membrane abuts upon an air-filled chamber or tube, part of the insect's tracheal respiratory system; and (3) sensory innervation by a chordotonal mechanosensory organ that can attach directly to the tympanum or indirectly through attachment to the adjacent air-filled trachea. The sensory unit of chordotonal organs is called a scolopidium, which is multicellular complex and may contain one or more bipolar sensory neurons, along with cap cells, support cells, and glial cells.

The respiratory tracheae play a central role in determining the directional properties of hearing in crickets, as shown by the pioneering work of Axel Michelsen and his bioacoustics laboratory in Odense, Denmark (Michelsen 1998). In brief, a four-input tubular system of tracheae, of which the tracheal tubes that adjoin the auditory receptor organ, the *crista acustica*, is part, imparts directional sensitivity to hearing by generating air pressure differences within the tubes. This was shown by Larsen and Michelsen (1978), in their Doppler laser vibrometry studies (Michelsen 1998).

2.2.5 *Evolutionary Convergence of Tympanal Hearing Organs: Crickets and Their Parasitic Flies*

Male crickets sing to attract females for mating, but their loud calling songs are also heard by parasitoid flies of the genus *Ormia* (Cade 1975). Interestingly *Ormia* flies evolved a tympanal hearing organ to hear crickets (Robert et al. 1992) nicely demonstrating the principle of convergent evolution. However, to localize the cricket based on directional acoustic cues, such as time and intensity, *Ormia* evolved an entirely novel mechanism for sound localization that surpasses the performance of its host in every way (Miles et al. 1995; Robert et al. 1996). The directional properties of hearing are fascinating but beyond the scope of this chapter. However, the bioacoustic principles “invented” in *Ormia* for sound localization, mechanical coupling, has turned out to inspire acoustic engineers to mimic its design principles for producing small, nanofabricated, directional microphones (Miles et al. 2009). Insect ears are fertile ground for physicists and engineers who deploy the strategy of biomimicry to “invent” useful biosensors in the field of biomedical engineering

2.2.6 *The Genetic Control of Cricket Song*

I was fortunate to stand on the shoulders of the founders of cricket bioacoustics. My postdoctoral mentor, David Bentley, at the University of California Berkeley, studied cricket song for his PhD. under the guidance of Richard Alexander, at the University of Michigan, after which Bentley did a postdoc on the central rhythm generating neural network in Franz Huber’s lab in Germany. Alexander had earlier shown (1962) that the calling song of male crickets is species-specific with respect to the temporal pattern of sound pulses in the call. The call rhythm was as predictable and stereotyped as any morphological trait (Alexander 1962) and was therefore genetically controlled. Bentley and I tackled the degree to which song rhythms were controlled genetically by hybridizing species of crickets that had distinctly different song rhythms and recording and measuring the call rhythms of the F-1 and back-cross hybrid males (Bentley and Hoy 1972).

Later, I became interested in how female crickets discriminate and recognize the songs of conspecific males which I pursued in my own laboratory. We deployed audio playback of natural recordings and electroacoustically synthesized models of calling songs to study the genetic control of cricket song rhythms, generally. We were able to induce hybridization between field cricket species with distinctly different call rhythms (Hoy and Paul 1973; Hoy et al. 1977).

As indicated earlier, field crickets, like many insects, live only a few months and so must mate and reproduce without ever having contact with the parental generation (Alexander 1957, 1962). Presumably, this means that the act of species-specific communication—singing and perceiving its species-specific calling song—must be largely specified by genetic instructions. This precludes the role of learning song

characteristics since there is no overlap with its progenitors, unlike longer lived birds and mammals, in which learning can occur because of overlapping generations. Thus, the cricket song system is an ideal model for investigating species-specific communication signaling that is primarily determined by nature (genetics) uncontaminated by nurture (learning from conspecifics).

2.2.7 The Acoustico-Motor Linkage in Species-Specific Phonotactic Behavior in Crickets

Regan's phonotaxis experiments showed that female crickets are attracted to the sound of the calling song of a male cricket but the degree to which her phonotaxis is dependent on the species of calling cricket would not be clarified until the 1950s and the studies of R.D. Alexander (1962) in field crickets and T.J. Walker (1957, 1962) in tree crickets. Their studies demonstrated that it is the temporal pattern of sound pulses in calling song that differentiates the calls of one species from another. It is the pulse rhythm of a calling song that the conspecific female detects and discriminates in making her decision to approach one call type over another call when both are simultaneously broadcast in a phonotaxis experiment. Of course, carrier frequency of the sound pulses also influences behavior but is less consequential because in both field and tree crickets, the spectral bandwidth of congeneric male calls shows considerable overlap and is shared among males of different species (Walker 1957, 1962; Alexander 1962), which became clear only after the commercial availability of the sound spectrograph in the late 1940s and 1950s.

The implications of this work led to a natural question of how the central auditory system processes the temporal pattern of species-specific calls and the degree to which call rhythms are under genetic control or whether some kind of learning is involved, as was known from the dialects of songbirds (Marler and Tamura 1964). In brief, how do female crickets become "tuned-in" and attracted to the temporal pattern of the calls of a conspecific male, ignoring the call of an equally audible heterospecific male whose call possesses a different temporal pattern of sound pulses? Learning was minimized if not simply dismissed because there is no overlap between parental generations and their offspring.

Especially in temperate climates, the parental generation completes its entire reproductive cycle in one season/year (lifespan is about 4–5 months, including 2 months of sexual, reproductive maturity as adult insects) and eggs are laid in the ground/vegetation to overwinter after the adult parental generation dies. It is not until the spring or summer of the next year that the eggs hatch and the immature instar larvae attain reproductive adulthood without ever hearing the calls of the male parent species—unlike birds, in which there is parent–offspring overlap and opportunities for immature males to "learn" from parental males. Undeniably, the acoustic behavior—both song production and its perception and "recognition" are under firm genetic control. Thus, the calling behavior of crickets—production of

species-specific call rhythms as well as the auditory perceptual processing of call rhythm—is a model system in which to study the neurobiological mechanisms that underlie the species-specific behavioral linkage that exists between conspecific male and female.

Such a linkage underlies auditory communication not just in crickets. It may exist for frogs, birds, and mammals, at least to some degree, as well as all acoustically communicating invertebrates. Thus, the cricket song system, a model for genetically determined communication coupling, cleanly separate from ontogenetic influences and learning. The detailed, elegant work of Bertil Hedwig et al. (2018; Schoeneich and Hedwig 2019) indicates that within the CNS of female crickets an identifiable network of interneurons serves as an auditory filter that is tuned to the temporal characteristics of its species-specific calling song. Other hypotheses such as template matching, a form of corollary discharge, remain speculative, absent experimental evidence (Hoy 1974).

2.3 Hearing Insects II: Moths and Neuroethology

Among the 1950s contemporaries of pioneering cricketeer, Franz Huber, were the noted insect physiologist, Kenneth Roeder at Tufts University (Boston, MA) and his colleague, acarologist (one who studies parasitic mites) Asher Treat, at the City College of New York. Huber and Roeder became spokesmen and co-founders of the emerging field of invertebrate neuroethology—a merger of ethology and neurobiology, the neural analysis of an insect's behavior, as performed in ecologically valid, natural habitats. Roeder's 1967 book, "Nerve Cells and Insect Behavior," is a classic, a canonical neuroethological text.

Noctuid moths are large (cricket size or more) nocturnally active insects that are commonly seen on summer nights, flying around porch lights or higher above, flying around street lamps. These large moths first attracted Treat's attention because they possess a pair of large, transparent membranes, one on each side of the insect's metathoracic body wall and normally hidden when the wings are folded in resting moths. Treat specialized in the tiny parasitic mites that infest moths. In particular, he was fascinated by the mites that infested noctuids because these mites formed family colonies that lived within a large, air-filled, thoracic chamber beneath the moth's wings. A large, transparent membrane forms the external wall of the chamber.

Even earlier, a German entomologist studying noctuid moths, had observed these membranes (Eggers 1919). He conjectured that the membranes served an auditory function because they looked like a vertebrate/mammalian eardrum. Aware of this, Treat presumed that he was studying ear mites, which inhabited/infested the air-filled chamber, internal and adjacent to the eardrum, and that this is where they lived their entire life cycle.

Even more intriguing, Treat was struck by the fact that these mites only and always infested one ear chamber, never two. His curiosity about the auditory functionality of noctuid eardrums led him to perform behavioral experiments that

showed noctuid moths in fact responded to sound mid-flight with brief, reflex-like turns at short reaction times (Treat 1955).

Such observations begged for rigorous physiological experiments which led Treat to collaborate with Roeder, a noted expert in insect sensory neurophysiology. Together, they demonstrated that the noctuid moth's hearing organ was sensitive only to sounds at ultrasonic frequencies. This led to their joint report in *Science* (Roeder and Treat 1957) that the moth's thoracic membranes indeed functioned as eardrums that were connected to an auditory organ consisting of just two scolopale sensory cells and an auditory nerve that projected to the CNS. Roeder recorded the nerve's auditory responses and discovered it responded to sound only at ultrasonic frequencies from 20 kHz to at least 60 kHz. From this, Roeder and Treat surmised that the Noctuid moth's ear is tuned to hear the biosonar calls of predaceous, insectivorous bats, which were known to include moths, including noctuids, in their diets. This minimalistic, two sensory-cell, ultrasound-sensitive hearing organ likely evolved as a special adaptation to predatory pressure from insectivorous bats, that hunt by emitting biosonar, echolocation signals (Roeder 1967).

In a classic and innovative series of studies, Roeder went on to study moth hearing as it occurs *au naturel*, out of doors and under the night sky, in his backyard and adjacent fields. He deployed powerful searchlights to cast intense beams of light high into the open sky which attract luxophilic flying moths. The phototactically attracted moths became illuminated and visible when they flow into the beams of the searchlight, at which time, Roeder directed beams of ultrasound at the illuminated moths. He stimulated the moths with playback of pulses of ultrasound within the bandwidth of Northeastern bats about 25–75 kHz, mainly *Myotis lucifugus* and *Eptesicus fuscus* (Roeder 1967).

In his experiments, Roeder precisely controlled where and when he wanted to stimulate the moths with ultrasound by mounting powerful loudspeakers on the end of long poles, thrust high into the air, to broadcast beams of ultrasound. Moths are attracted to light and so fly into these beams of light illuminating them against the background of the black, night sky, for photography. When Roeder stimulated high-flying moths with ultrasound, the moths abruptly steered away from the location of the speaker—this is an acoustic startle or evasive response (Roeder 1967).

As a devoted physiologist, Roeder augmented his field behavioral observations with neurophysiological recordings from minimally dissected moths from a recording setup on a table in his yard. He had built a little physiology lab in a shed in the yard—and that is why Kenneth Roeder is considered a pioneering neuroethologist! He was able to detect the presence of a bat chasing moths flying overhead by listening to the neural discharge of spikes from the auditory nerve of his lightly dissected, physiologically prepared moths whenever foraging bats homed in on the moths that were attracted to the searchlight beams—in effect, Roeder had “invented” an ultrasound-sensitive biological microphone!

Treat was especially delighted with his collaboration with Roeder because it helped solve his conundrum: why did moth ear mites inhabit only one ear chamber, but never both (Treat 1955)? Treat and Roeder found that ear mite infestation resulted in physiological deafness because the mites eat and destroy the moth's

“inner ear,” including its auditory nerve. But if the mites only devoured one ear the semi-deafened moth could still detect and perform evasive movements to escape from echo-ranging bats, permitting survival of both moth and mites. If mites infested both ears, the moth would be totally deaf—in effect, turning it into an insect version of the Titanic, for both mites and moths, but a meal for the bat (Roeder 1967).

2.3.1 All Night-Flying Insects Have a Bat Problem

Roeder’s foundational study opened the eyes of a new generation of neuroethologists to investigate auditory behavior in other insects. In the 1970s and early 1980s, graduate students and postdocs in my lab followed Roeder’s lead by investigating ultrasound-sensitive hearing in other night-flying insects. This led to multiple discoveries of ultrasound-sensitive ears in unexpected places and in surprising species, such as crickets (Moiseff et al. 1978), praying mantises (Yager and Hoy 1986), beetles (Forrest et al. 1995; Yager and Spangler 1997), katydids (Faure and Hoy 2000), and in many more moth species (Fullard and Yack 1993), and even in an acoustic-parasitic fly (Rosen et al. 2009). That may seem surprising until one knows that this fly’s host species are field crickets that they locate by hearing their mating calls (Cade 1975) and home in on the wing, at night, when male crickets sing and bats hunt bugs. Hence, to locate its host, a singing male cricket, the parasitic fly must share a female cricket’s predation risk from bats (Rosen et al. 2009). These phenomena have been reviewed in previous SHAR volumes (Hoy 1992).

2.4 Cockroaches Are Great Escape Artists, But Can They Hear?

Cockroaches are among the largest insects (one to several inches long) and infamously invade human dwellings, cohabiting with humans ever since humans sought protection from the elements in closed buildings. It might surprise readers that they are mentioned in a chapter on insect sonic behavior and hearing because they are not known to produce sound. In fact, early in the study of insect hearing, cockroaches were suspected to have a sense of hearing (Pumphrey and Rawdon-Smith 1936a, b).

Ironically, cockroaches lack recognizable tympanal membranes, unlike their sonically active insect relatives, crickets, cicadas, and katydids. The most familiar and common species of cockroaches such as the American cockroach (*Periplaneta americana*), German cockroach (*Blatella germanica*), and the oriental cockroach (*Blatta orientalis*) are very well known to humans as pests because they inhabit

human dwellings. Cockroaches are notorious and ruefully hard to catch and kill, to the point that frustrated housekeepers have attributed preternatural senses to escapees and, in particular, a suspicion that they can hear approaching threats.

In fact, cockroaches are extremely sensitive to air currents that perturb sensory hairs on their abdominal cercal organs (Pumphrey and Rawdon-Smith 1936a). Instead of tympanal ears cockroaches possess a pair of “hairy” appendages, cerci, on the tips of their abdomen, to which hearing was attributed. Biologists have also long admired the ability of cockroaches to detect local disturbances and avoid capture, even in dim light where vision is minimized, but their cercal sensory organs were regarded as short-range, “wind” detectors, not proper ears, with eardrums like orthopteroid insects such as crickets, katydids, and grasshoppers.

In the lab, where carefully controlled, gentle puffs of wind can be generated by a diaphragm-driven device, such as the cone of a low frequency speaker (woofer), a single puff or a brief puff-train is sufficient to startle resting roaches and send them scuttling rapidly away from the source of airflow (Camhi et al. 1978). The distance separating insect and the stimulus source is usually very short, on the order of up to 10 cm, but far beyond the range of actual touch or tactile contact. The roach’s mechanosensory organs, its cerci studded with fine sensory hairs, sense the bulk movement of air particles emitted from a nearby source, such as from acoustic audio speakers, placed close but not touching, and broadcasting low frequency tones, up to about 250 Hz (Pumphrey 1940).

As would be revealed in the 1970s, experimental work showed that cercal filiform sensilla of cockroaches (socketed cuticular hairs) are extremely sensitive to airflow. Further experimentation showed that the filiform hairs clearly sense the mechanical perturbations of air as shown by Juergen Tautz (1977, 1979), who studied the socketed filiform sensory hairs of moth caterpillars. These investigations made it evident that insects with mechanosensory organs bearing long, fine filamentous sensory hairs can detect airborne signals that are due to the movements of air particles and not from substrate vibrations or direct tactile touch.

The cercal organs of a roach bristle with dozens of long, thin, microscopic hairs that project into the air. These hairs are innervated by bipolar sensory receptor cells which serve as acoustic sensors. Thus, sensory hairs provide atympanate insects with another mechanism for sensing acoustic airflow; they detect the oscillatory movements of air particles that constitute the fluid flow of the propagating sound wave (Markl and Tautz 1975). These studies indicated that the role of filiform sensory hairs is to detect low frequency sounds over a few cm distance as well as responses to air puffs generated at slightly greater distances, and of course to respond to direct touch. Thus, cuticular hairs became associated with very short distance airflow detectors. In summary, although the commonest cockroach species have long been suspected to hear sound, based on biomechanics (Shaw 1994) and neurophysiology (Camhi et al. 1978) definitive behavioral evidence is still lacking.

2.4.1 *Supersized Sonic Roaches: The “Hissing Cockroaches” of Madagascar*

In the 1960s, the entomologist Louis Roth, at the Natick Laboratory Army Research, Development, and Engineering Center, (in search of the perfect insecticide, no doubt) in Massachusetts, famously maintained a cosmopolitan menagerie of cockroaches which he willingly shared with curious biologists. One such species, *Gromphadorhina portentosa* (the Madagascar hissing cockroach), has long captured the attention of entomologists (Roth and Willis 1960) as well as the public at large. This roach plays an outsized role in contemporary cultural awareness simply because it is nearly as big as a house mouse (2–4 inches long) and loudly announces its “displeasure” by audibly loud, startling hissing sounds when it is disturbed or picked up. This belies their usual docile nature—after a few disturbance hisses when touched, they do not run away when picked up and held in one’s palm where they remain in docile repose; a quality that makes them a children’s favorite at public science centers and museums.

However, *Gromphadorhina*, unlike all other roaches, also exhibits remarkable sonic and auditory behavior in its social interactions. During courtship and mating, male roaches make temporally patterned hissing sounds in the presence of females while competing males emit loud aggressive hisses at each other. Their acoustic behavior is like that seen in other auditive insects, like crickets and katydids. Yet, scrupulous visual and microscopic anatomical examination indicate that *G. portentosa* is atympanate, and moreover, its short, stubby abdominal cercal organs are grossly reduced in size and its sensory hairs are extremely sparse in number and short in length, by comparison with other cockroach species. However, this roach unequivocally emits audible acoustic signals in its social behavior (mating and territorial), and it hears contextually salient and distinctive social hisses, based on evidence from recordings made from behaving roaches and electroacoustic analogs of actual songs (Fraser and Nelson 1984; Clark and Moore 1994).

G. portentosa produces a loud, noisy, hissing sound by forcibly expelling air through its extensive respiratory tracheal system and released out of a specialized pair of horn-shaped spiracles on the second abdominal segment that are morphologically adapted (tuned) to produce a noisy hissing sound over a wide spectral range that “peaks” at 5 kHz (Barth 1968; Nelson 1979).

Remarkably, *G. portentosa*’s sound producing mechanism resembles that of a vertebrate’s, given its respiratory system origins. This hiss is produced by forcing air through the roach’s respiratory spiracular system located in its second abdominal segment that terminates to the outside in a reed-like valve (Roth and Willis 1960; Barth 1968; Nelson 1979). Muscles controlling the opening and closing of this valve allow this insect to modulate its sonifications, mainly through amplitude modulation (Nelson 1979; Nelson and Fraser 1980). While several large insects like cicadas or praying mantises emit audible disturbance sounds when picked up or perturbed, *G. portentosa* has also adapted its sonic system to subserve mating and

territorial behavior in its social communication (Nelson 1979; Clark and Moore 1994).

Social hissing signals are amplitude modulated in courtship/mating and aggressive (male-male) contexts. While no obvious tympanal membrane has been found yet nor reported, histological and functional modifications of its chordotonal subgenual organs in several of its legs suggest a possible auditory function (Fraser and Nelson 1984). Neural recordings made from the leg nerve indicate sensitivity to sound in a frequency band ranging from 1 kHz to about 8 kHz, with a broad peak from 4 to 6 kHz.

These data are consistent with Shaw's "missing link" hypothesis (1994). Shaw investigated hearing in the common house roach, *P. americana*, by focusing on mechanoreceptive subgenual organs in the legs of cockroaches, instead of the sensory hair-studded cercal organs. He proposed that these subgenual (beneath the "knee") organs are acoustic "missing links" that connect them, evolutionarily, to the tympanal scoloporous hearing organ of crickets and katydids, which these sonic orthopteran insects also possess. In addition, they have evolved a separate scoloporous organ that is associated with the foreleg tympanal membrane. Moreover, the orthopteran subgenual (SGO) and tympanal organs (TO) are adjacent to one another, lying beneath the "knee," in the forelegs of crickets (Michel 1974).

Shaw pointed out the remarkable sensitivity of SGOs to very low levels of acoustic airflow (1994) in making his argument for auditory function. It seems quite plausible that their SGO may explain hearing in the hissing cockroach, where its subgenual organs are modified from the typical SGO, in other roach species) by possessing many more sensory scolopales. The hissing cockroach is a testament to the remarkable and biodiverse themes that are presented in studying the acoustic behavior of insects. Among all cockroach species, it is unique in its respiratory system-derived sonic emitting mechanisms for social communication (Nelson 1979; Fraser and Nelson 1984). Importantly, hissing cockroaches are endemic to and found only in Madagascar. They represent an example of isolated island endemism giving rise to animals uniquely different from related continental species. Apparently, all members of the endemic genus *Gromphadorhina* emit hissing sounds, which is a unique sound among the world's cockroaches, so far as known (Roth and Willis 1960).

2.5 The Familiar, Aggravating, Hum of Mosquitos

Unquestionably, the relationship between humans and mosquitos has a very long history, ranging from annoyance to fear because of the habit of some species to "bite" humans. Mosquito bites are at least irritating and a nuisance but at worst cause serious illness and death due to the viruses and parasites that are carried in the salivary glands of infected mosquitoes and transmitted to human hosts. Viruses such as Yellow Fever, Zika, Malaria, and Dengue are but a few infamous examples of mosquito-borne diseases.

Since time immemorial humans have been aware of a mosquito's immediate presence by (barely) hearing its low-pitched, humming flight sound when flying around their heads especially annoying at bedtime, in the still of night. A mosquito's extremely soft flight tones are inaudible at distances of an arm's length, even in silence, but become perceptible at very close range as when it flies near its victim's head and ear, in preparation to land and bite. The fundamental frequency of the flight tone ranges from 300 to 800 Hz.

Mosquitos have always drawn the curiosity of entomologically inclined naturalists. An occupational interest possibly motivated the Baltimore physician and naturalist, Christopher Johnston (1855), to investigate mosquitos. He is credited with discovering the fly's donut-shaped hearing organ, the eponymously named Johnston's Organ (JO), at the base of each antenna. Johnston performed skillful anatomical studies of the mosquito JO and ascribed auditory functionality to it without any empirical proof, writing "...that the male should be endowed with superior acuteness of the sense of hearing appears from the fact that he must seek the female for sexual union either in the dim twilight or the dark night where nothing but her sharp humming noise can serve him as a guide" (Johnston 1855). As a medical doctor, Johnston is likely to have had first-hand experience with major epidemics of Yellow Fever and malaria, which were already known to be associated with having been bitten by mosquitos.

2.5.1 Are the Low-Pitched Tones of a Flying Mosquito Mating Signals?

Johnston's famous conjecture about mosquito hearing stimulated the imagination of other mid-nineteenth-century scientists and naturalists. Just a few decades after Johnston's paper was published it caught the attention of the scientist-inventor and naturalist, Hiram Maxim. Maxim was responsible for setting up the first night-time electrically illuminated exhibition in upstate NY, from the roof of adjacent buildings overlooking the exhibition site.

The next morning following a night of illuminated revelry and after the dynamo generator motors had been switched off, Maxim (1901) noticed that wherever the motors were located, the floor was carpeted with huge numbers of carcasses of mosquitos, all males. He astutely inferred from this that the loud, persistent, low-pitched hum from the dynamos lighting the exhibit grounds attracted the mosquitos by their sound. Maxim surmised that the sound of his dynamo motors emitted pitched tones resembling the flight tone of female mosquitos, on the wing, to which the males would be attracted for mating. Maxim, and earlier physicist A.M. Mayer (1874), demonstrated that male mosquitos could be attracted to tuning forks, for example, concert A or middle C (440 and 512 Hz respectively) both of which fall within 300–800 bandwidth of wingbeat frequency for female mosquitos such as *Aedes aegypti* and *Anopheles* species, both disease carriers.

It was not until the mid-twentieth century, that a definitive laboratory study was made of the mosquito's phonotactic behavior (in this case, *Aedes aegypti*) by the entomologist, Louis Roth (1948), and of the cockroaches mentioned above. Roth, like his predecessors, used tuning forks for simple experiments, but he also deployed newly available electronic audio oscillators and high-fidelity loudspeakers to demonstrate that sound in the frequency range of a female mosquito's wingbeats was sufficient to attract caged males to electronic and mechanical sound sources, in the absence of actual live females. Crucially, Roth found that amputating the antennae eliminated the mosquito's response to sound.

A few preliminary, crude, recordings were just being made in the 1950s from the JO and auditory nerves, setting the stage for a physiological approach to investigate behavior (Tischner 1953; Tischner and Schief 1955). However, the actual behavioral role of the mosquito's wingbeat as an acoustic signal in mating as well as truly rigorous biomechanical measurements of the sensitivity of the mosquito's JO hearing organ would not come until 50 years later (Goepfert and Robert 2001; Gibson and Russell 2006; Cator et al. 2009).

2.6 Loudest for Last: Cicada Songs

Since prehistoric times, humans and their hominid progenitors have likely associated the warmest months of the year with buzzing, crackling, whirring sounds that are emitted from male cicadas, calling from tall bushes or high above, in trees, during the hottest hours of summer days. Their songs are easily recognized as coming from individual males, but often nearby male cicadas in adjacent bushes or high in trees sing together, forming a deafening chorus. They are among the largest of the sonic insects and the loudest to inhabit human soundscapes during the day. No historical account of insect bioacoustics is complete without including cicadas.

Given the prehistoric fossil evidence as well as recent genomic research, it is safe to assume that all the sonic insects that ensonify our twenty-first-century environment are related, at least to the Family level, to ancient lineages of sonic insects that sang in the rise and sang out the fall of past ancient human populations and their civilizations. Clearly, cicadas have penetrated the consciousness of ancient cultures prominently enough to have left bountiful cultural footprints, in both cultural practice and as materially solid, symbolic objects in the form of jewelry and other statuary (Aldred 1971; Lim 2001), and they have been the muses for poets and philosophers for centuries.

Cicadas are large insects, fitting comfortably in the palm of one's hand and they are conspicuously the loudest. Like other sonic insects, it is the male that emits persistent, hours long calling songs. They can make their presence known by the sound produced by individuals, singing high in trees, but they undeniably dent even the most distracted human consciousness when males form local aggregations or

congregations in adjacent bushes and trees, where they produce a chorus of ear-shatteringly intense sonic calls. Chorus size can range from dozens to hundreds and thousands, and in the case of 13- and 17-year-old cicadas, to millions of calling males. It seems likely that humans have always associated the sound of cicadas with summertime.

2.6.1 *Cicadas as Human Fetish Objects*

Cicadas were always among the most prominent animals that inhabited the auditory, if not visual, scene of humankind's earliest civilizations, especially in temperate and tropical climates of the Mediterranean and the Near and Far East, during the hot, humid summer. Hence, they drew the attention of citizenry at all levels of society—they became fetishized. Whereas virtually all other sonic insects live their life cycles within only one seasonal year, some cicadas have a prolonged larval period in which they live and grow through multiple larval molts that span multiple years, from a few to seventeen, before emerging above ground and molting into their sexually mature, sonically active adult form. The recurrent cycles of death and larval emergence from the ground and metamorphosis into adults was a behavior well known in ancient civilizations and to their sages. The cicada's life cycle consisting of clamorously loud and very brief adult stage quickly followed soon by death and apparent "rebirth" after some years impressed all within earshot. Cicadas became fetishized as evidence of resurrection and came to symbolize immortality—a power attributed only to gods and other deities—in ancient civilizations as distantly separated in space and time as the Far East, Middle East (Egypt), and Western Europe. Cicada-shaped jewelry, sculpture, and art testify to their being spiritual or religious symbols. Such artifacts have been found in tombs and other burial sites (Aldred 1971; Lim 2001).

While cicadas may have lost their mystical religious symbolism today, they are still valued and regarded as tokens of good fortune and long life in some cultures. In fact, the ever-curious Greek philosopher and sage, Aristotle (1910), notably commented on cicadas. Aristotle was a noted naturalist and was well aware of the cicada's periodic life cycle and cited them as a symbol of immortality. His interest in them was not just naturalistic and spiritual, for he prized the tastiness of cicada grubs, dug from the ground and roasted. The ancient Greeks were not alone in valuing cicadas as a food, and in the tropical climes of Africa and Asia, they are even now featured as summer snacks and serve seasonal staples in food markets. Cicada grubs and adults are large and easy to dig up or catch. Hungry humans find adults by hearing them, since the adult male cicada's calling song is to predators a "dinner bell."

2.6.2 *The Scientific Study of Cicada Bioacoustic and Hearing*

Even in Renaissance and post-Renaissance academic circles and naturalist societies, the sonic insect that has historically attracted the most attention is the cicada, likely because its singing activities are limited to daylight hours, on sunny days in the hottest weeks of the summer. They are large, easily captured, and identified. However, most of the auspiciously sonic insects are crepuscular or strictly nocturnal creatures and hence mostly heard but not seen, making them far less easy to observe and study before artificial lighting was invented. In Myers' (1929) "Insect Singers," he cites obscure, early literature that the sound-making (tymbal) organs of cicadas were described by in the eighteenth century by Reaumur. Published descriptions of the cicada hearing organ, featuring a conspicuously large and transparent tympanal membrane, came much later with the detailed histological and anatomical studies of Vogel (1923). Clearly, even by early in the twentieth century, there was a notable literature on cicada auditory behavior.

Cicadas of both sexes possess a pair of typical chordotonal hearing organs, one beneath each wing. It consists of a clearly visible, externalized, eardrum that opens internally into a large air-filled chamber, and is innervated by a scolopophorous auditory sensory organ consisting of about 1000 sensory scolopidia (Young and Hill 1977). The tympanic membranes ("eardrums") are located in the abdomen and reside immediately adjacent to the smaller tymbal organ. The air-filled tympanal chamber is part of the air-filled abdominal sound radiator. The eardrum is attached to its scolopophorous auditory organ by a thin, stiff, apodeme, of cuticular origin that is interposed between the tympanic membrane and the auditory organ. Obviously, there must be a decoupling of auditory function from the intense acoustic emissions, given the anatomical proximity of tymbal membrane (sound emitter) and tympanal membrane (sound receiver) and it is thought that there is an efferent decoupling mechanism analogous to the stapedial reflex in the human cochlea to protect the sensitivity of the hearing organ, and indeed the auditory and tymbal tensor nerves contain both afferent and efferent axons (Wohlers et al. 1979). However, the mechanistic biomechanical and neural circuitry details are unknown and remain to be worked out.

2.7 The Age of Neurophysiology and Auditory Physiology

While functional morphology and behavioral studies were necessary to demonstrate the behaviorally adaptive functionality of hearing and ears, auditory function is incomplete without knowledge of how the biomechanics of auditory stimulation results in mechano-acoustic transduction into the neural activity, from the auditory nerve to the brain. There could be no auditory neuroscience until the invention of electrophysiology. That did not come about until the twentieth century and is

identified with pioneers such as C.S. Sherrington and E. Adrian in Britain, A. Forbes, H. Gasser, and J. Erlanger in America, and H. Berger and O. Foerste in Germany.

Edgar Adrian (Lord Adrian) and his supervisor, Keith Lucas, at Cambridge University (UK), were among the first physiologists to make recordings from sensory nerves in both vertebrates and invertebrates. Indeed, Adrian and Sherrington became the first neurophysiologists to become Nobel laureates, in 1932. Their pioneering work, and that of their American contemporaries, Herbert Gasser and Joseph Erlanger, at Washington University, St. Louis, who years later would themselves become Nobel laureates, set the stage for auditory neuroscience to emerge. Electrophysiological recording techniques exploded in labs, worldwide, including those groups that made recordings from auditory nerves in both vertebrates and invertebrates, including insects.

Starting in the 1930s, the great pioneer of auditory science, Ernest Glen Wever investigated the physiology of the grasshopper hearing organ with his colleagues and students, C.W. Bray and J.A. Vernon. They published papers on the acoustic sensitivity of the insect auditory nerves and organs of several species of *Orthoptera*, including crickets and katydids (Wever and Bray 1933; Wever 1935; Wever and Vernon 1957). Beginning in 1928, Wever and his colleagues published numerous first recordings from the auditory nerves of animals, a menagerie that included pigeons, frogs, lizards, as well as many mammals including cats and bats.

The fact that Wever also made the earliest auditory nerve recordings in insects is a testament to his insatiable curiosity, dedication to a truly comparative approach, as well as his bench skills. In fact, much later in life, Wever coauthored a paper with James Simmons on Brood X, of the 17-year-old cicada, about the possible adaptive significance of the cicada's explosive, simultaneous emergence and singing in painfully loud choruses consisting of millions of insects, to deter predation by birds (Simmons et al. 1971).

2.7.1 Insect Auditory Neurophysiology—Post-World War II and the 1950s

World War II spun off a revolution in electronic devices, for both industrial/research and consumer markets, to the benefit of auditory research science. For bioacoustics, the emergence of a giant consumer audio industry, led by tape recorders and audiophile quality amplifiers and speakers at affordable prices, enabled ethologists as well as physical scientists to more broadly explore bioacoustics and auditory neuroscience.

It is notable that important, post-war neurophysiological studies of insect hearing emerged from the Tokyo laboratory of Yasuji Katsuki and his very accomplished student, Nobuo Suga, in the late 1950s and into the early 1960s (Katsuki and Suga 1959; Suga 1966). They made recordings from the auditory tympanal organs as well as from the central nervous system in cicadas, katydids, crickets, and grasshoppers,

at the single unit level (Katuki and Suga 1960). They were among the first to record from the CNS, using KCl-filled micropipette electrodes, and they characterized large axon T cells believed to be associated with sound localization in katydids (Suga 1963).

G. A. Horridge (1960) in the UK and Katsuki's lab (Yanagisawa et al. 1967) studied locust hearing and were among the first investigators to show that insect neurons demonstrated true frequency discrimination, thus refuting the then-common belief that insects with tympanate auditory organs could not discriminate the frequency of an acoustic stimulus independently of level, as claimed by Pumphrey (1940).

Upon completing his doctoral training in Katsuki's lab, Suga embarked for post-doctoral work in the USA with Donald Griffin, at Harvard University (Cambridge, MA), and later, with Theodore Holmes (Ted) Bullock, at UCLA (Los Angeles, CA), where he applied his neurophysiological skills to the auditory CNS of bats. He went on to establish a distinguished, life-long, career studying how the bat brain processes biosonar signals in his laboratory at Washington University, in St. Louis. Suga's remarkable span of accomplishments as a neurophysiological recordist can be traced to his PhD studies with Katsuki, on the insect auditory system (Suga 1960, 1961, 1963).

The work of Kenneth Roeder (1967) on moth hearing and auditory physiology that took place in the 1950s and 1960s, discussed in Sect. 2.3, is arguably proto-neuroethological, as a paradigm for the field. As discussed in Sect. 2.2.2, Franz Huber's pioneering neurophysiological work in Germany in the 1960s established the field cricket as a model for insect bioacoustics. The 1970s saw the flowering of the field of neuroethology that ushered in a period of unparalleled investigation of the neurobiological basis of the insect senses of vision and olfaction, as well as audition. The auditory system of every known sonic insect was studied at the level of its neural systems, from sensory organs to the brain. To review this work is far beyond the scope of this retrospective. It is also the subject of two previous volumes of the SHAR series, (Hoy et al. 1998 and Pollack, Mason et al. 2016), to which the interested reader is referred.

2.8 Sizing Up Insect Hearing, a Reprise

I began this chapter by calling attention to how the extremely small size of insects, by comparison to vertebrate animals, can drive differences in the mechanisms of hearing, particularly in the "outer ear," and noting that insects do not need a middle ear. Hearing in small insects like mosquitoes and other small flies makes membrane-constrained outer ears problematic. Instead, these tiny insects deploy thin, filamentous, nanoscale airflow detectors that are sensitive to the velocity of local movements of surrounding air particles that are set into oscillation by the propagating sound waves. These particle-velocity-sensitive hairs or hair-like antennae are innervated by mechanoreceptive sensory cells that perform sensory transduction. Insects like

cicadas, grasshoppers, katydids, beetles, moths, and praying mantises that possess the sense of hearing are large enough to deploy tympanal membranes (eardrums) substantial enough to detect pressure differences in the sound wave.

To summarize, hearing in both vertebrates and insects involves sensing an aerial mechano-acoustic disturbance that radiates from the vibrating noise source. The sound wave propagates through oscillatory movements of air particles that impinge upon the animal's outer ear structure, which is set into movement. In vertebrates, the outer ear may be as simple as thinned patch of epithelium/skin or an internalized tympanal membrane—in either case, it is an eardrum. The vertebrate eardrum senses the vibrating airflow as oscillations in air pressure, integrated over its surface. Large sonic insects, such as cicadas, locusts, and crickets also possess tympanal membranes which detect oscillating changes in air pressure, just like vertebrates.

However, minutely small insects, such as mosquitos and drosophila, are insensitive to changes in air pressure but instead detect the velocity of air particle oscillations in the impinging sound wave, which they sense with long, thin cylindrical mechanosensory hairs. Importantly, such sensory hairs can sense particle velocity even at relatively long distances from the source where sound propagates as a pressure wave, the acoustic far-field, and not just in the immediate vicinity of a vibrating source, the near acoustic field.

The ability of a sensory hair to detect air particle movements in the pressure field is limited only by its mechano-neural sensitivity, and its auditory threshold is determinant. As long as its sensitivity is above thermal noise, particle velocity can be neuro-acoustically transduced into action potentials and a sensory hair would be an adequate acoustic organ.

Mosquitos can hear sound in the range of 400–700 Hz over relatively long distances (meters). This is the case for the mosquito antenna-Johnston's organ complex, as elegantly demonstrated in the biomechanical experiments of Goepfert and Robert (2001) and much later, in neurophysiological recordings from the Johnston's organ auditory nerve (Menda et al. 2019). Thus, the customary use of the terms, acoustic “near-field” and “far-field,” where the former implies detection of air particle velocity at close range and the latter, detection of air pressure at long range, needs to be reconsidered.

There is a tendency to think of acoustic transducers as being pressure detectors, whether in the world of commercial audio microphones or in comparative bioacoustics labs investigating the animal ear. This is an understandable but implicit anthropocentric bias. In fact, all commercial microphones are based on the human hearing mechanism and are constructed to detect sound pressure. But this is not so for the hearing organs in minute insects (nor in fishes—see Sand et al., this volume).

Retracing the history of discovery in insect hearing, it was conjectured or known by the 1930s, that cockroaches and mosquitos sensed sound with cuticular sensory hairs on cercal organs or antennae, but functionality was thought to be limited to very close distances. Behavioral reactions could be induced by local puffs of wind or near-field acoustic excitation. Long range acoustic sensitivity was assumed to be the province of pressure-sensing tympanal organs, as exemplified in crickets and

cicadas. It was not until the twenty-first century that the sensitivity of hairs or antennae was demonstrated at distances where sound is propagated as changes in air pressure, thus demonstrating that sensory hairs detect the velocity of air particles oscillating in the pressure field (Goepfert and Robert 2001; Menda et al. 2019).

2.9 After Words

There remains much to be discovered about insect hearing because of the diversity of hearing organs and mechanisms, especially those in small insects that operate at nanoscale-to-microscale dimensions. They can be studied with new imaging, biomechanical, and neurophysiological tools that are now available. While this chapter has emphasized differences in hearing mechanisms and organs between vertebrates and insects, very recent work points to functional convergence in the biomechanical workings of hearing organs, especially those possessed by katydid (Tettigoniidae). This chapter will conclude with some recent studies that are food for thought when considering convergence and divergence in the structure and function of insect hearing organs.

Insect cuticular sensory hairs serve as remote sensors that detect action at a distance. Goepfert and Robert (2001) demonstrated the exquisite sensitivity of the mosquito JO to particle velocity in acoustic flow. However, sound is not the only force acting at a distance that is an adequate stimulus to stimulate sensory hairs. All that is required is a force to stimulate the hair into movement, however slight. Daniel Robert's lab (Clark et al. 2013) has recently shown that an electrostatic force will cause (charged) cuticular hairs to move and generate action potentials. They showed that bumblebees can detect and even learn the configuration of the electrostatic field of flowers and leaves and utilize this information for efficient foraging. This work opens a new window into the sensory ecology of insects—that of terrestrial electroreception—and a new role for sensory hairs. Thus far, it has been shown that sensory hairs are superb models for detecting weak forces at a distance, such as air particle movements in acoustically driven airflow, as well as weak electrostatic force fields—mechanoreceptive hairs can also electroreceptors—as long as they are moved by an external force they can be excited to respond.

It has been known for several decades that the scolopidia cells in a chordotonal hearing organ (such in crickets and katydids) form linear arrays in the organ and that they are organized tonotopically, analogous to that in the vertebrate cochlea (Oldfield 1982). This is an interesting convergence of structure and function in the cricket and katydid ears with vertebrates.

However, an even more interesting story has emerged in the recent investigations of the hearing organs of tropical, South American katydid (tettigoniid), *Copiphora gorgonensis* (Montealegre-Z et al. 2012). The work of Montealegre-Z, also in the Robert lab, on the tympanal hearing organ of this katydid reveals an even greater degree of convergence of structure and function, with mammalian hearing. Not only did they demonstrate tonotopy, but they also discovered traveling waves within a

fluid-filled chamber that contains the sensory scolopale cells. Presumably, this sets up a vertebrate-like impedance matching problem and indeed, they discovered a structure called the tympanal plate which seems to act like the vertebrate middle ear (Montealegre-Z et al. 2012). These discoveries were enabled by micro-CT scanning techniques and laser vibrometry. A new technique for investigating the micro-mechanics within the miniscule katydid ear with even higher resolution optical coherence tomography vibrometry increases the spatio-temporal resolution of measurement, which reinforces the convergence in vibrational mechanics between insect and vertebrate ear, at the level of micromechanics. It will be interesting to know if a similar structure-function mechanism occurs in the ears of crickets and other sonic insects that have tympanal hearing organs (Vavacou et al. 2021). Traveling waves are also a feature in the ears of locusts, but the parallelism with vertebrates and katydids is far less pronounced (Windmill et al. 2005).

Another interesting parallel between vertebrate hearing and an insect is the discovery of metabolically dependent acoustic amplification and the discovery of spontaneous acoustic emissions in the hearing organs of mosquitos (Goepfert and Robert 2001) and grasshoppers (Koessler and Boyan 1998). There is evidence that efferent control of sensitivity may occur in insect hearing and that the phenomenon of stochastic resonance appears to play a role in enhancing sensitivity in insect hearing (Windmill and Jackson 2016).

I conclude with these “reports from the front,” which I hope testify to the value of investigating hearing at nano-to-microscale in insects as well as the continuing value of comparative studies at the neuroethological level of sensory ecology and behavior. It is obvious that such program of basic research studies also provides rich ground to till for the applied acoustical engineering field, through the application of the strategy of biomimicry for discovery. We live in an age of novel applications of audio in the age of the internet, and the need for new designs for microphones and audio transducers is alive and well in the world of the internet. For tomorrow’s students: study insect hearing—It has much to offer.

Acknowledgments I am grateful to the 25 grad students and 26 postdocs I was lucky enough to attract to my lab at Cornell and regret that I could not cite the work of every one of them in this chapter. However, this book focuses on the historical roots of insect hearing up to about 1970 which is when I opened my lab. Special thanks are owed to the editors: Arthur Popper, without whose prodding and encouragement, I would not finished this chapter, and Darlene Ketten whose support encouraged me to keep on trucking. Lastly, to my wife Margy who said I was crazy to take this on alone—she was right.

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