

# Chapter 1

## Introduction to Insect Acoustics

Andrew C. Mason and Gerald S. Pollack

**Abstract** Insects are the most diverse taxonomic group of animals, and this is reflected in the number and variety of anatomically and evolutionarily distinct ears to be found within this group. In general terms, all auditory systems must accomplish the same basic tasks of detecting, discriminating, and localizing sound sources. Insects, therefore, present many examples of alternative mechanisms for fundamental auditory processes, and research on insect auditory systems addresses all aspects of hearing and acoustic behavior. This research is also highly integrative. Insects provide important models for studies of biophysical and molecular mechanisms of auditory transduction. The relative simplicity of insect nervous systems (compared with those of vertebrates) allows for auditory mechanisms to be studied at the level of explicitly resolved neural circuits and identifiable neurons, and these can be linked to specific behavioral functions.

**Keywords** Acoustic communication • Active hearing • Auditory mechanics • Auditory processing • *Drosophila* hearing • Evolution • Insect hearing • Mechanoreception • Mechanotransduction • Predator detection • Scolopidia

### 1.1 Hearing

Hearing, or auditory perception, refers to the detection of mechanical waves (or vibrations) propagating through a surrounding medium. These vibrations induce movement of specialized body structures (ears) and in turn activate sensory neurons to generate an auditory percept. Hearing is widespread among two disparate animal taxa: vertebrates and insects. A major goal of auditory research in general is to understand the mechanistic basis of human sound perception: as a model for the neural basis of sensory experience more generally and as a basis for maintaining normal auditory function or correcting dysfunction. In this volume, we focus on

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comparative studies of hearing in insects, with the goal of providing an overview of current research on all aspects of hearing in the most diverse and numerous animal taxon. Coverage includes the origins, evolution, and adaptive function of hearing in insects; mechanical and molecular mechanisms of auditory transduction; and organization and computational function of the auditory pathway.

All auditory systems must accomplish the same basic tasks. Sound is a source of information that can guide behavior. In a few taxa, self-generated sound or vibration is used as a mechanism for “sounding” to acquire information about the environment (Surlykke et al. 2014). In general, however, the information derived from sound refers to an external sound source. This may be a predator (to be avoided), a conspecific (to be approached), or another source that might signal the presence of a resource (such as a prey item or a host). The function of hearing, therefore, is to detect, recognize, and localize relevant sound sources, possibly among numerous irrelevant ones. This applies to insects as well as vertebrates. Whereas vertebrate hearing has a common ancestry (single evolutionary origin; Manley 2012), hearing has evolved independently many times among insects (at least 24 by current estimates; see Greenfield, Chapter 2). Thus insects are a useful group for comparative studies aimed at identifying common functional principles of hearing and auditory processing. In addition, the relative simplicity of insect nervous systems, and their “economical” design, often make these questions much more experimentally tractable than in vertebrates. Research on insect auditory systems has uncovered a variety of novel and elegant solutions to classic problems in hearing and neuroscience, including selective attention (Pollack 1988), refference (Poulet and Hedwig 2002), categorical perception (Wytenbach et al. 1996), and sound localization (Robert et al. 1996). Insect hearing research also makes more directly practical contributions, as their elegant solutions to some of these sensory tasks frequently inspire novel strategies for technology development (Robert et al. 2010).

## 1.2 Hearing in Insects

### 1.2.1 *Sound Pressure and Tympanal Ears*

The chapters in this volume represent a relatively inclusive view of “hearing.” The narrowest definition of the term (by analogy with human hearing) refers only to detection of the pressure component of airborne waves by means of a tympanal organ (Hoy and Robert 1996). Insects, largely as a consequence of their small size, operate at a wider range of spatial scales than most vertebrates. It is true that the insects that are most obviously recognizable as having an auditory system are those that communicate using acoustic signals over long distances. Examples of these include the Ensifera (crickets and kaytdids) and cicadas, and in these groups hearing is mediated by tympanal organs detecting sound pressure—unambiguously fitting the narrowest definition of hearing. The obvious acoustic signals, easily detectable to the human ear, produced by many of these species (usually males advertising to

or courting females; see Balakrishnan, Chapter 3) have resulted in a long history of research on their hearing (see Pumphrey 1940). In addition to their role in intraspecific communication, the tympanal ears in many insects function in the detection of predators (mainly echolocating bats; see Pollack, Chapter 4).

### ***1.2.2 Near-Field Hearing and Particle Displacement Ears***

For many insect species, however, behaviors mediated by sound occur within the acoustic near field (see Windmill and Jackson, Chapter 6 and Kamikouchi and Ishikawa, Chapter 10), and the relevant cues are derived from the particle displacement component of sound. Examples of these include fruit flies (*Drosophilidae*) and mosquitoes (*Culicidae*), and among these groups near-field sound is detected with nontympanal ears, usually Johnston's organ, a mechanosensory structure located on the second segment of the antennae. In some species, such as fruit flies, this sensory system mediates an acoustic communication system broadly similar to those based on long-distance calls (i.e., males signaling to court females) despite the short-range nature of the signals. Others, such as mosquitoes, do not produce specialized acoustic signals, but hearing functions to allow males to detect the low-frequency tones produced by female wingbeats when they are in flight. A closely related sensory modality is fluid flow sensing, which is mediated by mechanosensory hairs activated by air particle movement over a wide range of frequencies (Bathellier et al. 2012). The hairs are often abundant and widely distributed over the insect body, but in many species they are also concentrated in specialized organs, the cerci, with functions that parallel those of the auditory system in some respects (Jacobs et al. 2008; Casas and Dangles 2010). Fluid flow senses are, nevertheless, considered a distinct modality from near-field hearing and are not discussed in this volume.

### ***1.2.3 Sound and Vibration***

Mechanical waves that function as signals or cues may also propagate in solid substrates. Sensitivity to such substrate-borne signals is ubiquitous in insects, and many species have well-developed communication systems using substrate vibration signals. There is a close relationship between sound and substrate vibration in some insect taxa. In the Ensifera, there is a close anatomical relationship between auditory and vibratory sensory structures (Strauss and Lakes-Harlan 2009). Among the true bugs (Hemiptera), cicadas make extensive and obvious use of acoustic signals that they detect using tympanal ears, whereas other closely related species communicate via signals propagated through solid (plant) substrates (Cokl and Virant-Doberlet 2003). The relationship between substrate vibration sense and tympanal hearing of airborne sound is a major question in the evolution of hearing (see Greenfield, Chapter 2).

Most reviews of insect hearing begin with a statement of the scope of material to be covered that specifically indicates the categories of “hearing” that will be included. This volume includes the full spectrum, with an admitted emphasis on airborne sound detected by tympanal ears (Hoy and Robert 1996)—this being the most extensively studied area and representing the most common and clearly acoustically active insect species. Nevertheless, the striking diversity of insect auditory systems is unified by the common underlying structure, at the cellular level, of the scolopidia comprising the sensory organs themselves (Field and Matheson 1998). In addition, a growing body of research (largely on the nontympanal ear of the fruit fly) has demonstrated a broader homology at the molecular level that encompasses both insects and vertebrates (Senthilan et al. 2012). Likewise, increasingly fine-grained analyses of the mechanics of insect tympanal organs have identified other commonalities with vertebrate systems, including traveling waves in the locust eardrum (Windmill et al. 2005), cochlea-like mechanics in katydid ears (Montealegre-Z et al. 2012; Udayashankar et al. 2012), and active amplification in a number of insect ears (Mhatre 2014). All of this highlights the value of the broadest comparative approach. There is a continuity of structure and function across the full spectrum of insect auditory mechanoreception that justifies this inclusiveness. Where this volume is slightly more conservative, on the other hand, is taxonomic scope. Unlike the previous SHAR volume on insect hearing (Hoy et al. 1998), we do not include spiders, another major arthropod group that makes extensive use of sensory information derived from substrate-borne vibrations. A number of recent reviews have covered vibrational communication in spiders (Elias and Mason 2014). Likewise, there is little mention of underwater hearing (Sueur et al. 2011).

The contents are broadly organized around three areas. Chapters 2–5 review topics on the origins and functions of hearing in insects. Chapters 6 and 7 cover mechanisms of acoustic transduction at the mechanical and cellular levels, respectively. The remaining chapters (Chapters 8–10) focus on the neural basis of hearing and auditory behavior.

## 1.3 Origins and Functions of Hearing

### 1.3.1 *Evolution of Acoustic Communication in Insects*

This striking diversity of ears has, at times, seemed to defy logical explanation, as (Oldroyd 1962, p. 63) observed:

There is little rhyme or reason about which insects have tympanal organs, and whereabouts on the body they are placed. The short-horned grasshoppers have them on the first segment of the abdomen, but the long-horned grasshoppers and crickets have them on the fore-legs. Many bugs and moths have them in the thorax, but cicadas and some moths have them in the abdomen; no butterflies have them at all.

Based on current evidence, hearing (i.e., a sensitivity to airborne sound) has arisen independently at least 24 times among different insect taxa, and this list is

now known to include also butterflies (Lucas et al. 2014). Studies of the origins and evolution of hearing provide an important foundation for comparative analyses, and current evolutionary and phylogenetic analyses have provided insight on origins and patterns of insect auditory diversity. In Chapter 2, Greenfield reviews current research on the evolution of hearing and communication in insects. A long-standing issue has been the question of whether insect hearing evolved in the context of intraspecific communication or predator detection. The numerous independent origins of insect hearing would suggest that there need not be a single answer to this question.

Nevertheless, within a number of large insect taxa, there are alternative models for the evolution of hearing. Among groups such as the Ensifera, where hearing is reliably associated with sound production and acoustic communication, the question remains whether hearing arose first and communication later and what evolutionary processes (e.g., sensory bias, sexual selection) resulted in the elaboration and diversification of these systems. Among insect lineages with auditory systems devoted to the detection of predators (mostly echolocation signals of bats; see Pollack, Chapter 4), the nature of selection for the evolution of hearing is clear—a set of acoustic cues highly correlated with a danger of predation makes possession of an auditory system highly advantageous. These broad generalizations are complicated by the fact that in many groups where the origin of hearing appears to have been predator detection, hearing has secondarily evolved to function in intraspecific communication. The opposite pattern is also common, in which acoustically mediated predator avoidance has evolved as an elaboration of auditory systems whose primary function is communication. Finally, the anatomical diversity of insect ears must be understood in light of the relationship between auditory organs and the other mechanoreceptive systems from which they are derived (proprioception, tactile, substrate vibration). Thus, tracing the evolutionary origins and diversification of insect hearing is a complex task but one that is central to answering the broad comparative questions.

### ***1.3.2 Behavioral Ecology of Insect Acoustic Communication***

In addition to the evolutionary origins and diversification of hearing and auditory systems in insects, much research has focused on the current functions of hearing. These fall broadly into the two categories considered in Chapter 2: intraspecific communication and predator detection. The behavioral ecology of insect hearing is reviewed in Chapter 3 by Balakrishnan. The focus here is mainly on long-distance acoustic communication, taking an integrative approach that considers production, transmission, and detection of acoustic signals. Variation in the costs and benefits of signal production and processing for both partners in a communicative exchange leads to a diversity of behavioral strategies (and signal structures) that is, to some extent, independent of the taxonomic diversity of the auditory systems involved. Behavioral studies therefore add another layer of complexity to the study of insect hearing. In addition to addressing important questions in animal behavior and

evolution, clear understanding of behavioral function, and therefore the information content of signals, is vital to the broader comparative study of hearing.

In many acoustic insects, sound production serves primarily in pair formation, with males producing advertisement calls and (usually) females recognizing and localizing these signals. In some species females produce a specific response to male calls, and it is males that localize. Both sound production and movement toward a sound source may be costly because of the energetic expenditure and increased predation risk that these conspicuous activities entail. The partitioning of these costs among the sexes and across different phases of communication and mating can have a strong influence on signaling strategies and adaptations of the auditory system. In addition to mate identification, insect acoustic signals also function in aggressive contests and aggregation. In each of these contexts, individual variation in signal characteristics may carry relevant information for a receiver. Thus behavioral studies may identify multiple levels of discrimination of signal parameters that must be mediated by the auditory system—species-specific cues that identify the source as a conspecific and individual-level variation in signal parameters that correlate with some aspects of phenotypic quality. Finally, all of this information exchange relies on signal propagation through the environment. Filtering and distortion of signals due to environmental effects, and the presence of noise from other sources (anthropogenic noise is recognized as an increasingly important factor in many systems), impose further constraints on signalers and receivers.

### *1.3.3 Hearing for Defense*

Just as for intraspecific communication, a clear understanding of the behavioral function, the relevant acoustic parameters, and the costs and benefits of alternative behavioral strategies are essential to comparative studies of the diverse insect auditory systems (in fact, the majority) that function in predator avoidance. Hearing that functions in this defensive context is reviewed in Chapter 4 by Pollack. The major difference between hearing in predator defense and in intraspecific communication is the absence of mutual interest between sender and receiver. In some contexts, there may be conflicting interests between sender and receiver in intraspecific communication. For example, signalers may benefit from exaggerating indicators of quality or competitive ability, whereas receivers will benefit from accurate information. Nevertheless, signals are by definition adapted to the function of transferring information (Bradbury and Vehrencamp 2011) and intraspecific communication will always entail some form of sender–receiver coevolution (Balakrishnan, Chapter 3). Acoustic detection of predators, on the other hand, is more purely an evolutionary arms race (Conner 2013). Acoustic predator detection in insects largely refers to the detection and avoidance of the ultrasonic echolocation calls of bats. Behavioral responses tend to be more uniform in this context—avoidance is always the adaptive response. Nevertheless, a range of avoidance tactics may be available (including eluding detection by the predator, evasive maneuvers, or defensive behaviors

that may include sound production) and selection of the appropriate action is mediated by auditory analysis of the relevant acoustic cues. In addition, selection on receivers will favor rapid responses that require reliable detection and discrimination of broad classes of signals (to identify danger) but not necessarily finer, individual-level variation among examples of signals (as may often be the case for communication). A further layer of complexity arises from the fact that many species that have evolved hearing in the context of predator detection have secondarily co-opted these systems for intraspecific acoustic communication. The reverse is also true, with auditory systems whose primary function is intraspecific communication being adapted to an antipredator function. Predator avoidance hearing, therefore, provides a wide variety of examples of auditory processing with different “weighting” on the same basic components of auditory function (detection, recognition/discrimination, and localization).

### ***1.3.4 Vibrational Signaling***

It has long been recognized that substrate-borne vibration is an important source of sensory information to many animals, perhaps especially insects, and that there is a close relationship between the sensory organs that detect vibration and airborne sound in some of the most extensively studied acoustic insects (Ensifera). Nevertheless, vibration sense has tended to be less studied than hearing. At least in part, this has been due to the technical challenges of measuring and controlling vibrational stimuli. Recent decades have witnessed something of an explosion of research in substrate vibration senses in diverse animal taxa, including insects. Chapter 5 by Yack covers this important topic. Substrate vibration senses are used in many of the same behavioral contexts as airborne sound. A very different set of physical constraints, however, govern waveform structure and propagation in solids and, consequently, the detailed structure and mechanics of the associated sensory organs. These factors, in turn, affect behavioral adaptations to exploit sensory information from vibration as well as the underlying neural mechanisms. This chapter provides an overview of all these aspects of the rapidly advancing field of vibrational “hearing” in insects.

## **1.4 Mechanisms of Acoustic Transduction**

### ***1.4.1 Mechanical Specializations of Insect Ears***

All auditory systems must work within the common constraints of physical acoustics. Some of these constraints are particularly severe for insects because of their generally small size, and the most striking aspect of the diversity of insect auditory systems is the variety of mechanisms they have evolved to convert the energy of

propagating waveforms into movement of scolopidia in the auditory sensory organ. The mechanical aspects of audition in insects are reviewed in Chapter 6 by Windmill and Jackson. Because the scope of this volume includes hearing of both near- and far-field sound, two fundamentally distinct mechanisms of acoustic transduction are considered (displacement and pressure detectors, respectively). Displacement receptors are essentially fine hairs (or antennal segments), jointed at the base, which oscillate with the bulk movement of air molecules in a sound field (Robert et al. 2010). These are typically localized to the antennae and in some groups (particularly Diptera—the true flies) are associated with the complex Johnston’s organ. There is no clear analogue for this transduction mechanism in vertebrate hearing. Nevertheless, beyond this initial transduction step, near-field auditory systems accomplish the same processing tasks as all auditory systems do and represent some important model systems (see Chapter 10 by Kamikouchi and Ishikawa). A thorough understanding of the mechanics of transduction in these systems is therefore of great interest.

Auditory systems functioning in the acoustic far field typically include a tympanal membrane (eardrum) as the primary input of acoustic energy. The insect body plan, a rigid exoskeleton richly supplied with mechanical extero- and proprioceptors, combined with a respiratory system consisting of a distributed network of air-filled chambers, has made for a wealth of evolutionary “opportunities” for the development of audition. This principle is clearly represented in the phylogenetic and anatomical diversity of tympanal ears among insects (Yack and Fullard 1993). The mechanics of auditory transduction represents the initial step in extracting information from relevant parameters of the sound field. Insect ears, like those of vertebrates, require mechanisms of impedance matching between the sensory structures and the medium of sound propagation to allow efficient capture of acoustic energy. Frequency analysis and directionality are important categories of information that rely on auditory mechanics. Active mechanics is emerging as a more common feature than previously appreciated across diverse auditory systems in insects.

### ***1.4.2 Auditory Transduction***

It is at the level of mechano-electrical transduction—the conversion of mechanical energy to electrical signals at the level of primary auditory receptors—that some of the clearest commonalities among auditory systems spanning insects and vertebrates can be recognized. This topic is covered in Chapter 7 by Eberl, Kamikouchi, and Albert. At the cellular level, the tympanal membrane (or antennal flagellum) is coupled to the basic sensory units of insect hearing, scolopidia. Each of these consists of a group of cells comprising a sensory neuron with dendrite inserted in a specialized scolopale cell and a surrounding group of glial and support cells (Yack 2004). Mechanical displacement of scolopidia induces a deformation of the sensory dendrite that activates the neuron via mechanically sensitive ion channels.



The physiological properties of receptor neurons have been examined in insect auditory systems representing a range of complexity—from the relatively simple ears of some moths, comprising only a few sensory neurons, to the complex antennal ears of flies, with hundreds of sensory cells. These studies have demonstrated considerable variation and specialization in primary auditory responses. Not surprisingly, different ears may be specialized for different stimulus parameters (e.g., frequency, directionality, or temporal resolution) that may correspond with specialization of the mechanical transduction apparatus (see Windmill and Jackson, Chapter 6). But individual receptors within a single ear may also show distinct tuning and response properties, suggesting a complex interplay between the mechanical and molecular (neural) stages of auditory transduction.

Physiological studies have provided some resolution of the electrical events of transduction at the level of the multicellular structure of scolopidia. Much current research is now focused on the molecular basis of auditory transduction, and the Johnston's organ of *Drosophila* has emerged as an important model system for these studies. A number of genes affecting mechanosensory function have been identified that are homologous across insects and vertebrates. Some are implicated in specific types of hearing disorders in humans (Senthilan et al. 2012). The wealth of genetic techniques available for *Drosophila* makes this a very active and rapidly progressing area of study.

There is considerable evidence that mechanoelectrical transduction must ultimately rely on mechanically gated ion channels, that is, force generated by the mechanical transduction apparatus acting directly on the neuronal membrane to alter channel configuration. Although such a channel has not been specifically identified, molecular and genetic studies have uncovered a number of membrane channels that contribute to auditory sensitivity in *Drosophila*, and these are distributed among the multiple cell types within the scolopidia. This diversity of molecular elements and developmental mechanisms in *Drosophila* auditory transduction reflects the complexity of auditory responses observed at the level of receptor physiology. Similarly, a number of molecular elements contributing to active auditory mechanics have been identified. Unraveling these individual elements and identifying their specific contributions (Riabinina et al. 2011) to develop an explicit model of the process of mechanoelectrical transduction is an active area of research.

## 1.5 Neural Basis of Hearing and Auditory Behavior

### 1.5.1 Central Neural Processing of Sound Signals in Insects

Hearing mediates a number of important behaviors in insects (see Balakrishnan, Chapter 3 and Pollack, Chapter 4). How are these behavioral tasks accomplished by the nervous system? As mentioned previously (Sect. 1.1), the essential processing tasks of the auditory system are universal. Relevant sounds must be detected,

classified (discriminated), and assigned to source locations. Nevertheless, these tasks apply to a rich variety of auditory stimuli in a wide range of behavioral contexts, and current research continues to emphasize common underlying principles of auditory function that make insects informative models. Chapter 8, by Hedwig and Stumpner, covers neural mechanisms of auditory processing in insects. Following the initial steps of mechanical and electrophysiological transduction of acoustic energy (Windmill and Jackson, Chapter 6 and Eberl, Kamikouchi, and Albert, Chapter 7), auditory information is represented in the spiking output of a population of sensory neurons. All of the information available to subsequent processing stages must be encoded at this stage. The spectral content, amplitude, and temporal patterning of acoustic stimuli all may carry information relevant for behavioral decisions, and these parameters are represented in the identities and activity patterns of auditory afferents. Sound amplitude, or intensity, is typically represented in the activity levels (spike number or rate) of auditory afferents, whereas sound frequency is usually represented in differential activation among a population of auditory sensory afferents (Mason and Faure 2004). There is, however, considerable variation across species in the design and complexity of ears and therefore in their capacities to encode and represent variation in sound parameters. Some insects, such as notodontid moths, have ears with only a single sensory neuron (Surlykke 1984), whereas others, such as mosquitoes, have auditory organs comprising thousands of receptor neurons (Field and Matheson 1998). In all cases, information encoded at the periphery is transformed as it progresses through the auditory pathway, usually with a significant reduction in the number of neurons involved in processing at higher levels in the auditory pathway. Temporal patterning of amplitude modulation is an important parameter in the classification of sound sources in many systems, and temporal processing—from the temporal resolution of the auditory periphery to the filtering of species-specific song patterns in the brain—has been an important area of research. Another important function of hearing is localization of sound sources, and extensive work has focused on neural mechanisms to extract directional information from differences in binaural responses. Auditory information must be integrated with ongoing behavior, which often in itself is a source of noise that may interfere with the ability to process auditory information. A female cricket approaching the call of a singing male by phonotactic walking must contend with the effects of her own walking movements on her ears, which are located on her front legs (Schildberger et al. 1988). A singing male cricket must have an analog to the stapedius reflex to avoid being deafened by his own sound production (Poulet and Hedwig 2006). Furthermore, these issues may be complicated by the fact that insect acoustic signals are often highly stereotyped and sustained for long periods with high redundancy, with the inevitable consequence of adaptation in auditory responses. Receivers must have mechanisms to selectively track individual sources, often among many competing simultaneous sources (Schul and Sheridan 2006). Thus insects provide a number of important examples of fundamental mechanisms of auditory processing (tonotopy, selective attention, temporal filtering, feature detection, sensorimotor integration) that have been analyzed at the level of individual neurons in explicitly mapped neuronal circuits.

### ***1.5.2 Information Processing in the Auditory Pathway of Insects***

Understanding the nature of higher level processes in the nervous system is an active area of neuroscience, and insect hearing makes important contributions here too. A practical understanding of processes such as feature detection, temporal filtering, pattern recognition, and decision making requires that the specific details of neuronal connectivity and response properties be translated into a formal description of the underlying algorithms that are implemented by neural circuitry. But this must be built from a thorough understanding of the information content of acoustic signals and its behavioral significance as well as a detailed analysis of how this information is encoded at different levels of the auditory pathway. The topic of computational models of insect auditory processing is covered by Ronacher in Chapter 9. A large number of insect taxa (especially among the grasshoppers, crickets, and katydids) communicate using acoustic signals that are highly stereotyped and sustained over long time periods. There is a huge diversity of temporal structure and spectral content among different species. Because these groups are some of the most numerous and noticeable (to humans) acoustic insects, they have been the subjects of a long history of research into the behavioral and neurophysiological aspects of acoustic communication. Thus, there is sufficient diversity of models to inform a broadly comparative approach as well as sufficiently detailed behavioral and neurophysiological data to test theoretical models for general principles of neural computation. Chapter 9 examines information coding at multiple levels in the auditory pathway, the significance of inherent variability in neural responses for the robustness of sensory coding, and modeling approaches for feature detection in auditory responses that correspond with behavioral preferences.

### ***1.5.3 Hearing in *Drosophila****

Other chapters in this volume have reviewed research on a variety of systems and emphasized the importance of comparative studies and the diversity of insect hearing. Chapter 10 by Kamikouchi and Ishikawa reviews research on hearing in fruit flies (*Drosophila* sp.) and presents an overview of research in a single, well-studied system. Acoustic communication in *Drosophila* has been described since the 1960s (Ewing and Bennet-Clark 1968), and contemporary studies of hearing in fruit flies range from the molecular basis of auditory transduction to the development and function of central circuitry. The availability of extensive genetic tools makes *Drosophila* an important model system in integrative auditory neuroscience (Kittlmann and Goepfert 2014). Fruit fly males produce complex acoustic courtship signals that elicit responses in females as well as other males, and these responses can be manipulated in behavioral and genetic experiments (Coen et al. 2014). Fruit fly courtship signals function in the acoustic near field. Thus, unlike the

majority of taxa included in this volume, the auditory system detects particle displacement via a nontympanal ear (Windmill and Jackson, Chapter 6). As mentioned previously (Sect. 1.2.3), however, the sensory mechanisms at the cellular and genetic levels are common across all types of insect ears. Genetic tools now available for *Drosophila* allow for detailed analyses of the development and neuroanatomy of the auditory system, from primary receptors to central circuits as well as the manipulation of specific elements within these circuits. Mechanical transduction by the complex antennal ear activates auditory sensory neurons in Johnston's organ, a highly complex sensory chordotonal organ comprising hundreds of receptor neurons in fruit flies. It is now understood that active amplification plays a significant role in Johnston's organ, and research in *Drosophila* has made important contributions to our understanding of the cellular and molecular mechanisms of active processes in hearing and their role in determining auditory tuning and sensitivity (Windmill and Jackson, Chapter 6; Eberl, Kamikouchi, and Albert, Chapter 7). As in any auditory system, information from sensory inputs is processed by central neural circuits to drive appropriate behavior. Studies of the development, organization, and function of auditory circuits are emerging as an important area of research in *Drosophila* (Lai et al. 2012).

## 1.6 Future Directions

Early research on insect hearing included a certain amount of debate on the question of whether sensory terms, such as "hearing," necessarily implied humanlike perception and therefore whether these terms could be applied to insects (which could not be assumed to possess anything analogous to subjective perception). This issue was summarized briefly by Pumphrey (1940), who argued for an operational definition of hearing as responsiveness to sound. Versions of this debate have continued, however. These might be broadly defined as the question of what studies of insect hearing (or neuroethology in general) have to say about mammalian (or human) systems. Clearly, the common structure and function of neurons and the composition of nervous systems means that simpler nervous systems, such as those of insects and other invertebrates, can be very informative about fundamental neural mechanisms from membrane biophysics to circuits. Research on insect hearing continues to make significant contributions in a number of areas including basic neuroscience, the genetics and cell physiology of hearing disorders, and sensor and signal processing technology (Wessnitzer and Webb 2006; Akcakaya et al. 2011; Liu et al. 2013).

Likewise, no one would dispute that behavioral biology, ecology, and evolution have been greatly advanced by studies of acoustic communication in insect models. But when it comes to linking specific neural mechanisms with behavior, there is sometimes debate (or confusion) about what definitions apply in the two domains. For example, discussions of neural mechanisms that underlie decision making often assume (implicitly or explicitly) that decision mechanisms must reside in the central nervous system. This reasoning has fed back to discussions of behavioral and evolutionary questions. Understanding of the role of female choice in the evolution of

signals and communication has been obscured by unnecessary disputes about whether an effect of peripheral sensory filtering could be considered as part of a mechanism for “choice” (in the evolutionary sense). From an evolutionary point of view, adaptation refers to mechanisms that sort alleles between one generation and the next. Choice, in the context of sexual selection (Darwin 1871), was defined operationally—without reference to any particular internal mechanism (or subjective experience) on the part of the “chooser.” Patterns of female behavioral responses that reliably discriminate among variants of a male call, with the effect that some male phenotypes are more likely to reproduce than others, constitute female choice in the evolutionary sense. If it is subsequently determined, for one species (or signal parameter), that the neural mechanism mediating this female “choice” behavior is a bias in the peripheral sensory system that makes some male call variants more effective stimuli than others (e.g., males calling with different carrier frequencies), and for another species (or parameter) that female “choice” behavior requires the activation of network of brain neurons sensitive to the rate of amplitude modulation in the male call, does this distinguish qualitatively distinct categories of mechanism (Parker 1983)? Both contribute consistently to a female-mediated bias in male mating success, and both are ultimately mediated by a stronger or weaker stimulation of the same sensorimotor pathway.

An (arguably) unbiased perspective on insect neuroethology sees insects as providing a wealth of natural examples of mechanisms for generating adaptive behaviors in autonomous agents with an elegant efficiency of neural (and other) resources. Wehner (1987) provided a number of beautiful examples to show that apparently complex sensory processing tasks are accomplished with elegant simplicity thanks to the organization of peripheral sensory organs as environmentally matched filters. As the field progresses, more complex sensorimotor mechanisms are understood in more explicit detail at multiple levels of analysis (behavioral, neural, algorithmic), and this understanding can be validated in “real-world” models through robotics. At the same time, the active field of biologically inspired robotics demonstrates the utility of understanding the biological systems (Pfeifer et al. 2007). This inherently operational approach to sensorimotor processing and autonomous behavior shifts the debate to questions of what insects (or robots) might have to say about cognition (Wilson and Foglia 2011; Pfeifer et al. 2014). This might be considered a question of semantics (how to define “cognition”), but it might also be worth considering whether a given definition is identifying a boundary between qualitatively distinct categories (Webb 2012) or setting an arbitrary threshold across a continuum of variation (van Swinderen 2005).

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