Chapter 5
Vibrational Signaling

Jayne Yack

Abstract Vibrational communication is widespread in insects, yet scientists are only beginning to appreciate the importance and complexity of this communication channel. Substrate vibrations are widely available to insects living on plants, sand, soil, leaf litter, or fabricated materials such as beehives, termite mounds, or silk. Sources of vibrations important to insects may be abiotic (e.g., wind, rain) or biotic (e.g., signals or cues arising from conspecifics, predators, and even plants). This chapter focuses primarily on insects and specifically on adults that exploit plant-borne vibrations, reflecting most of the research to date. Some consideration is paid to other invertebrates such as spiders and scorpions, as well as juvenile stages such as eggs, larvae, and pupae. Topics covered include the diversity of taxa exploiting substrate-borne vibrations, the complexity of their vibratory environments, and the multitude of ways that vibrations are generated and used in social communication, finding food, avoiding predators, and monitoring the environment. Vibratory sense organs, including subgenual organs, lyriform organs, and Johnston's organs and their constituent mechanosensilla are described. The vibratory landscape of insects and other invertebrates is poorly documented for most taxa, and all lines of investigation, from "identifying the players" to understanding how complex vibratory signals are detected and processed to recognize and localize sources, are unchartered territories ripe for further investigation.

Keywords Behavior • Chordotonal organs • Communication • Insect • Mechanoreception • Scolopidia • Sensory • Subgenual organ • Substrate vibration • Vibration signals

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5.1 Introduction

Most people are familiar with insect acoustic communication signals, particularly those used for advertisement over long distances, such as the calling songs of crickets or cicadas. Insect acoustic signals have been studied for centuries, with thousands of scientific reports documenting a wide diversity of signals and their respective functions and sensory mechanisms (see Alexander 1957; Ewing 1989; Drosopoulos and Claridge 2006; Hedwig 2014). Despite this plethora of literature, the vast majority of research focuses on stimuli that are accessible to the human ear: airborne sounds transmitted as pressure waves. What many do not realize is that insects generate and tap into acoustic stimuli that are not easily detected by humans, and it has been convincingly argued that such stimuli are far more abundant and ubiquitous than airborne sounds (Cocroft and Rodríguez 2005; Hill 2008).

Acoustic signals can be broadly defined as vibrations transmitted through an elastic medium. When this occurs in a fluid (air or water), the signals are generally defined as "sound"; in solids they are generally referred to as "vibrations" or "substrate vibrations" (Windmill and Jackson, Chapter 6). There has been much discussion and debate concerning the nomenclature used to define acoustic stimuli (Hill 2014). This chapter uses the terms sound to mean airborne vibrations, near- and far-field sounds to distinguish between the displacement and pressure components, respectively, and vibrations or substrate vibrations to describe waves traveling through solids. Figure 5.1 illustrates three main types of acoustic stimuli using the example of a honeybee. If attacked, the bee can generate a buzzing or hissing sound by vibrating its wings rapidly (Rashed et al. 2009). These warning signals can be transmitted as pressure waves (far-field sounds) that are detectable by the pressure-sensitive ears of a vertebrate predator (Sen Sarma et al. 2002). Alternatively, a forager bee can communicate information about profitable food sources to a colony mate by generating oscillations of the wings and abdomen that are detected as near-field sounds by the antennae of a recruit (Kirchner 1997; Tsujiuchi et al. 2007). Recruits in turn can signal back to the forager to stop dancing and offer food samples by producing substrate-borne vibrations through the honeycomb surface (Kirchner 1997). These vibrations are detected by specialized receptors in the legs of the bee (Sandeman et al. 1996). Most research on insect acoustics has focused on communication by far-field sounds, and comparatively less is known about how insects and other arthropods use near-field sounds or solid-borne vibrations. This dearth of knowledge is partly owing to the fact that the latter types of acoustic stimuli have not been accessible to humans without the use of specialized equipment. But this is rapidly changing, at least for vibratory signals, which is the subject of this chapter.

There is an increasing awareness that animal communication through solid-borne vibrations is widespread and important. The number of published reports on vibratory communication has increased steadily over the past 20 years (Cocroft et al. 2014b). In insects and spiders, vibratory communication continues to be discovered in organisms previously thought to be "nonacoustic," for example, some

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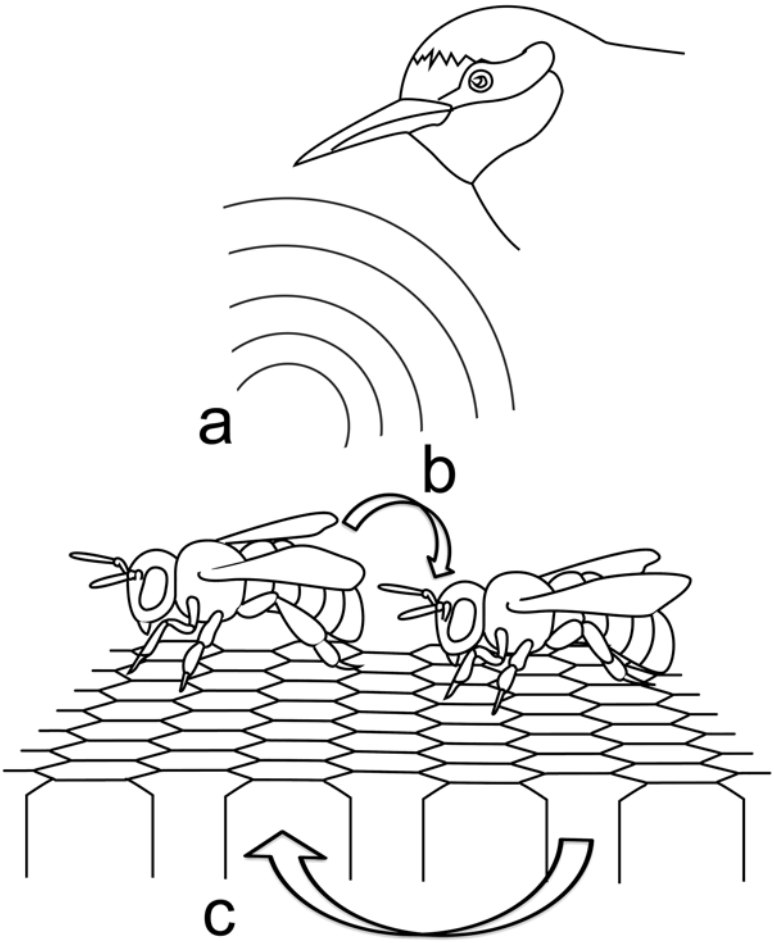

Fig. 5.1 Different types of acoustic signals produced by the honeybee. (**a**) Hissing sounds that function as antipredator signals are generated by vibrating wings and are detected by the pressure-sensitive ears of a vertebrate predator, such as a bird. (**b**) A dancing forager communicates information about a food source to a recruit through dorsoventral oscillations of its wings. These near-field sounds are detected by the recruit bee's antennal receptors. (**c**) A recruit can transmit substrate-borne signals through the wax comb to the leg receptors of a forager by pressing its thorax against the substrate and vibrating (Adapted from Kirchner 1997)

caterpillars (Scott et al. 2010), sawfly larvae (Fletcher 2007), and beetle pupae (Kojima et al. 2012). Even in those taxa already studied extensively for their use of sound communication (e.g., crickets, cicadas), vibratory communication can play an important role in their sensory ecology (Hill 2008). There are few comprehensive reviews on the subject of vibratory communication. Those with an exclusive or heavy emphasis on arthropods include Markl (1983), Virant-Doberlet and Čokl (2004), Hill (2008), and Cocroft et al. (2014a). These are highly recommended to

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readers wishing to explore the topic in detail. Notwithstanding the growing awareness of the vibratory sensory modality in insects, there are many unanswered questions concerning which taxa use vibrations, how they use them, the characteristics and transmission properties of signals and cues in natural habitats, and the sensory mechanisms used to detect and process vibratory stimuli.

This chapter is an introduction to the "up-and-coming" field of vibratory communication in arthropods. The focus is primarily on insects and mostly those communicating through plant tissues. However, some consideration is given to vibratory communication and reception in other arthropods such as spiders and scorpions that share similar environments and behaviors with insects. The first topic (Sect. 5.2) provides an overview of the vibratory "landscape" of an insect, including the common sources of abiotic and biotic vibratory stimuli encountered. Section 5.3 summarizes methods used to record and play back vibrations. Section 5.4 discusses the diversity of insects reported to generate and detect vibrations, and Sect. 5.5 reviews the many ways that vibrations are important to an insect's survival. Section 5.6 reviews the main sensory organs used to detect vibrations.

The objective is to introduce readers to the literature on these topics and, importantly, to ponder unsolved problems and avenues of investigation to inspire further research.

5.2 Vibratory Landscapes

Vibrations that an arthropod might encounter in its environment are abundant and complex. There are many different vibration-generating sources, ranging from "passive" wind noise to "specialized" communication signals. Vibrations traveling through solids are far more complex than those traveling through air, and their transmission properties vary depending on the composition and geometry of the many substrates occupied by an organism in its natural habitat.

5.2.1 Types of Vibrations

Vibrations transmitted through solids have physical properties that differ from those of airborne sounds in ways that are relevant to insect communication. First, whereas airborne sounds generated by an insect can travel over long distances [e.g., >1 km in bladder grasshoppers (*Bullacris membracioides*; Van Staaden and Römer 1997)], insect-generated vibrations typically occur on a local scale, within a meter from the source. This is due to a number of factors, including the small size of an insect in relation to the size of the substrate and filtering and damping properties of the substrate (Michelsen et al. 1982; Cocroft and Rodríguez 2005). Second, airborne sound communication is not an option for many small insects because they produce high-frequency sounds that are highly attenuated in natural

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environments (Bennet-Clark 1998). Consequently, many small insects use solid-borne vibrations because they are the least costly for them to produce over short distances (Bennet-Clark 1998). Third, substrate vibrations are far more complex than airborne sounds. In air, one wave type (longitudinal) is propagated through a more or less uniform medium. In contrast, there are several types of vibration waves, and their transmission can be affected by substrate properties, including the type of material (e.g., herbaceous plant stems, wood, sand, rock, silk), geometry (e.g., long thin stems, flat leaves, silk strands, tree trunks), and composition and condition (e.g., heterogeneity, density, moisture content). Waves traveling through solids have been categorized based on their mode of transmission, shape, energy distribution, and motion in relation to the direction of propagation, speed, and attenuation. The main wave types used by insects include longitudinal (and quasi-longitudinal), bending, torsional, and transverse, and the type(s) that occurs in any particular scenario depends on factors such as the mechanism of signal production and the aforementioned substrate properties. This complexity has important implications for the generation and reception of vibrations and how scientists record and playback stimuli. For more detailed accounts of vibration wave types used by invertebrates, see Michelsen et al. (1982), Markl (1983), Hill (2008), and Elias and Mason (2014).

5.2.2 Sources of Vibrations

Vibration sources relevant to insects can be broadly categorized as abiotic or biotic, and biotic sources can be subdivided into passive cues or active signals (Fig. 5.2). A number of authors have reviewed the types of vibratory signals, cues, and noise relevant to animals (Cocroft and Rodríguez 2005; Hill 2008; Caldwell 2014; Virant-Doberlet et al. 2014). This section introduces a few of the many different vibration sources used by insects. Two main abiotic vibration sources relevant to insects are wind and rain (Barth et al. 1988; Casas et al. 1998; Cocroft and Rodríguez 2005; Virant-Doberlet et al. 2014). Wind is a major source of noise for insects communicating on plants. It induces trembling and collision in leaves and stems, resulting in a noisy vibratory environment. Wind interference, comprising vibrations typically below 200 Hz, is thought to play an important role in the selection of signal characteristics and the time of day that species living in open habitats or in the forest canopy will signal (Cocroft and Rodríguez 2005; Virant-Doberlet et al. 2014). There is also evidence that plants have evolved mechanisms, such as trembling, to enhance wind noise as a deterrent to herbivorous insects (Yamazaki 2011). Rain drops falling on plants cause intermittent and high-amplitude waveforms with most energy below 1 kHz (Fig. 5.2a) (Barth et al. 1988; Casas et al. 1998). Some insects may cue in on the vibrations to avoid activity during rainfall, while others living in geographic regions with heavy rainfall may have evolved signals with long pure tones to overcome low-frequency background interference, as suggested by Cocroft and Rodríguez (2005). Other sources of abiotic vibrational noise that may affect

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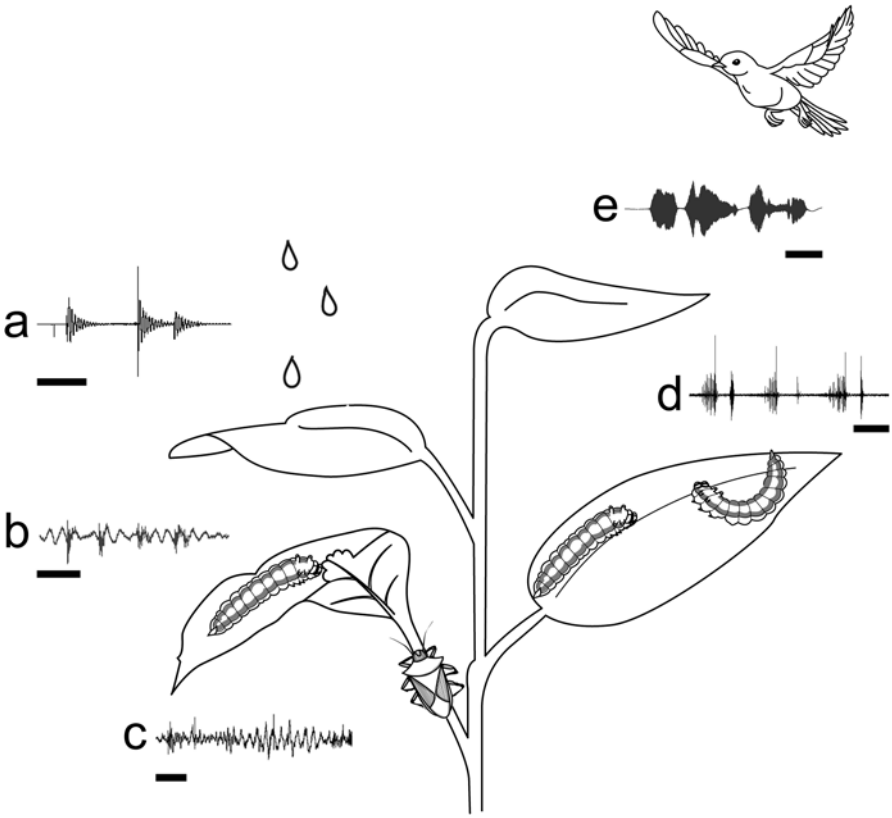

Fig. 5.2 Hypothetical "vibration-scape" of a plant-dwelling caterpillar. (**a**) Abiotic stimuli such as rain droplets may be a source of background noise or provide information about weather conditions. Various biotic sources, such as incidental vibrations generated by a caterpillar (*Drepana arcuata*) chewing (**b**) or a predator (*Podisus maculiventris*) walking (**c**), may provide useful information to a predator or prey, respectively. (**d**) Communication signals, such as those produced by resident territorial caterpillars (*D. arcuata*), inform intruding conspecifics that the leaf is occupied. (**e**) Vibrations may also be caused by airborne sounds, such as the call of a bluebird (*Sialia sialis*). All vibrations were recorded by the author in a laboratory setting on birch leaves, using a laser-Doppler vibrometer. Scale bars are 5 s (**a**), 500 ms (**b**, **c**, **d**), and 200 ms (**e**)

insects include anthropogenic noise (e.g., traffic, wind turbines) (Morley et al. 2013; Virant-Doberlet et al. 2014) and water flow (e.g., rivers, waterfalls).

Vibrations originating from biotic sources can be broadly categorized as (passive) cues and (active) signals. Although the distinction between signals and cues is not always clear, one explanation is that cues have not evolved to alter the behavior of other animals, whereas signals have evolved for that effect (Maynard Smith and Harper 2003). Vibrations from nonsignaling behaviors include those resulting from locomotion (walking, crawling, flying), feeding (chewing), or digging (Fig. 5.2b, c) (e.g., Guedes et al. 2012). There is mounting evidence that unintended receivers use such cues to escape predators or to capture prey (see Sect. 5.5.2).

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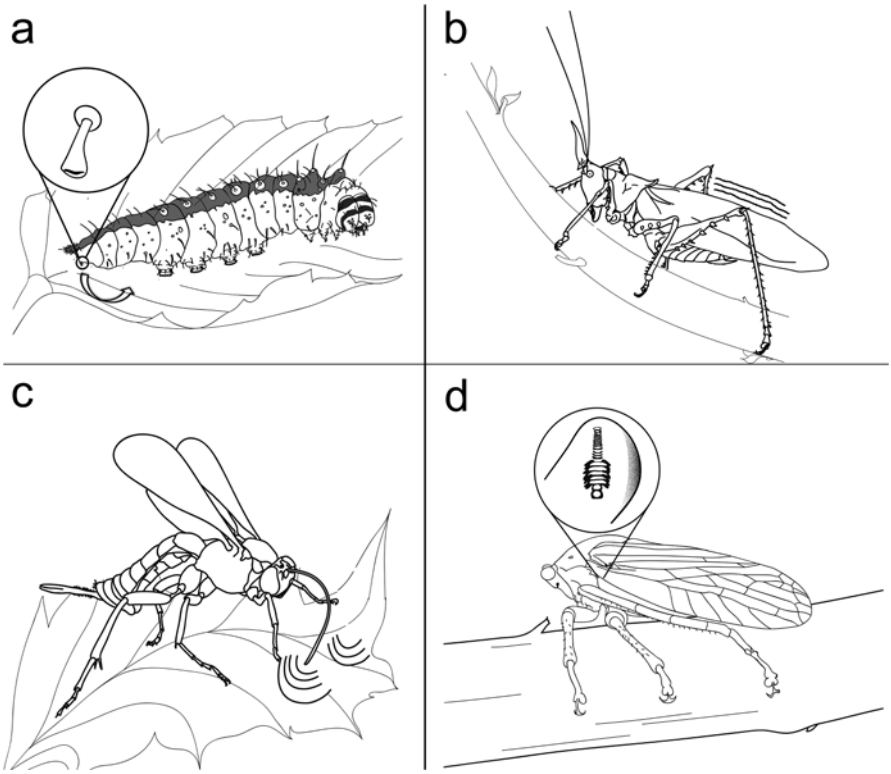

Fig. 5.3 Mechanisms for generating substrate vibration signals in insects. (**a**) Stridulation: Vibrations are generated by friction as one body part rubs against a substrate or another body part. In the caterpillar *Drepana arcuata*, bilateral anal "oars" are scraped against the leaf surface to generate vibratory signals used in territorial encounters with conspecifics. (**b**) Tremulation: Body movements such as jerking, trembling, and shaking transfer vibrations to the substrate. A male neotropical katydid, *Copiphora rhinoceros*, tremulates by bobbing up and down in a stereotyped manner during its courtship display (redrawn and adapted from Morris 1980). (**c**) Drumming: Signals are produced by striking a body part against the substrate. In this example, a parasitoid wasp (*Pimpla turionellae*) strikes its antennae against a leaf surface to echolocate (vibrational sounding) to locate a host. (**d**) Tymbal buckling: Tymbals are specialized, often ribbed, regions of exoskeleton that are popped in and out in a clicking motion by muscles attached to the inner surface of the structure. The example is a treehopper (*Aethalion reticulatum*). The tymbal inset is redrawn from Evans (1957)

In contrast to cues, signals have evolved to convey messages to intended receivers and therefore are typically conspicuous, highly redundant, and stereotyped (Johnstone 1997) (Fig. 5.2d, e). Mechanisms used to generate vibration signals in the Arthropoda are diverse, involving almost every body part imaginable. According to Hill (2008, 2014), they can be categorized into four types: stridulation, tremulation, drumming, and tymbal buckling (Fig. 5.3). Stridulation produces signals by the friction caused by one body part rubbing against another body part or against a substrate (body-substrate stridulation) (Fig. 5.3a). Mechanisms employed to

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generate these signals range from nonspecialized structures such as mandibles rubbing against the substrate (e.g., Ishay et al. 1974; Yack et al. 2001) to specialized file and scraper mechanisms (e.g., Uetz and Stratton 1982; Cokl and Virant-Doberlet 2003). Tremulation describes repetitive body movements such as trembling, shaking, and swaying without the insect hitting the substrate (Hill 2014; Fig. 5.3b). Such signals have narrow bandwidths compared to those produced by drumming (see later in this section). Tremulation is often used by plant-dwelling insects and spiders that signal on homogeneous substrates that permit the passage of narrowband signals (Hill 2014). Drumming, or percussion, involves some nonspecialized body part (mandibles, head, antennae, legs, abdomen) striking the substrate (Fig. 5.3c). Drumming produces broadband "noisy" signals that are most often associated with heterogeneous substrates, where the filtering characteristics of the substrate are unpredictable. With such broadband signals, temporal patterns are believed to be more important than spectral features in conveying information (Hill 2014). Tymbals are modified regions of cuticle that are buckled rhythmically by specialized muscles attached to their inner surfaces (Fig. 5.3d). Although best known for producing airborne sounds in cicadas (Cicadidae) and tiger moths (Arctiinae), they are also common in many Hemiptera that communicate primarily using plant-borne vibrations (Wessel et al. 2014). Other types of biotic signals relevant to arthropods that do not fit into the aforementioned categories include plucking a silk shelter or web (e.g., Fletcher et al. 2006; Wignall and Taylor 2011; Mortimer et al. 2014) or vibrations generated by airborne signals that are transferred and propagated as solid-borne vibrations (Fig. 5.2e; Caldwell 2014).

5.3 Vibration Recording and Playback

Over the past 50 years, scientists have developed and refined instrumentation to broaden the understanding of the extraordinary sensory capabilities of animals that communicate using ultrasonic, infrasonic, ultraviolet, infrared, geomagnetic, and chemical stimuli (Bradbury and Vehrencamp 2011). Although such instruments are portals to learning about other sensory modalities, it is crucial to be aware that each instrument imposes its own characteristics on the signal that was "intended" by the organism. Given the aforementioned complexity of substrate-borne vibrations and the heterogeneity of the substrates on which insects and other invertebrates signal, the need to take precautions for recording and playback experiments is particularly important (see Elias and Mason 2014).

A variety of instruments are available to record substrate vibrations (Cocroft and Rodríguez 2005; Elias and Mason 2014). Sensors vary in their sizes, frequency ranges, what they measure, costs, and sensitivities. Each has advantages and disadvantages, and the choice of sensor should be based on a number of factors including the size of the insect, the type of substrate, and how the recordings are to be used. Two main sensor types are used to record vibrations from insects: laser vibrometers and piezoelectric elements. Laser Doppler vibrometers (LDVs) reflect a light off the

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surface of a vibrating structure, providing a measure of the velocity of movement based on the Doppler shift. LDVs are ideally used in the laboratory to record vibrations from small organisms and in particular those on lightweight substrates such as herbaceous plants or spider webs. Piezoelectric elements are solid materials, usually quartz crystals or ceramic, that generate an electrical signal in response to a mechanical force. When the mass is vibrated, it produces a force that generates an electrical charge proportional to the acceleration of movement. Piezoelectric elements are often packaged as accelerometers that vary in size, bandwidth, and sensitivity. Other low-cost piezoelectric elements (e.g., guitar pickups, phonocartridges) can be adapted to monitor vibrations but are limited in that they are difficult to calibrate and couple with the substrate.

Playback devices, or actuators, also vary in their size, how they attach to the substrate, type of motion they transmit, frequency range, portability, and effects on the substrate (Cocroft and Rodríguez 2005; Elias and Mason 2014). There are three main types commonly used for invertebrate studies: mini-shakers, electromagnets, and speaker cones. Mini-shakers are acceleration actuators that use a coil and magnet to vibrate the substrate. The substrate can be coupled to the shaker using a pin or nail that is glued to the substrate or the substrate can attach directly to the shaker. Small magnets can be glued to the surface of a plant and are vibrated remotely by an electromagnet. Speaker cones are small audio speakers with their diaphragms removed to reduce the generation of airborne sounds. They are used to vibrate a lightweight substrate such as a leaf by attaching a pin to the central coil and gluing the pin to the substrate. Although playback of substrate vibrations is far more complex than playback of sounds, there are a number of solutions to common problems encountered (Cocroft et al. 2014c; Elias and Mason 2014).

5.4 Diversity of Insects Using Vibrations

Among the different forms of acoustic cues and communication signals used by insects and other arthropods, substrate vibrations are considered to be the most ancient and taxonomically widespread (Cocroft and Rodríguez 2005; Hill 2008). Cocroft and Rodríguez (2005) estimate that vibratory communication has been reported in 195,000 described insect species across 18 orders and that of all families using some form of mechanical communication, 80 % use vibrations either alone or with another mechanosensory modality. For reviews of invertebrate taxa reported to use vibrations, readers should consult Virant-Doberlet and Čokl (2004), Cocroft and Rodríguez (2005), Hill (2008), and chapters within Drosopoulos and Claridge (2006) and Cocroft et al. (2014a).

Why are substrate vibrations more commonly used by arthropods than are airborne sounds? There may be several reasons but a few in particular stand out. First, there are many sources of solid-borne vibrations that may not necessarily produce detectable airborne sounds. These include abiotic sources (e.g., wind, rain) or inadvertent body movements and activities (e.g., crawling, chewing). Such vibrations

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may be used as information sources even by species that have not evolved specialized communication systems. For example, some caterpillars (*Semiothisa aemulataria*) can detect the leaf vibrations induced by foraging predators (Castallanos and Barbosa 2006), and ant lion larvae (Myrmeleontidae) are extremely sensitive to the sand-borne vibrations generated by passing prey (Devetak 2014). Second, and not unrelated to the first point, is that vibration signals are typically less costly to produce than airborne sounds owing to the better impedance matching between the signaler's body and substrate compared to that of the signaler's body and air (Caldwell 2014). Very small insects, including some ants (Formicidae, Hymenoptera) and lice (Trogiidae, Psocoptera), that may be incapable of sound production can generate substrate-borne vibrations (Dumortier 1963; Kirchner 1997). Third, it may be easy to "evolve" a vibration receptor. Substrate-borne vibrations induce movements of body parts, such as legs and antennae, that are in direct contact with the substrate, and because these structures are already well "endowed" with mechanoreceptors that function to detect body movements (as proprioceptors), the evolutionary transition from proprioceptor to exteroreceptor may be relatively simple. Indeed, the borderline between the vibration sense and other forms of mechanoreception is not always clear (Kalmring 1985).

Current estimates of the number of arthropod species using vibrations are believed to be low, and researchers are still in the process of "identifying the players" (Cocroft and Rodríguez 2005; Hill 2008). Where then, should we be looking? Some taxa, including those within the Hemiptera (true bugs), Neuroptera (mayflies, ant lions, and relatives), Plecoptera (stoneflies), and Arachnida (spiders, scorpions, and relatives) have been studied in detail and are emerging as models for exploring both proximate and ultimate questions on vibratory communication. Taxa moderately represented in the literature include the Orthoptera (crickets, grasshoppers), Hymenoptera (bees, wasps, ants), Isoptera (termites), and Crustacea (crabs, lobsters, and relatives), but most others are underrepresented. Furthermore, the vast majority of reports focus on sexual behaviors of adults (Virant-Doberlet and Čokl 2004). Considering that a large portion any insect's life cycle is spent as immature, the lack of literature on the eggs, nymphs, grubs, caterpillars, maggots, and pupae that use vibratory communication is surprising. There are an increasing number of examples of juveniles using vibratory signals for a diversity of functions, including territorial behavior (e.g., Fletcher et al. 2006; Yack et al. 2014), recruitment of conspecifics or heterospecifics for foraging or defense (Cocroft and Hamel 2010), mimicry to exploit food resources (e.g., Sala et al. 2014), and parent–offspring communication (Cocroft 2001; Mukai et al. 2014). Research on acoustic communication in juveniles lags far behind that for adults and requires further investigation.

5.5 How Do Insects Use Vibrations?

Solid-borne vibrations are used by arthropods in a variety of contexts. Vibratory stimuli may be used for communication between conspecifics or heterospecifics or to gain information by monitoring abiotic events, eavesdropping on signals or cues

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generated by others, or through echolocation. The multitude of ways that insects and other arthropods use vibrations are discussed in Hill (2008), Virant-Doberlet et al. (2014), and chapters within Drosopoulos and Claridge (2006) and Cocroft et al. (2014a). Here, the functions are discussed under three broad categories, which are not necessarily mutually exclusive: communication signals, monitoring the environment, and obtaining food.

5.5.1 Communication Signals

Communication has been defined as the process whereby individuals exchange information using signals that have evolved for this purpose (Lindstrom and Kotiaho 2002). According to this definition, communication signals are distinct from other stimuli that may be used by an organism to gain information about its environment, which are not intended for communication. Invertebrates use vibration signals in a variety of contexts, including those involving interactions between mates, parents and offspring, heterospecifics, predators and prey, and colony members. Why use substrate-borne vibration signals over other sensory modalities? Although there are different factors that influence the evolution of one form of communication over another (Bradbury and Vehrencamp 2011), four explanations for why insects may use vibrations include the following. (1) As discussed in Sect. 5.4, vibration production can be energetically less costly than sound production, particularly for small insects signaling on plants; (2) vibrations are used in environments where chemical and sound vibration are not viable options (e.g., inside logs, soil, or termite mounds); (3) vibrations may offer a private communication channel so that a signaler avoids being exploited by predators or conspecifics that may eavesdrop on airborne or chemical signals (see Virant-Doberlet and Čokl 2004; Hill 2008 for discussion of the advantages of vibratory communication). Keeping in mind that there are a variety of ways to classify the functions and contexts of insect acoustic signals (Alexander 1967), this chapter divides the functions of vibration signals into three broad categories: reproductive behavior, predator–prey interactions, and group behavior. These categories are not intended to be mutually exclusive and are by no means comprehensive.

5.5.1.1 Reproductive Behavior

Vibratory communication signals have been implicated in a number of functions in the context of mating and reproduction, including attraction, locating a mate or rival, species recognition, courtship, competition between rivals, and pair maintenance. Signals are produced by all four previously discussed mechanisms (stridulation, drumming, tremulation, and tymbal buckling), and some species have complex signaling repertoires using multiple mechanisms [e.g., the treehopper *Ennya chrysura* (Membracidae) produces eight distinct signals (Miranda 2006)]. Other species use vibratory signals as part of a multimodal display in combination with visual or chemical signals [e.g., male jumping spiders, *Habronattus dossenus* (Salticidae), signal to females using complex

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visual and vibratory displays (Elias et al. 2003)]. The vast majority of studies on vibratory communication in insects and other arthropods have focused on reproductive behaviors, and reviews on the topic are included in Barth (1997), Cokl and Virant-Doberlet (2003), Virant-Doberlet and Čokl (2004), Hill (2008), and chapters within Drosopoulos and Claridge (2006) and Cocroft et al. (2014a).

5.5.1.2 Predator–Prey Interactions

Vibratory communication signals can be employed by prey to stop an attack by a predator, or by predators to facilitate prey capture (Cocroft 2001; Hill 2008; Cocroft and Hamel 2010). Antipredator signals may be directed toward the predator as aposematic or deimatic displays (Masters 1979), although there is little direct experimental evidence that vibrations alone function in these contexts. Alternatively, signals can be directed toward conspecifics or heterospecifics as alarm signals to recruit help (Cocroft and Hamel 2010). Predators may deceive prey by mimicking vibrations that attract prey. Examples of aggressive mimicry include the assassin bug (*Stenolemus bituberus*), which hunts web-building spiders by mimicking the vibrations of a struggling prey (Wignall and Taylor 2011), and the jumping spider (*Portia fibriata*), which mimics vibratory courtship signals of other species (Jackson and Wilcox 1990). Predators also locate prey by vibratory echolocation; technically, these are considered signals, as there is a sender and a receiver, although it is the same individual doing both. Echolocation is discussed further in Sect. 5.5.3.

5.5.1.3 Group Behavior

Many insects benefit from living in social groups ranging in size from two individuals to large eusocial colonies with thousands of individuals. It has been convincingly argued that vibratory communication plays an important role at all levels of group interactions and that we have just begun to explore these functions in different insect groups (see Cocroft 2001; Hrncir et al. 2006; Hill 2008; Cocroft and Hamel 2010; Hunt and Richard 2013). Reported functions of vibratory communication amid group members include recruitment to food or nesting sites (Hrncir et al. 2006), alarm signaling (Cocroft 1996; Rosengaus et al. 1999), communicating social status (Casacci et al. 2013), coordination of activities (Fletcher 2007, 2008), and parent–offspring communication for food exchange (Savoyard et al. 1998) or to stimulate egg hatching (Mukai et al. 2014).

5.5.2 Monitoring the Environment

Beyond using vibrations for communication purposes, some arthropods monitor vibration stimuli in their environments to gain information. Sources of these vibrations may be abiotic, such as wind or rain, or biotic, such as incidental cues resulting

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from body movements, or even communication signals that are intercepted and exploited by unintended receivers.

Vibrations caused by abiotic sources, in addition to introducing background noise (see Sect. 5.2.2), may also be information sources (Virant-Doberlet et al. 2014). Rain-induced vibrations have been reported to evoke escape responses or inhibit activity in some insects (e.g., Casas and Magal 2006; Guedes et al. 2012). Although to date there is no evidence that hatching or eclosion events are stimulated or inhibited by rain-induced vibrations, as seen in some frog embryos (e.g., Caldwell et al. 2010), this is possible for insects. Wind vibration noise has been reported to influence the activity patterns of some insects and spiders, including predators that use wind noise as a "smokescreen" to mask self-generated vibrations from their prey (Wilcox et al. 1996; Wignall et al. 2011).

Vibratory stimuli arising from biotic sources can be used by an unintended receiver. These might be incidental vibrations caused by body movements, such as chewing or walking on a plant surface. Such stimuli are used by prey or hosts to detect and avoid predators or parasitoids (e.g., Castallanos and Barbosa 2006) or, in turn, by predators and parasitoids to locate their respective prey or hosts (e.g., Pfannenstiel et al. 1995). Another intriguing possibility is that insects may acquire information from the incidental vibrations generated by plants, such as those resulting from water stress (e.g., Haack et al. 1988). The topic of plant bioacoustics is fascinating (Gagliano et al. 2012; Appel and Cocroft 2014) and is certain to reveal more ways that insects are using vibrations. Finally, insects can exploit communication signals that are intended for other recipients. Receivers may eavesdrop on the calls of conspecifics to intercept mating or to locate competitors, predators may localize prey by their calling signals, or, in turn, prey may detect potential predators (Hill 2008).

5.5.3 Vibrations for Obtaining Food

Invertebrates may use vibrations to help them obtain food in a number of ways. Predators may eavesdrop on communication signals or passive vibrations generated by prey, or colony members may recruit one another to good-quality food sources. In addition, some insects actively generate vibrations to facilitate food gathering through echolocation, buzz pollination, or even creating a "vibratome" to facilitate leaf cutting (Hill 2008). Some wasps use echolocation (or vibrational sounding) to locate a concealed host, such as a caterpillar or pupae located inside plant material or soil (Fig. 5.3c). The female wasp drums on the substrate surface using modified antennae and receives the returning vibration through subgenual organs in her legs to assess differences in the density of the substrate and thus the location of the host (Broad and Quicke 2000; Otten et al. 2001). Other insects proposed to use echolocation to assess food include termites (Evans et al. 2005) and insects living on the water surface (e.g., whirligig beetles) (Hill 2008; cf. Voise and Casas 2014). Some bees actively vibrate their flight muscles to release pollen from flower anthers, a

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phenomenon called buzz pollination (Hill 2008; De Luca and Vallejo-Marín 2013). Flowers and bees have formed mutualistic relationships whereby the flowers release pollen only when stimulated by a particular vibration frequency produced by the insect. In this sense, buzz pollination could be considered a form of communication between plants and insects, with plants "hearing" and responding to specific vibration signals. Finally, there is an interesting example of ants generating vibrations while feeding on leaves to facilitate leaf cutting (Tautz et al. 1995). While cutting through a leaf with their mandibles, leaf cutter ants drag their gasters on the leaf surface, causing a high-frequency vibration that stiffens the leaf to facilitate cutting, effectively functioning as a vibrotome.

5.6 Sensing Vibrations

Although most arthropods are likely capable of detecting substrate vibrations, the sensory organs have not been identified in most species. Moreover, in those species for which receptors have been identified, our understanding of how they function to detect, localize, and recognize stimuli or filter out background noise remains limited. Our knowledge of vibration receptors lags far behind that for insect tympanal ears, and there may be several reasons for this. First, unlike for tympanal ears that typically have a conspicuous tympanal membrane, there is often no distinctive external manifestation of a vibration receptor. Second, the distinction between vibration reception and other forms of mechanoreception such as touch and proprioception is not always clear (Kalmring 1985; Lakes-Harlan and Strauss 2014). Third, insects communicating with vibrations can be quite small compared to those that possess tympanal ears, making it sometimes technically challenging to conduct neurophysiological recordings to confirm vibration sensitivity. Such obstacles notwithstanding, there has been progress in understanding vibratory sensory reception in selected taxa, including those within Hemiptera, Orthoptera, Hymenoptera, Arachnida, and Crustacea (Kalmring 1985; Hill 2008; Lakes-Harlan and Strauss 2014).

5.6.1 Types of Sensilla

Like all acoustic sensory receptors in animals, those sensitive to substrate vibrations belong to a broader class of receptors called mechanoreceptors. Arthropod mechanoreception has been reviewed by several authors, including McIver (1985), Keil (1997), Barth (1997, 2004), and Field and Matheson (1998). Those specialized to detect acoustic stimuli have also been the subject of several reviews (e.g., Ewing 1989; Fullard and Yack 1993; Yager 1999; Greenfield 2002; Yack 2004; Strauss and Lakes-Harlan 2014), albeit most of these focus primarily on tympanal hearing. Mechanosensory sensilla most commonly employed as vibration receptors are hairs

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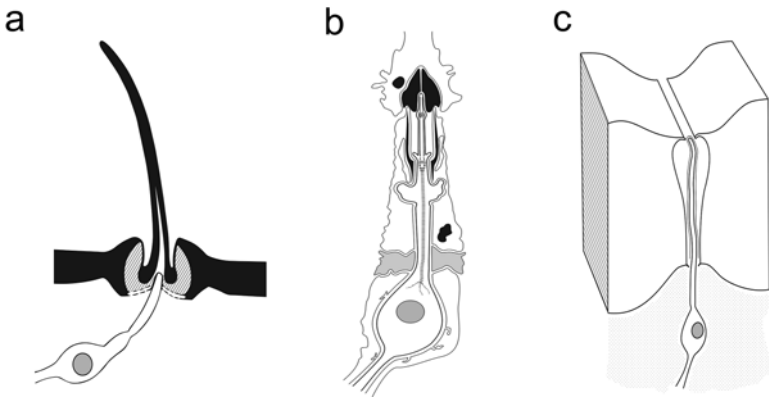

Fig. 5.4 Types of invertebrate mechanoreceptive sensilla known to function as vibration receptors. (**a**) Hair-type sensillum comprising a cuticular extension (hair shaft) innervated at its base by the dendrite of a bipolar sensory neuron. The cell responds to deflections of the hair shaft. (**b**) A scolopidium comprising a bipolar sensory neuron, a scolopale cell, and surrounding accessory cells. The dendrite tip inserts into a bullet-shaped scolopale cap produced by an attachment cell. The sensory cell is stimulated by vibrations transmitted through accessory structures. (**c**) Slit sensillum comprising a region of flexible cuticle innervated by the sensory cell dendrite. Deformation of the cuticle stimulates the sensory neuron

and bristles, scolopidia, and slit sensilla (Fig. 5.4). Other types suggested to function in vibration detection include campaniform sensilla and multipolar receptors (Lakes-Harlan and Strauss 2014).

5.6.1.1 Hairs and Bristles

Mechanosensory hairs are proposed to function as vibration receptors in insects, spiders, and scorpions (Barth 1998; Lakes-Harlan and Strauss 2014). These sensilla comprise four cell types: a hair shaft cell that secretes a hair-like cuticular projection, a socket cell, a sheath cell, and a sensory neuron (Fig. 5.4a). Hair shafts come in a variety of different forms and are variously named trichobothria (very long thin projections), hairs, bristles, and trichoid sensilla. The hair shaft typically sits in an articulating socket, into which inserts the tip of one or more sensory cell dendrites. Deflection of the hair in a particular direction deforms the dendritic tip, causing depolarization of the sensory neuron. In most cases these mechanosensory hairs are responsive to touch, but some are specialized for detecting near-field sounds, water surface vibrations, air currents, and substrate-borne vibrations (Keil 1997; Hill 2008; Lakes-Harlan and Strauss 2014). Hairs and bristles that have been implicated or confirmed to function as substrate-vibration receptors in spiders, scorpions, and insects are reviewed in Barth (1998), Hill (2008), and Lakes-Harlan and Strauss (2014).

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5.6.1.2 Scolopidia

Scolopidia are internal mechanoreceptors found in the Insecta and Crustacea (spiders do not have scolopidia) (Howse 1968; Field and Matheson 1998; Yack 2004). Each scolopidium comprises one or more bipolar sensory neurons with a distal ciliated dendrite that inserts into a scolopale cap or tube (Fig. 5.4b). A scolopale cell envelopes the distal tip of the dendrite, creating an extracellular space called a lumen. Attachment and glial cells connect the sensory neuron and scolopale cell to internal anchor points. It is generally believed that deformation of the dendritic cilium leads to depolarization of the sensory cell (Mhatre 2015; Eberl, Kamikouchi, and Albert, Chapter 7). Scolopidia are extremely sensitive to vibratory stimuli. They are located throughout the body and, depending on their location and association with peripheral structures, may function as proprioceptors (detecting self-induced movements) or exteroreceptors (detecting gravitational forces, near- and far-field sounds, or substrate vibrations) (Field and Matheson 1998). Although individual scolopidia may function as vibration detectors, they are usually organized into groups called chordotonal organs that occur in the legs (subgenual organs in insects, Barth's organs in crustaceans) or antennae [Johnston's organs (JOs) in insects] (see Sect. 5.6.2).

5.6.1.3 Slit Sensilla

Slit sensilla are integumental mechanosensory sensilla that commonly occur in arachnids (Fig. 5.4c) (Barth 1997, 1998; Hill 2008). They are analogous to campaniform sensilla in insects and, similarly, function like strain gauges that detect deformation of the body wall. Each slit sensillum comprises an externally manifested elongated pit on the surface of the body wall. One or more dendrites attach to the cuticle at the base of the pit and are stimulated when the body wall is deformed. Slit sensilla occur all over the body and function mostly as proprioceptors. Some, however, are specialized to detect solid-borne vibrations and occur in organized groups such as in the lyriform organ of spiders or the basitarsal compound slit sensilla (BCSS) organ of scorpions (see Sect. 5.6.2).

5.6.2 Vibration Sensory Organs

Although there may be constituent physiological and ultrastructural properties of certain mechanosensilla that render them more sensitive to substrate vibrations, it is their associations with accessory structures and their positions and orientations within the body that play key roles in vibration sensitivity. They need to be coupled to the substrate, and therefore often occur in the distal leg regions, and are positioned such that they are sensitive to vertical displacements or acceleration caused by movements of the substrate. Vibratory sensory organs most thoroughly studied

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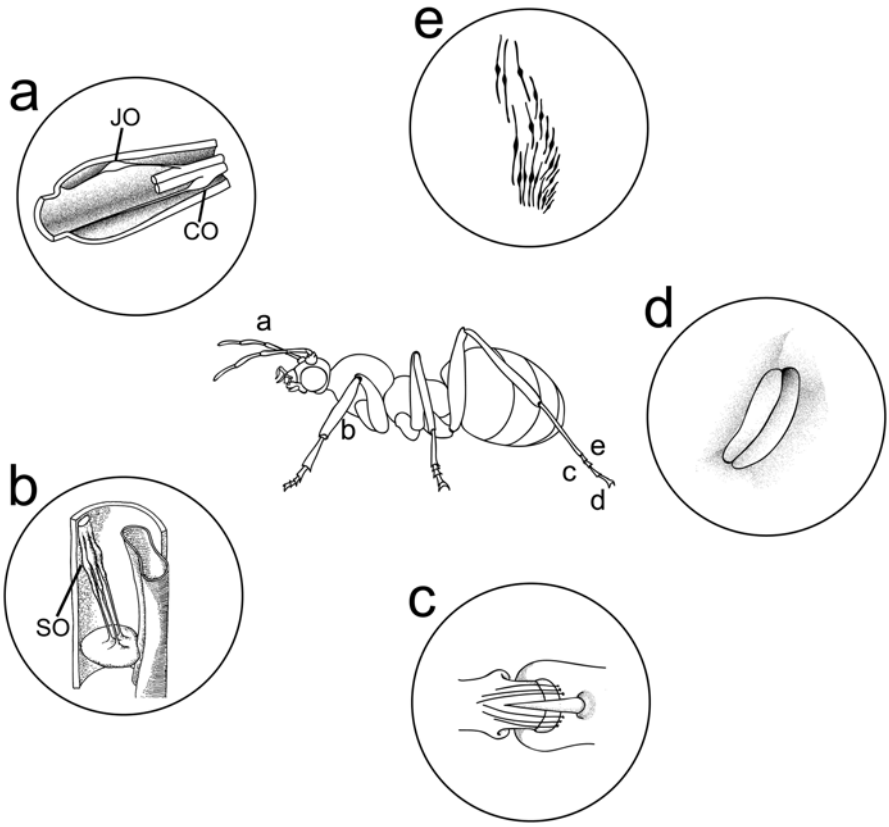

Fig. 5.5 Schematic drawing of a "generic" arthropod showing different types of vibratory sense organs and their general locations. (**a**) Antennal vibration receptors. The inset shows Johnston's organ (JO) and central organ (CO) in the third antennal segment (pedicel) of a green stink bug (*Nezara viridula*). Each sensory organ comprises several scolopidia (redrawn from Jeram and Pabst 1996). (**b**) Subgenual organs (SO) are located below the "knee" in several insects and may be developed for vibratory detection in one pair of legs or all six legs. The inset depicts the SO in the green lacewing (*Chrysoperla carnea*). Attachment cells of the scolopidia connect to a septum, and vibrations of the leg hemolymph result in stimulation of the sensory cells. (Image redrawn from Devetak and Pabst 1994). (**c**–**e**) Different vibration-sensitive cuticular sensilla on a spider leg (redrawn from Speck-Hergenröder and Barth 1988): cuticular hairs at the tarsus-metatarsus joint (**c**), a single tarsal single-slit sensillum (**d**), and the metatarsal lyriform organ (comprising several slit sensilla) (**e**)

to date in arthropods include chordotonal organs (subgenual organ, JO) and those comprising groups of slit sensilla (lyriform organ, BCSS) (Fig. 5.5). These are briefly described in Sects. 5.6.2.1–5.6.2.4. Other structures proposed to function as vibration-sensitive organs include larval antennae, prosternal organs, pleural discs, and other leg scolopidial organs such as the intermediate and femoral chordotonal organs (Saliba 1972; Meurgey and Faucheux 2006; Hill 2008; Lakes-Harlan and Strauss 2014).

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5.6.2.1 Subgenual Organs

Subgenual organs (SOs) are considered to be the primary vibration receptors of insects (Field and Matheson 1998; Hill 2008; Lakes-Harlan and Strauss 2014). They are chordotonal organs located in the proximal tibia of the legs in most orders, with Diptera and Coleoptera being possible exceptions. Each SO comprises a group of scolopidia that is suspended in the hemolymph of the leg cavity but not connected to the leg joint. There is considerable morphological diversity among taxa in the shape of the organ, the number of constituent scolopidia, and the means by which they attach to the integument. Usually there is no external manifestation of the SO, but in some organisms such as parasitoid wasps that use vibrations for echolocation, the region is greatly enlarged (Broad and Quicke 2000). Although SOs can respond to a variety of mechanical stimuli, including leg movements and sounds, the best known function is vibration detection. They respond to external transient stimuli transferred through the leg from the substrate. The best studied SOs include those of selected taxa within the Neuroptera, Hemiptera, and Orthoptera (Lakes-Harlan and Strauss 2014). In green lacewings (Chrysopidae, Neuroptera), substrate vibrations stimulate the scolopidia by setting into motion the hemolymph in the leg cavity, which in turn vibrates a diaphragm to which the scolopidia are attached (Fig. 5.5b) (Devetak 1998). Localization of a vibration source may be achieved by comparing the arrival time of the signal between different legs (Virant-Doberlet et al. 2006; Lakes-Harlan and Strauss 2014).

5.6.2.2 Johnston's Organs

JOs are chordotonal organs that occur in the second antennal segment (pedicel) of pterygote insects (Field and Matheson 1998). The number, types, and arrangement of scolopidia vary between taxa. These organs have been implicated in wind detection, proprioception, and in many Diptera and Hymenoptera they are highly specialized to detect near-field sounds (Field and Matheson 1998; Eberl, Kamakouchi, and Albert, Chapter 7). In the green stinkbug (*Nezara viridula*), the JO, along with the central organ (another chordotonal organ in the pedicel), detects solid-borne vibrations (Fig. 5.5a). A male touches the branches of the fork of a plant twig with its antennae while trying to localize a female, and it is hypothesized that the antennal chordotonal organs, in conjunction with the SO, are involved in mate localization (Ota and Cokl 1991; Jeram and Pabst 1996).

5.6.2.3 Lyriform Organ

Lyriform organs are the main vibration receptors of spiders (Barth 1997; Hill 2008). They are located on the tarsi and distal ends of the metatarsi (Fig. 5.5e) and comprise parallel bundles of slit sensilla arranged such that they respond to vertical and horizontal movements of the substrate. In the wandering spider (*Cupiennius selei*),

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vibrations are required for detecting prey, predators, and courtship signals (Barth 1997, 1998; Hill 2008). The metatarsal lyriform organ sensilla are tuned to conspecific calls and are capable of crude frequency discrimination. The position of the legs has important implications for increasing the sensitivity and localization capabilities of lyriform organs. Spiders may take on a particular stance to enhance the transfer of vibrations to the legs, and localization of a vibration source is achieved by comparison of wave arrival times between legs.

5.6.2.4 Basitarsal Compound Slit Sensilla

In scorpions, the BCSS is considered to be homologous to the lyriform organ in spiders. The BSCC occurs on all eight legs and comprises groups of eight slit sensilla at the distal ends of the basitarsus. In the nocturnal scorpion (*Paruroctonus mesaensis*), these organs, along with tarsal sensory hairs, are used to detect and orient toward prey that cause disturbances that are propagated through sand. Scorpions position their legs in a hunting stance to optimize their ability to assess the direction of a source. Distance is assessed based on differential propagation of waves through the sand (Brownell and Farley 1979; Hill 2008).

5.7 Summary

Vibratory communication has been described as a "gold mine" for continuing research and innovation and "an exciting frontier in the study of animal behavior" (Cocroft et al. 2014b). During the past decade, as a result of increased awareness of this sensory modality and improved recording techniques, scientists have discovered that the vibratory landscape of arthropods is busy and complex. An insect can be bombarded with vibratory stimuli from multiple sources, including wind, rain, an approaching predator, or complex communication signals from a colony member, potential mate, or rival. Vibrations are used to communicate with other organisms (including plants), for orientation, to eavesdrop on potential predators or prey, or to avoid bad weather. Research to date has focused mostly on plant-dwelling insects and spiders and among those, only a select few taxa have been examined in any detail. According to Hill (2008), we are still "identifying the players" and scientists should continue to record from the natural vibratory environments of many species that have not yet been tested for vibratory sensitivities. The vibratory environments of immature insects and those residing in logs or soil are all unchartered territories ripe for exploration. The richness and complexity of this vibratory world is attributable not only to the sheer number of vibration sources but also, owing to the complexity of the communication channel, to a diversity of wave types that vary with different natural substrates. We need to understand better how waves travel in different substrates using modeling and what a receiver is experiencing by refining recording and playback methods. Finally, despite the burgeoning number of

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discoveries of species using vibrations and the purported importance of this sensory modality, our understanding of the sensory organs and capabilities lags behind what is known for insect hearing, vision, and chemoreception. In most taxa, vibration sensory organs have not even been identified, and there are many exciting questions to address concerning how the peripheral and central nervous systems function to process vibrations to mediate biologically relevant responses. The field is indeed a gold mine of opportunity to make new discoveries at all levels of analysis, and the potential to do so exists even in our own backyards.

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