Vibrational Communication in Animals

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Vibration as a Channel for Information Transfer

ONE OF THE most compelling outcomes of the process of science is that we tend to find what we seek. This observation is not meant to suggest that we search for support for a pet hypothesis while intentionally ignoring other alternatives, but that we tend to look for things when we already have a pretty good idea that they are there. The “normal science” of Kuhn (1996) is spent in working on small questions within the larger framework of a paradigm. We have a good general idea of how things work, but we question the smaller details, and we follow leads, looking for inconsistencies—the anomalies that lead us to other questions. Answers bring a new doorway with a heretofore-unknown world on the other side. We say, “The more I learn, the less I know.” However, rarely does an answer shift a paradigm. Only with major insights, or the use of new tools, or with a question asked of exactly the right person who is prepared to think of it in a novel way do we break away from the nested boxes that define most of our work in normal science.

Such is the story of animal communication through substrate vibration: the idea that individuals send and receive signals using the substrate as the medium. Our study of vibrational communication is in its infancy, but the glimpse we have of the mechanisms employed leads us to believe that this is a very ancient system, that it is perhaps the primary channel of communication in some animal groups, and that it is ubiquitous, at least in vertebrates and arthropods (Hill 2001a,b). For example, the very loud signaling via airborne sounds in cicadas is actually a derived modality that evolved from a substrate vibration precursor.
still employed by its “little cicada” relatives in the Hemiptera (Claridge, Morgan, and Moulds 1999). Cocroft and Rodríguez (2005) conservatively suggest that 150,000 described species of insects communicate exclusively through substrate vibration, and another 45,000 species use vibration signals together with other forms of mechanical signaling.

Those who work outside the field of animal communication may justifiably be skeptical that humans could have missed stumbling on this phenomenon before, even if by accident, were it really as widespread and primary as we now argue. The answer, of course, is that we have encountered it, but we were not looking for it. We described and documented the function of all sorts of mechanical receptors that could detect substrate vibrations in a large number of arthropod and vertebrate taxa, and we observed animals drumming or thumping appendages, heads, and abdomens against various substrates while producing no sounds audible to humans. We attributed the anomalies that led us to suspect something else was going on to anything more plausible than communication through vibration signals—or the anomalies persisted as anomalies, to be examined again later when it was more practical to do so. For example, Jones and Dambach (1973) reported that the cricket *Gryllus campestris* was able to respond to load airborne signals even after the tympanal organs, antennae, and cerci had been removed. They did not speculate that the airborne sounds might have been picked up by the substrate and channeled to the cricket nervous system as vibration, but two decades later Kalmring et al. (1997) cite the Jones and Dambach paper as reporting on a vibratory communication system—not just vibration detection, but vibratory communication. Likewise, an early description of maternal care in the short-tailed cricket, *Anuragryllus muticus*, mentioned that the very aggressive female only retreated in response to “violent substrate vibration” (21) and that in her aggressive displays she “shook her body in the manner characteristic of aggression in many kinds of crickets” (West and Alexander 1963, 21). This behavior might strongly suggest the use of substrate vibration as a communication channel, but at that time, this interpretation was not really as intuitive as it might appear today.

The community bound by a paradigm does not purposefully make square pegs fit round holes, but through the carrot-and-stick approach of peer review of publications and grant proposals, practitioners determine
which questions are worth pursuing. Sometimes the weight of accumulating data is required to shift interpretations of events.

Some investigators in the first half of the twentieth century were studying vibrational communication, especially in invertebrates, but the scientific community was not fully engaged. For example, Ossiannilsson (1949) published an extensive treatise on leafhoppers that suggested vibrations produced by the tymal apparatus were conducted through the substrate. He summarized the literature to date, including a 1907 paper that reported “sounds” of the otherwise “silent” leafhoppers that had been transferred from a leaf to the air. Ossiannilsson himself used musical notation to describe substrate vibration of some leafhoppers that he was able to hear by inducing individuals to signal from leaves in a test tube that he held to his ear. He also analyzed recordings of signaling species and published the waveforms in his monograph, including one of two alternating males. He described substrate vibration signals used in a chorus, suggested that male-female duets were important mating signals, and determined that pitch varied with temperature (1949). However, up through the 1970s, conventional wisdom held that substrate-borne vibration could not transfer any biologically meaningful information among organisms, especially the very small. The medium of soil or water or plant stems was too inelastic, and propagation speeds were too great to provide anything more than a nonspecific alerting mechanism to inform the animal of a disturbance nearby (Schwartzkopff 1974).

Then technology in the form of faster, cheaper computers and seismic sensors, such as the geophones that had been developed for oil exploration (and detecting advancing enemy troops in the jungles of Southeast Asia), became accessible to more scientists. Affordable transducers made detection, simulation, and manipulation of signals possible. Faster, smaller, cheaper computers provided the opportunity for rigorous analyses of the data gathered (Hill 2001b). Sometimes the right person was in a position to think of a new way to test an anomaly (see Miles et al. 2001). At the same time, perhaps, the anomalies encountered in asking other questions became too massive to be set aside for another time.

My own interest in vibration began with a frustrating experience trying to manipulate male prairie mole crickets (*Gryllotalpa major*) in the field using a playback experiment (see Hill and Shadley 2001). These rare burrowing endemics of the south-central United States construct
burrows from which they project airborne sexual-advertisement calling songs to attract flying females for mating. Males sing from a fixed location inside an underground "acoustic horn" for about 30 min just at sunset on spring evenings when it is not too hot or too cold, not raining and not too windy. I wanted to test a scramble competition model that required me to evoke a response from a male when I simulated a competitor. Anecdotal reports were that prairie mole cricket males did not respond to conspecific song when the playback methods used to study other orthopterans and frogs were employed, but to test my hypothesis, I had to try. Males ignored the taped sounds I played for them, but as I moved about the area as darkness settled in night after night, males stopped singing whenever I was within 1–3 m of their burrow openings. It was entirely within my worldview at the time that these males could detect my footsteps and consider my presence a threat, but it took some investigation before I could ask whether they could also use this same sort of information to interact with conspecific neighbors.

Could a person in the twenty-first century A.D. hope to write an account of animal communication through any other sensory modality? Would it be possible to describe visual or hearing or olfactory pathways that included a short history of use of the channel, background of the nature of the signal, production of signals as well as reception of them, and the contexts within which the signals were used by species known to use them across Kingdom Animalia? Yet even with the groundswell of interest in vibration since the dawn of the twenty-first century, we still speculate about the breadth and depth of the importance of substrate vibration as a communication pathway. We may know something about a behavior, but nothing yet about the signal or the neurophysiology of how the behavior is elicited and controlled. We may understand the technical aspects of a receiver, but not the ecological context that might have promoted its selection, or the selection for production of the signal, or even the behavioral interactions that were influenced by its selection. The ecologist with questions is not likely to be trained as a neuroethologist, a histologist, or a neurophysiologist. The functional morphologist may not have the tools to pursue questions beyond a point, and luring colleagues with these tools away from their own chosen research lines to help pursue a potential illusion is difficult, at best.

An examination of the literature reveals early descriptions of anomalies and guarded suggestions of a link to substrate vibration. As recently
as the 1980s, experiments in anatomy, physiology, ecology, and behavior still bolstered support for only tentative interpretations that animals really are using substrate vibration detection in as many contexts as they would use any other major sensory pathway.

The pioneering work of Philip Brownell and Roger Farley (Brownell 1977; Brownell and Farley 1979a,b,c) showed us that scorpions not only can detect prey but can use information contained in substrate-borne vibrations created by the prey themselves to locate and capture them. It was Brownell and Farley’s carefully controlled and executed experiments, published in the best mainstream journals, that encouraged others to examine the possibility that baffling behaviors observed in their study species might be linked to sensory input via a substrate vibration channel. Hadley and Williams had already reported in 1968 that scorpions appeared to use tactile senses rather than vision to recognize prey and would attack forceps drawn along the substrate nearby (Hadley and

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**Figure 1.1.** Dorsal-anterior view of right fourth leg of the sand scorpion, *Paruroctonus mesaeensis*, showing tarsal hairs (H) and the basitarsal slit sensillum (SS). B = bristle hairs, BT = basitarsus, LC = lateral claw, MC = medial claw, PS = pedal spur, T = tarsus.

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Williams 1968). Yet Brownell knew that the sandy substrate on which he observed scorpions was supposed to absorb, or damp, low-frequency sound rather than transmit it, because sand is granular and would not support propagation of a wave from one particle to the next in the fashion of a more homogenous substrate. Further, waves traveling at higher frequencies would have a wavelength similar to the size of the sand grains, and these waves would be scattered as they traveled through the medium. What he found, however, was that sand was a good conductor of both compressional (P) waves and Rayleigh waves, that these waves traveled much slower in sand than predicted by current theory, and that in the range of several decimeters, animals with the right sort of receivers should be able to use information contained in these waves to make decisions that promote fitness. Specifically, he concluded that Rayleigh waves were detected by the basitarsal compound slit sensilla (BCSS) in scorpion legs (Figure 1.1) and used by scorpions to determine source direction, whereas P-waves were detected by mechanosensitive tarsal hairs and used to determine source distance (Brownell 1984).

We now have uncovered evidence of use of the substrate vibration channel, especially in the Arthropoda, in contexts from predation or pathogen defense, to foraging coordination, to mate location and choice, to family dynamics. Of special note is the observation that if we find an unusual morphological feature that empirical evidence supports as a sender or receiver in substrate vibration communication, we then can find behavioral contexts in which this communication can be shown to occur, and vice versa. In examining related taxa, we often will find the same behavior or morphology, and sometimes an evolutionary trail can be followed by studying a feature in a phylogenetic framework. Again, if we find that a species gathers substrate vibration cues in one context, we often can find that it also uses vibration signals in conspecific communication. When our worldview expands to suspect that substrate vibration might be a key to explaining a behavior or morphology, we very often find that it is.

What the Fossils Tell Us

The fossil record and comparative morphology studies tell us a great deal about the possibilities for sensory input in ancient taxa, even if the central nervous system (CNS) does not fossilize. We can fall back on
comparative evidence from the skeletal material in which the nervous system has been housed, as we do with modern forms, and modern taxa may not be that much different from their extinct ancestors. Morphologists can see that ancient amphibians, the first vertebrates on land, would have been able to detect substrate vibrations as their massive heads lay on the ground. Their lower jaws, coupled with the soil, could conduct vibrations through the quadrate bone to the inner ear through a bony pathway (Hildebrand and Goslow 2001). Thus, the earliest land vertebrates could “hear” substrate vibrations before they had the acoustic apparatus required to hear airborne sounds as terrestrial forms do today. Furthermore, the vibration pathway is still in use by amphibians, and the sacculus and lagena of the inner ear of modern frogs are the sites of their exquisite sensitivity to substrate-borne vibrations (Ashcroft and Hallpike 1984; Caston, Precht, and Blanks 1977; Lewis 1984).

The story of the evolution of vertebrate animals and their head skeleton is a fascinating one (see review in Northcutt and Gans 1983). The process of cephalization that accompanied the earliest bilateral symmetry in invertebrates not only defined the head end of an individual, but it focused sensory structures, and then feeding structures and a brain, in this region. Details of the head so define vertebrates as a group, and in turn the classes into which they are sorted, that a well-reasoned and logical argument can be made to call them the Craniata. All vertebrate animals have a brain enclosed by a skull, but not all have jaws, and the earliest jaws in the fishes were integrated into the rest of the head skeleton in a different way than the jaws later seen in terrestrial forms. Elements of the visceral skeleton, which supported gills in the fish, were freed up by terrestrial life where the gill arches had no role. Some of these elements were incorporated into new hearing structures, the auditory ossicles of the middle ear, and others were incorporated into the vocal apparatus of the larynx and hyoid apparatus, which anchors the tongue and supports the floor of the mouth (Figure 1.2). At the same time, the number of elements in the lower jaw, or mandible, was dramatically decreased in a manner that gained stability but lost flexibility. The jaw joint itself was “reinvented” and was moved forward, while the muscles that closed the jaw shifted to a position where they attached outside the skull, rather than inside, as they had in the earlier fishes. The skull developed windows, or fenestrae, to accommodate these external muscles, and the options for food choices were
rather suddenly, for geologic time, increased. We might also argue that the options for communication also were multiplied by these changes in the head skeleton.

In primitive bony fish (Class Ostechthyes) skulls, the visceral skeleton includes an element, the hyomandibula, in association with the quadrate bone in the jaw joint. In the early amphibians, this hyomandibula was reduced and took on a new role as an early ear ossicle, the stapes, or columella (Hildebrand and Goslow 2001). Modern amphibians and

![Diagram of phylogeny of vertebrate jaw articulation and ear ossicles](image)

Figure 1.2. Phylogeny of the vertebrate jaw articulation and ear ossicles. Note angular/ectotympanic, articular/malleus, quadrate/incus, and hyomandibula/stapes relationships between lobe-finned fish and mammal. Reprinted with kind permission of John Wiley & Sons, Inc., from Hildebrand and Goslow (2001, 128).
reptiles that lie flat on the soil in direct contact with the Earth over much of their body surface have not developed a tympanum (ear drum) or middle ear cavity that promotes the most efficient conduction of airborne sound. They, like their ancient, extinct ancestors, are more suited to receiving information from vibration in the substrate than from sounds transmitted through the atmosphere.

Aberrant Behavior and Vibration Sensitivity

Humans have actually taken note of various animal responses to substrate vibration for at least 3,000 years (Snarr 2005). Tributsch (1982) rather extensively discussed documented reports of anomalous animal behavior that occurred minutes to days prior to an earthquake, beginning with a detailed description of the 373 B.C. destruction of Helice in ancient Greece for which the primary source has been lost. Many people have heard that animals “act funny” before, after, and during earthquakes (see Anderson 1973), and I, myself, have been interviewed by the BBC on how animals might be able to predict earthquakes. However, after the 2004 tsunami in Southeast Asia, most of us were surprised to hear anecdotal reports that animals such as elephants and tigers did not die from the wave as humans did (i.e., Kenneally 2004, 2005), and even the indigenous people did not die as the more “civilized” ones did (Parker 2004; McAdoo et al. 2006; Nowak 2006). Before the tsunami arrived in Thailand, elephants carrying tourists reportedly broke free from handlers to move away from the area. Elephants, their riders, and the handlers who chased them survived, while other humans who stayed did not (Kenneally 2005). Of the survivors of the tsunami in Thailand who responded to a formal survey within three months of the event, only 21% remembered any unusual animal behavior prior to the arrival of the first wave, but only 24% recalled noticing unusual shaking of the ground (Gregg et al. 2006). Even though interest in this phenomenon is high, empirical evidence is sparse, especially in what would be considered natural, nondomestic, or noncaptive settings.

Two radio-collared Asian elephants (*Elephas maximus*) being monitored with their herds at Yala National Park in Sri Lanka provided an unplanned opportunity to gather data on 26 December 2004. No evidence in their movement behavior suggested either was using anything other than immediate environmental cues as they avoided the wave
(Wikramanayake, Fernando, and Leimgruber 2006). However, the wave did not reach either area where the two herds were actually located, unlike the situation of the elephants in Thailand in the anecdotal reports, whose position was inundated and human lives were lost.

Mantled howlers (*Alouatta palliata*) in northeast Honduras that were being studied in Cuero y Salado Wildlife Refuge provided an opportunity to gather opportunistic data when an earthquake occurred in El Salvador in February 2001 with its epicenter at a distance of 341 km from the field site. Because behavioral data were already being collected on these habituated, but free-ranging, individuals at 10 min intervals, trained observers were on hand to document precisely the sequence of population responses to the surprising occurrence of the earthquake. Individuals responded much as they had been noted to do to a threat from the ground and rapidly moved higher into the trees, switching from a resting to an alert state. This behavior was in response to Modified Mercalli Intensity Scale Level IV motion at the site, or an incident where automobiles would rock visibly and dishes, windows, and doors would be disturbed but not broken. Although individuals did not display any anomalous preseismic activity, seismic body waves were detected by the howlers almost instantly, as "the P-waves arrived at the field site approximately 60 s post-origin, with the S-waves arriving 87 s post-origin" (Snarr 2005, 281).

Kirschvink (2000) made an interesting argument that even with a short life span that would preclude an animal’s being able to “remember” a seismic event and respond to it, individuals might “inherit” an ability to respond appropriately to a seismic event. “A population-genetic model indicates that such a seismic-escape response system can be maintained against random mutations as a result of episodic selection that operates with time scales comparable to that of strong seismic events” (312). The oldest known fossils of mammals that survived the Permian extinction are most commonly found as pairs in a collapsed burrow; therefore, selection pressure for a response to seismic events was present at least 250 million years ago (Kirschvink 2000). We speculate that those burrowing mating pairs that did not respond were killed where their remains were found, whereas those that exited the burrow complex survived to be parents. If individuals detect P-waves, as reported for the mantled howlers by Snarr (2005), they might avoid death by responding rapidly before
the S-waves arrived. The greater the distance from the epicenter of the earthquake, the more time individuals would have to respond because P-waves travel through the crust at about 2–4 km/s faster than S-waves (Kirschvink 2000). The response time provided by the difference in the arrival of these two wave types would have been sufficient to allow the escape from the 2004 tsunami, as well.

We thus know a bit about a lot with regard to the substrate as a communication channel. More data must be gathered before we can convert anecdotal reports into questions with testable hypotheses in many areas. Evidence from the fossil record and behavior associated with earthquakes has mostly been incidentally gathered, rather than being in response to the question driving the research. Very few systems have even been superficially studied. A handful of research groups are linking communication studies with morphology and neurophysiology and asking questions about selection for a particular type of signal in a given habitat or social environment. However, an entire planet full of potential research subjects awaits our interest. One purpose of this book is to document what we do know, in the broadest possible sense, from others’ work to identify promising areas for future research. Another is to simply provide a glimpse into a fascinating world of animal interactions that we otherwise might happily continue not to see.
ANIMALS GENERATE a broad range of potential signals merely as incidental events, or byproducts, or epiphenomena, of routine activities. These events can only be labeled signals after empirical testing to confirm that they transfer information among or between individuals (see Bradbury and Vehrencamp 1998). Animals generate airborne, or waterborne, or substrate-borne vibrations; display colors or patterns; and emit chemicals as they live their lives. However, even if an event is stereotypical and species specific (Doherty and Gerhardt 1984), it cannot be classified as a signal unless it functions to transfer information from the sender to a receiver and then modifies the behavior of the receiver in a predictable way that has adaptive value for one or both (Markl 1983). This concept of a signal, though by all means not the only one available in the literature, will be used throughout this book. The definition clearly applies to conspecific communication used in mating, parental care, and coordinated group living, but it would also include information transferred incidentally between prey and predators. The signal need not be directed toward a specific individual; in other words, it may be broadcast in hopes of its encountering a receiver. Further, the time delay between sending and receiving may be rather short, or the signal could be persistent, as in scent marking of a mammal’s territory. A signal could even be a thread spun and deposited by a spider (Krafft 1982). The essential requirements, then, of any communication system include that an individual acts to initiate an event that encodes information (intentionally or incidentally), that the informa-
tion is carried through some medium in a format that will deliver it to a receiving individual, and that the receiver is able to both detect and decode the message, ultimately acting on the information received. All of these steps must be present and detectable by a researcher for the event to be formally classified as a signal. However, signals may also be multimodal, and scientists must remain open to the idea that cryptic signals, or certain aspects of signals, may be repeatedly overlooked.

Determining the range of information that can be transmitted via vibration in solids of all kinds, translating the signals, and estimating the contribution of such signaling to overall fitness will likely be a focus of study for some time, as will determining which anatomical features are specialized for sending and receiving the signals, and whether the same behaviors and features are present or absent in related taxa. A further challenge is to communicate to the reader a concise view of a complex, hidden process, where, for example, signal intensity “can be expressed either in terms of acceleration (m/s²), velocity (m/s), or displacement (m)” (Dambach 1989, 179). Still, the search for these answers and our attempts to incorporate them into our communication paradigm are rather young.

Ehrenberg’s mole-rat, or the Palestine mole-rat, *Spalax ehrenbergi* (but work also reported under the generic name *Nannospalax*, or *Nanspalax*: see Mason and Narins 2001), has been observed to bang its flat head against the top of its subterranean tunnel in a way that could be explained as part of tunnel building activity. However, when individuals were shown to respond in a highly repeatable way to playback stimuli of thumping by conspecifics (Heth et al. 1987) and to respond to simulations in artificial tunnels as well as in the field (Rado et al. 1987), this head banging could be referred to as signaling. Thus, the first confirmation of vibrational communication in terrestrial mammals was as recent as 1987.

Our information on invertebrate communication via vibration signals is currently restricted essentially to the literature of Arthropods, but behavioral observations of other taxa at least suggest that looking for such signals might be worthwhile (i.e., Beesley, Glasby, and Ross 2000 on the extreme vibration sensitivity of feather-duster worms in Annelida, and Newbury 1972 on use of vibration in prey detection by the Chaetognatha). Vibrational communication has only been a research focus of primarily the last 30 years, even though we have been
able to build on century-old observations of novel, or anomalous, behaviors.

One example is our study of the fiddler crabs in the genus Uca, which inhabit intertidal beaches around the world. Males have long been of interest to those studying communication because they have one larger claw, or chela, which they are seen to wave and also to rap on the ground. Male *Uca pugilator* have been observed in both laboratory and field settings as they drummed their large chelae against the substrate. Teasing apart the waveforms showed that drumming created three types of waves. Study of this and related species is providing a great deal of information on how substrate vibrations contribute to animal communication. If conspecific animals, in particular the females targeted by male courtship, are able to perceive waves with different properties and propagation velocities as different vibration events, they should be able to use the information encoded in the drumming signal to locate the male who is producing them (Aicher and Tautz 1990). However, what does this drumming say to other males, or to any members of the population in a context other than mating? Again, work continues to reveal a fascinating world of information transfer.

Distinguishing strictly between sound and vibration may not be a useful enterprise. We can somewhat distinguish them based on sensory perception, if we hold that sound is detected by pressure, or pressure difference, receivers, and vibration by particle displacement in a medium (Kalmring 1985). Vibrations that propagate through both the air and the substrate are produced simultaneously by the same action (Gogala 1985a). Especially in the Orthoptera (Markl 1983), it appears that airborne sound and substrate-borne vibration signals are used in combination in both mating and aggressive interactions. The tympanal organ used for "hearing" and the subgenual organ that detects substrate vibration are located adjacent to each other in the cricket prothoracic legs. The sensory cells in the subgenual organ are "structurally indistinguishable from those in the ear; and these sensory cells respond to substrate vibration as well as to low-frequency sound" (Ball, Oldfield, and Rudolph 1989, 391). Not only is teasing apart the signal functions a daunting task, but it is entirely possible that the two function in combination, as well. Therefore, the more we learn about the channels animals use to gather information about the environment,
the less valuable a distinction between sound and vibration becomes. Ossiannilsson (1949) commented on this distinction as follows:

This discussion has been made more complicated by many workers having felt obliged to separate a perception of air-born vibrations by a specific auditory sense from a perception of the vibrations by the tactile sense. This presentation of the problem will, in my opinion, very easily turn into a battle of words. Even in insects with a well-developed tympanal organ apparently specially constructed for the interception of vibrations of the air, we shall of course never be able to gain a real conception of how the animal subjectively apprehends these . . . I believe that the vibrations produced by the symbal organ of one specimen are conducted to other individuals mainly by the solid substratum—as a rule some part of a plant—and only in a less degree by air. If it could be established that the animals do in this way apprehend calls of each other as such—is this to be termed hearing or not? A matter of taste! (136)

The Problem of Ambiguous Terminology

Within the context of human interactions, we all have a fair understanding of what is meant by words such as sound, hearing, vibration, song, acoustic, and audible. However, one of the greatest challenges of trying to organize and review what is known about communication via substrate signaling has been the lack of a consistent, cohesive vocabulary that is used by researchers studying disparate taxa. A common experience of any emerging academic discipline is to borrow terminology from mostly compatible, or closely related, fields, and then to develop jargon when the established vocabulary fails. In the case of vibrational communication studies, terms have been imported from, for example, physics and mechanical engineering, but their use has evolved and definitions have been sculpted in isolation to the point that communication among groups of researchers is impeded. In many cases first descriptions were published before substrate signaling was suspected, and then the same terms were subsequently used, even after confirmation that the signals were carried via the substrate. Merely repeating the terms that authors have used to describe their systems creates a jumble of roadblocks for the intended audience of a review. Trying to translate the authors’ descriptions by substituting standard terms carries with it
all the dangers inherent in any translation and may unintentionally alter or misrepresent the original observer’s perspective. However, after first relying on individual authors’ use of terms for this book, the decision was made to convert them, and accept the criticism, by using terminology based on the considerations discussed here.

A large and comprehensive literature exists on senders and receivers used in animal communication via airborne or waterborne compressional waves (i.e., the Springer Handbook of Auditory Research volumes), but that literature and other conventional literature on hearing do not include substrate-borne vibration communication. The topics covered in this book are mostly distinguished from that literature by the medium (substrates of one kind or another) and the direction of particle motion detected by receivers (perpendicular to the direction of propagation), where detection of the particle motion usually involves some sort of inertial motion sensor, or sensing mass (see Lewis 1984). However, attempting to strictly separate airborne sound from substrate-borne vibration signaling leaves a gray, or fuzzy, area of behaviors that we have yet to successfully categorize, especially when the same words are used to describe very different phenomena.

The first distinction must be made between sound and vibration. Use of these terms is not as clear-cut as we might think (e.g., Webster 1992; Lewis and Fay 2004), even though they are generally understood to be distinct when used in a popular connotation. Sound is typically used to describe airborne or waterborne compressional acoustic waves that can be “heard” after detection by some specialized sensory organ (such as an ear), but authors may also use sounds to describe substrate-borne vibrations detected by other sensory organs. The use of sound has thus been minimized in this book, even when it is the term most used in the source material to describe signals.

Using the strictest definition, vibration can be airborne, waterborne, or substrate-borne in that it represents particle motion in a fluid or elastic body. Particle motion, rather than the medium, is the issue in defining vibration. Further, vibrations in a fluid always accompany vibrations in a solid with which it is in contact. We tend to use vibration to refer to substrate-borne waves, and this convention is followed in this book, even though this is an ambiguous usage that engineers will find appalling.

Vibration signals that are propagated via the substrate, atmosphere, or surface waves of water, as well as airborne and waterborne signals propa-
gated as compressional waves, could all be considered *acoustic*, and so *acoustic* is not used in this book except in direct quotations. Likewise, for those who study animals whose signals are carried in soil or sand, *seismic* and *substrate* are synonymous. However, vibrations carried in plants are not seismic, by strict definition, because they are not carried through the earth. For all those authors who wrote of seismic signals, the alternatives *vibration signal* or *substrate-borne vibration signal* have been used.

The terms *song* and *noise* are also not restricted to medium. Signals can be songs, or they can be noisy, but they are distinguished by whether they contain a fundamental frequency with harmonic overtones (song) or whether energy is broadly represented in frequencies that are not whole number multiples of the fundamental. Songs can be propagated via the substrate, air, or water and are distinguished in this book with terms such as *airborne song* or *vibrational song*. Somewhat easier to elucidate, but not significantly so, is the distinction among the types of waves produced and detected by animals in their communication.

### A Primer on Wave Theory

Markl (1983) distinguishes among vibration events that induce contact vibrations (when one individual directly touches another with varying pressure: tapping, drumming, antennating, etc.), nearfield medium motions (generated in the fluid medium surrounding the sender and perceived by movement detectors such as hairs or cerci), or boundary vibrations (substrate vibrations at the interface between solid/air, water/air, solid/water, solid/solid, etc.). Most of our focus is on boundary vibrations; however, examples of both contact and nearfield motion are included in subsequent pages, especially when they are difficult to tease apart from other events, or where an evolving story would be truncated and incomplete without their inclusion.

Markl (1983) subdivides boundary waves into subcategories: pure longitudinal, quasi-longitudinal, transverse, torsional, and bending waves. However, we are cautioned to remember that “different wave types are characterized by their different kinds of motions in relation to the direction of wave energy propagation, by their different speeds of propagation and—depending on the conducting material and its geometry—by the different attenuations with which they are propagated” (Markl 1983, 338) (Figure 2.1). Likewise, one disturbance
Figure 2.1. Types of waves in elastic solids: (1) compressional, or P-waves, (2) shear, or S-waves, (3) Rayleigh waves, and (4) Love waves. The arrow shows the direction of propagation.

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event may excite different types of vibrations in the same substrate, and
when passing through some sort of junction (e.g., where a twig meets a
larger stem) a given wave may even be converted into an entirely differ-
et type (Markl 1983).

Pure longitudinal waves, also known as compressional waves
(Brownell 1977), are restricted to "the interior of a medium that extends
over many wavelengths in all directions" (Markl 1983, 338), and particle
oscillation is in the direction that the wave is propagating. A variety of
surface waves are produced when pure longitudinal waves arrive at
boundaries, and the ideal vibration pattern is changed (Gogala 1985a).

Quasi-longitudinal waves, also known as symmetric waves, are pro-
duced by pure longitudinal waves at the boundary with rod- or plate-like
structures and have a slightly lower propagation velocity than the pure
longitudinal waves (Gogala 1985a). Quasi-longitudinal waves are often
propagated through structures such as plant stems or leaves, or spider
web strands, where one or two dimensions are small in relation to the
wavelength. The displacement perpendicular to the surface, where an
animal might be found, would only be 1/100 to 1/1000 times the dis-
placement in the longitudinal wave's propagation direction, but very
sensitive receptors could perceive that level of displacement (Markl
1983). Quasi-longitudinal waves are thought to be a likely candidate
when looking for a mechanism for vibrational signaling (Gogala 1985a).

Transverse waves only exist in solids (Gogala 1985a) and "can only
be propagated in solid materials, which are able to sustain and trans-
mit elastic shearing forces. Particle motion in them is perpendicular to
the direction of wave propagation and in the plane of the surface of a
body boundary" (Markl 1983, 339). The propagation velocity of plane
transverse waves is about 60% that of quasi-longitudinal waves (Markl
1983). Rayleigh waves are produced by a combination of longitudinal
and transverse waves at boundaries of solids and have a shear compo-
nent that is perpendicular to the plane of the body surface. Their prop-
agation velocity is even lower: 4–13% less than transverse waves
(Gogala 1985a). Love waves are transverse surface waves (Markl 1983).

Torsional waves, which appear similar to transverse waves and are likely
to be seen in parts of plants (Gogala 1985a), have not been explored as a
source of biologically relevant information. They are "the type of trans-
verse vibrations transmitted in long structures whose diameters are small
in comparison to their length. If the structure has rotational symmetry
(as in a circular rod) there is no component of motion perpendicular to the surface and wave propagation along the rod's axis is the same as that for a plane transverse wave" (Markl 1983, 339).

Bending waves appear similar to transverse waves and are sometimes referred to as transverse waves, but in the strictest interpretation they are quite different. One difference is that their propagation velocity is frequency dependent, and bending waves are propagated with dispersion (Markl 1983). This means that the different frequency components in dispersion waves travel at different speeds, are not in phase with each other, and arrive at a given distance from the source at different times. Animals might be able to use these phase differences in locating the signal source (Gogala 1985a). A second difference between bending waves and plane transverse waves is that "the phase and group velocity are not the same, the latter being twice the phase velocity" (Gogala 1985a, 119). The group velocity "can be regarded as the propagation velocity of the carrier wave envelope of a wave bundle or wave packet" (Markl 1983, 339). Bending waves occur in a structure with a small diameter in relation to either the structure's length or the wavelength: the diameter must be less than 1/6 the wavelength (Markl 1983). "Particle motion in bending waves is perpendicular to the structural surface at rest because the whole structure is rhythmically bent" (Markl 1983, 339).

Boundary waves on the surface of water present a special case. A disturbance event will generate waves in which particle movement (in ellipses or circles) is dependent on water depth in relation to the wavelength. Likewise, propagation velocity at wavelengths greater than or equal to 10 cm (or frequency of less than or equal to 4 Hz) is dependent on gravity (gravity waves), whereas at higher frequencies (greater than or equal to 46 Hz or wavelength less than or equal to 0.6 cm) it is dependent on surface tension (capillary waves). In between, propagation velocity is dependent on both (capillary-gravity waves). Gravity waves in shallow water, like bending waves, are propagated with dispersion, while the dispersive waves in deeper water are more complicated. Attenuation of surface waves is also frequency dependent (Markl 1983).

Since this book is intended as a study of vibrational communication in animals, the focus has been on substrate vibrations, whether those are via the surface of water, soils of various kinds, plant tissues, or spider webs. These vibration signals all involve at least some particle motion that is perpendicular to the direction of propagation. The
distinction between sound and vibration underwater is not a clear one, and the discussion of communication through water has been limited to very specific cases, as has that of infrasound and tactile (contact) communication signaling.

The Issue of the Medium

Animals create substrate vibrations, including those used in communication, through a variety of behaviors. Substrates can be soils, plants, water, honeycombs, and spider webs, but even within these broad groupings, great variation often exists in the characteristics of any given substrate (i.e., sand vs. clay soils, wet vs. dry sand, soft vs. rigid stems, leaves with parallel veins vs. leaves with netted veins, or even leaves vs. stems of the same plant). How much damping or filtering of the emitted signal occurs during propagation? How much of the signal is reflected, and do vibrations composed of energy across broad frequency bands propagate with dispersion, or are they phase locked? We have made progress in 30 years of study of vibration signaling, but much is still unknown.

Further, the same behavior generates different kinds of waveforms, depending on the substrate, and different behaviors create waves of varying types even within the same substrate. For example, drumming is a percussive event, and we would expect that a drumming individual would produce longitudinal, or compression, waves (Morris 1980). Drumming on sand, or tree bark, or dry leaves are similar events from a behavioral perspective, but the transmission of the signals may be quite different, or they may not. Do drumming on a plant stem and stridulating while standing on a plant leaf create the same type of wave? Should and might are still part of the discussion until more data are gathered. Can we account for the tendency of animals to tremulate on plants but drum on sand because of the types of waves created by the behavior? Perhaps.

Soils

Soil is not a static substrate. Propagation properties of soil change from day to day with changes in temperature and moisture content (Hill and Shadley 2001). Further, generalizations and extrapolations
from one habitat to another are difficult to make (and to support empirically) because of variations in such things as particle size, degree of heterogeneity, and overall complexity of a soil. Some animals, such as the jumping spider *Habronattus dossenus*, routinely traverse an environmentally heterogenous substrate on a daily basis. *H. dossenus* can be located on sand, rock, and leaf litter in the Sonoran desert of North America and will court on all three substrates. The three substrates have very different filtering properties, and most successful courtship was on leaf litter, which was also the most favorable signaling substrate of the three (Elias, Mason, and Hoy 2004).

In observing animals and designing simulations to test their responses, characteristics of the medium must be considered and incorporated into the design because "seismic waveforms (observed with geophones) produced by impulsive mechanical stimuli (including those produced by the thumper) are largely determined by the physical properties of the ground and largely independent of the stimulus source" (Lewis et al. 2001, 1195). In studying terrestrial or burrowing vertebrates or invertebrates, in rain forest or desert or prairie, the issue of the medium is nontrivial. As long as the temporal pattern and intensity of the simulated signal are a good approximation of a naturally produced one, the receiving animal will respond, whether the signal is produced by a living source or a mechanical one (Brownell and Farley 1979c; Hill and Shadley 2001; Lewis et al. 2001).

In grasslands soils, attenuation of vibration signals is strongly dependent on frequency. For example, in a test of signal propagation at a frequency of 142.5 Hz, "the vibration level fell off at a rate of 44 dB per decade increase in distance" (Hill and Shadley 1997, 462). In addition, the soil is not a noise-free environment. Soil organisms produce vibrations as they move, forage, and perhaps communicate. Anyone who has ever listened to the Earth using a geophone in a desert or grassland when the wind is blowing knows the sounds of the tugging of grasses against the soil, which are much like the creaking and groaning of a wooden ship, or an old house, in the wind. There is also incidental noise in most inhabited regions due to vehicle traffic, and engineers are aware, even if biologists are not, of a rather ubiquitous 60 Hz vibration signal (50 Hz in Europe) from transducers in both substrate and atmosphere that could be interpreted by the unwary as evidence of vibration produced by animals. "It is not uncommon for recordings
from electrical transducers to contain noise at 60 Hz and multiples of 60 Hz. In outdoor measurement, these are often due to emissions from electrical power transmission lines” (Hill and Shadley 2001, 1204). Thus, collaborative research across disciplinary lines is a wise choice for all those hoping to disentangle the part of a putative signal that is from the animal and the part that is from its environment.

Even though Brownell (1977) knew that sand was supposed to absorb low-frequency vibrations instead of propagate them, he identified two separate waves propagating through desert sand when a piezoelectric crystal generated displacement pulses on the sand surface (Figure 2.2). A fast wave varied in velocity with sand compaction from 95 to 120 m/sec and was determined to be a compressional body wave, or P-wave. The slower wave velocity was 40 m/sec in loose sand and 50 m/sec in lightly compacted sand. This slower wave was determined to be a Rayleigh wave, and both wave types traveled at about 1/10th their documented velocities in other natural substrates. Both waves were detected when the receiver axis was placed radially to the source, but amplitude of the Rayleigh wave increased, and that of the P-wave decreased, when the receiver was oriented perpendicular to the surface. Likewise, the Rayleigh wave could be damped by placing an absorbant object between source and receiver, whereas the P-wave was not affected (Brownell 1977). Rayleigh waves and Love waves, which are boundary waves, are the principal components of the vibrations produced by drumming fiddler crabs, and the surface P-waves, or primary waves, carried much lower energy (Aicher and Tautz 1990).

<table>
<thead>
<tr>
<th>Vibrational Wave Transmission in Sand</th>
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<tr>
<td><strong>Source</strong></td>
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<td>Rayleigh (R)</td>
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<td>Love (L)</td>
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*Figure 2.2. Physical properties of surface and body waves propagating away from a source disturbance in dry sand. Adapted and reprinted with kind permission of Oxford University Press and the authors from Brownell and van Hemmen (2001, 1232).*
Plants

Female planthoppers in the species *Nilaparvata lugens, Laodelphus striatellus,* and *Sogatella furcifera* signal on rice plants from which they are feeding using substrate-borne vibrations. They elicit responses from males even with no airborne component to the signal. These signals can be effectively transmitted at distances of 60–80 cm, and signals can be perceived even from adjacent plants as long as leaf blades from the two are in physical contact (Ichikawa 1976). Natural and synthetic signals that mimic those from a female will stimulate a male to search for her, even when a thin paper substrate is used to replace the rice leaf (Ichikawa and Ishii 1974). In general, the small planthoppers and leafhoppers do not respond to any high-frequency airborne component that might exist for their signals, even when the sound is detectable at a distance of 1 cm. However, the substrate component of this same signal may travel 1 to 2 m and will elicit a response from the target recipient (Claridge 1985).

Michelsen et al. (1982) studied vibrational songs of three species of non-cicada Hemiptera (leafhoppers *Euscelis lineolatus* and *Euscelidius variegatus* and the planthopper *Euides speciosa,* all from Germany) and four cydnid bugs: *Sehirus (Cantephorus) impressus,* *S. (C.) dubius* and *S. (C.) melanopterus* from Slovenia and *Sehirus (Triomegas) bicolor,* collection site not stated but perhaps also from Slovenia. Their study also included simulations and tests of mechanical properties of a range of plants, from fresh and dry tree leaves, to reeds, bean plants, and wild herbaceous species. Songs recorded were courtship, rivalry, and female acceptance songs for the bugs and calling and alternating mating calls of the “small cicadas.”

Their results were quite different from what one would expect to find for airborne signals. Vibrations could be transmitted over distances of 1–2 m with very little loss of energy at the carrier frequencies, and a signal might pass up and down a stem several times before it was no longer detectable by a receiver. The amplitude did not decrease in a predictable way with distance from the source, and attenuation and amplification of specific signal frequencies were hard to predict. Further, even though the mechanical properties of the plants in the study were quite different, the signal propagation velocities were rather similar (Michelsen et al. 1982).
Perhaps the most interesting finding was linked to both the unexpectedly similar filtering properties of the plants and the identity of the vibrations, which were bending waves. Bending waves are dispersive and "distort" a signal, so that frequencies emitted by the sender travel at different velocities. Over some distance, different frequency components of the song arrive at a receiver at different times. Songs produced by the "small cicadas" and bugs all contained energy in broad frequency bands, regardless of variation in the song function or temporal characteristics. Thus, regardless of the filtering or loss of song components due to conditions such as body position or vagaries of the substrate, some signal components will pass through the filter and reach the receiver. Further, if multiple frequencies from the song do arrive, the receiver could potentially use the differences in arrival times to estimate distance to the singer (Michelsen et al. 1982).

A newer technique allows a two-dimensional characterization of the plant stem by using two perpendicularly positioned transducers (McNell et al. 2006). A single transducer is sensitive to particle motion in a single axis, but use of two transducers aligned in perpendicular planes provides a better picture of the signaling environment of the animal perched on the plant, and likely integrating sensory input from all its legs.

Tree crickets in the genus *Oceanthus* were hypothesized to frequent specific plant species because of their high resonance qualities (Bell 1980b). An experiment tested species of Canadian plants on which tree crickets do and do not mate. Orchard grass (*Dactylis glomerata*), raspberry canes (*Rubus* spp.), Canada thistle (*Cirsium arvense*), and goldenrod (*Solidago* spp.) are all known tree cricket perches and "had nearly flat vibration transmission curves" (Bell 1980b, 212). Common cattail (*Typha latifolia*) and toadflax (*Linaria vulgaris*) are not known perches for mating tree crickets, and these both showed signal distortion and rapid decay (Bell 1980b). So, the question then becomes, "Are host plants chosen as perches because they efficiently propagate signals, or are substrate signals used in communication because they work well on the plants where tree crickets typically perch?"

Within a rapidly diverging group of cryptic species that differ primarily in their vibrational mating signals transmitted through plant stems, we logically assume that natural selection would contribute to adaptations for more efficient signaling on the preferred substrate. In the green lacewing *Chrysoperla carnea* group, 15 cryptic "song species"
from around the world were tested for convergence of substrate vibration songs on the preferred plant substrate, and for transmission through the preferred and alternative substrates (Figure 2.3). Surprisingly, the songs of a species associated with conifer branches and one that signals from grasses propagated equally well through either substrate. Frequency spectra did not change in the songs of either species.

Figure 2.3. Maximum parsimony bootstrap phylogeny of 15 song species of green lacewings of the *Chrysoperla carnea* group and three outgroup taxa, which sing from conifers (*) or grasses. Numbers at the nodes are bootstrap values. A 12-s oscillograph is shown for the song of each species; vertical arrows indicate where the partners would sing during a duet. Reprinted with kind permission of Elsevier and *Animal Behaviour* from Henry and Wells (2004, 881).
when transmitted through either substrate. Even though examples were found of convergence of song type based on substrate preference, tentative conclusions were that natural selection appeared to play no part in selection for a match between song and substrate. Instead, sexual selection acting on arbitrary song differences was probably the mechanism driving speciation in this group (Henry and Wells 2004).

This preliminary evidence leads us to think that insects perch on preferred plants and signal there, but they would still signal in much the same way if displaced and forced to use alternative perches. Further, even those species of plants that promote rapid, focused communication between mates might lose their beneficial transmission characteristics with age and loss of hydration (Bell 1980b). This interpretation is supported by evidence from the southern green stink bug, *Necara viridula*, which lives and signals on a variety of agriculturally important host plants throughout the world. There can be a difference of as much as 10 times in attenuation of their signals in plants from the same family. For example, propagation of signals through green bean is much more efficient than through soybean or pea (Virant-Doberlet and Čokl 2004), yet *N. viridula* uses these three legumes and others as host plants. Likewise, when the treehopper *Umbonia crassicornis*, which feeds and signals from a variety of host plants, was recorded on host and nonhost species, spectral and temporal characteristics of their signals were influenced by distance, but effects were small. Signal traits were repeatable and could be reliably associated with the individual singer (Cocroft et al. 2006).

Work that focused only on the dicotyledonous leaf as a signaling substrate was able to reduce the complexity of the system. The functional area of a leaf surface could be subdivided into sectors bounded by veins of diameter greater than 0.2 mm. Within sectors, whether they were crossed by minor veins or merely consisted of rather homogeneous leaf lamina, the energy losses based on distance and frequency were essentially the same. Regional differences in signal dissipation could be attributed to the larger veins closer to the leaf petiole (Magal et al. 2009). Yet the harlequin bug, *Murgantia histrionica*, which is a pest of more than 50 plants, such as cabbage, collards, and mustards that do not have an actual stem, exploits the leaf vein as a preferred signaling perch. On cabbage, attenuation of both male and female *M. histrionica* signals was in the range of 2.5–4 dB over 5 cm, whereas attenuation
through the leaf lamina was on the order of 21–23 dB at distances of 5–6 cm (Čokl et al. 2004).

Unlike many insect species that signal from plants on which they are feeding, spiders that do not build webs use the substrates on which they perch to detect prey, as well as to signal to potential mates. *Cupiennius salei* is a tropical wandering spider of Central America that hides in leaves of its closely associated plant during the day and emerges at night to feed and court on the leaf surface (Rovner and Barth 1981; Barth 2002). In Mexico they live closely associated with banana (*Musa*) or bromeliad leaves. Two other species, *C. getazi* and *C. coecinus*, were found on the same or similar plants in Costa Rica. Whereas those animals adapted to signaling from dicotyledonous leaves use broadband vibrations, use of narrowband vibrations would not be disadvantageous to an animal signaling from monocotyledonous leaves. On these the veins are all parallel and running the length of the elongated leaf, instead of partitioning the leaf blade in a netted pattern as in dicotyledonous plants. Members of the genus *Cupiennius* are sit-and-wait predators that live, hunt, and court exclusively on monocots. Attenuation is only about 0.8 dB/cm for vibrations up to 500 Hz on the bromeliad *Aechmea fasciata* and a comparable 0.5–1.0 dB/cm on the agave *Agnus americana*. Banana leaves show even less attenuation: 0.3–0.4 dB/cm at 75 Hz (Dierkes and Barth 1995).

Further, when experiments were designed to identify mechanisms to disrupt communication among mating leafhoppers, *Amrasca devestans*, on cotton and planthoppers, *Nilaparvata lugens*, on rice, there was a difference in the transmission of pure tones and harmonic overtones between the dicotyledonous cotton and the monocotyledonous rice. The focus of the study was to find a vibration source for frequencies that would interfere with necessary mating signals from the pest species without being obnoxious to humans. When harmonium tones were played into the air, they were transduced to plant-borne vibrations in both cotton and rice leaves. A broad range of frequencies was propagated through the cotton plant, whereas the best propagation frequencies for rice were very narrowly focused between 178 and 200 Hz. Likewise, pure tones were less effective in disrupting mating on cotton plants than sounds with harmonic overtones; however, pure tones were effective in disrupting mating on rice (Saxena and Kumar 1980). Conclusions were that mating could be disrupted with intro-
duced vibrations that humans could tolerate. However, the frequency and intensity of the sound would have to be determined in each case. I suggest that differences in frequency filtering and propagation of vibrations through monocot and dicot leaves must be taken into account in any such experimental design.

The southern green stink bug, *Nezara viridula*, from Slovenia leaves little to chance as both males and females signal from the stems of multiple host plants. Both male and female calling songs have both narrow- and broadband components (Čoki, Virant-Doberlet, and Striž 2000a). Signal effectiveness of the female calling song is so great that a male has been observed to respond from a sedge separated from that of the female by 2 m simply via coupling of the roots and soil between the plants (Čoki and Virant-Doberlet 2003).

Being able to distinguish among potential mates, meals, and abiotic factors, such as wind or rain, is possible because of the differences in the physical properties of vibrations generated by these forces in the leaves on which the wandering spider *Cupiennius salei* sits and waits. Vibrations produced by wind are typically narrowband and low in frequency (below 5 Hz), and even wind gusts that blow leaves about generate vibrations up to only about 50 Hz if we consider a threshold of −20 dB. Rain drops at the same threshold show frequency bands up to 250 Hz and maximal acceleration at about 1,000 Hz. Prey, on the other hand, produce higher-frequency and broadband vibrations in the range of 150 to 900 Hz on banana and just a few Hz to 900 Hz on bromeliad, with peaks at 600 Hz and 250 Hz, respectively. Courtship signals produced by males and females fall somewhere in between: females, 20–50 Hz frequency range, but more broadbanded than wind; males, peaks at 75 Hz and 115 Hz and delivered as a train of up to 50 syllables. Temporal patterns in the male signal allow them to be recognized by females as conspecifics, but other temporal patterns are useful in discrimination, as well. Interestingly, passing trucks on a nearby road generated long-trained continuous vibrations similar in spectral characteristics to prey without eliciting a response, while a creeping grasshopper generated vibrations much like wind and was able to slip by undetected on the same leaf as the spider. The banana plant is able to transmit courtship signals and is well suited to transmit all the investigated vibrations with an average attenuation of only 0.35 dB/cm (Barth et al. 1988). The greatest transmission distance
measured for a male’s signal on banana plants was 3.8 m in Costa Rica (Barth 2002).

The courtship signal of Cupiennius salei can be broken up into a narrower-band (60–100 Hz) train of syllables produced by the abdominal (opisthosomal) bobbing of a tremulation signal, and a broadband scraping, drumming percussive signal produced by the pedipalps, which are a pair of appendages between the jaws and front pair of walking legs. On bromeliads, the attenuation of pedipalpal signals varies with frequency, so that frequencies above 1 kHz are attenuated by more than 30 dB, frequencies in the range of 250–550 Hz by 15–30 dB, and those less than 200 Hz are transmitted more readily. Thus, “[T]he highest detectable frequency of a pedipalpal signal therefore is a measure for distance to the signaling male” (Baurecht and Barth 1992, 242). The opisthosomal signal is carried via bending waves and “[B]ecause the frequency contents of the male syllables hardly varies, propagation velocity in the plant is about the same for all syllables. As a consequence, the temporal pattern of consecutive syllables is well preserved during propagation” (Barth 1997, 257). Attenuation of the opisthosomal signal varies with acceleration amplitude, thus syllables having higher initial acceleration amplitudes attenuate more than those with a lower initial level. However, females respond to a wide range of acceleration amplitudes in synthetic signals, and this attenuation would not pose a communication constraint for C. salei (Baurecht and Barth 1992).

Water

Insects that live on the surface of still water, such as waterboatmen or backswimmers (Hemiptera: Notonectidae), waterstriders (Hemiptera: Gerridae), and whirligig beetles (Coleoptera: Gyrinidae), can use vibration waves produced on this boundary to communicate with conspecifics or detect prey. The waterboatman, or backswimmer, Notonecta glauca is able to use phase differences in components of signals reaching multiple vibration receptors to localize prey (Wiese 1974). These generalist predators can distinguish prey and nonprey using the frequencies of surface waves created by their movements. Depending on the prey type and its behavior (i.e., the struggling of terrestrial species that fall into the water or the diving of aquatic prey), N. glauca could detect and orient to them at distances greater than 14 cm, while effec-
tively ignoring the lower-frequency waves created by conspecifics and abiogenic (not produced by living things) factors such as wind (Lang 1980). Prey species all produced waves in the frequency range of 60–140 Hz, whereas conspecifics, wind, rain, or falling leaves produced waves with frequencies of 40–50 Hz. Energy maxima in the waves created by prey were consistently above 15 Hz, and for nonprey, consistently below 15 Hz. Although it is true that “every displacement of the water surface generates a wave packet that propagates with group velocity” (Lang 1980, 236), the story is still not completely one of frequency discrimination because some species that generate waves within the range of prey did not actually attract foraging backswimmers (Lang 1980).

Waves produced by skating of the waterstrider *Gerris lacustris* have essentially the same characteristics as those produced by fully aquatic prey (frequencies up to 70 Hz and well above the vibration amplitude threshold) of *Notonecta* and can be detected by this predatory backswimmer at distances above 14 cm (Lang 1980). In addition, pre- and postcopulatory struggles between aggressive males and unwilling females (Arnqvist 1989) would likely create waves similar to those described by Lang (1980) when *Notonecta*’s terrestrial prey fell into the water. In 30 species of waterstriders examined, 23 species showed clear postcopulatory struggling to terminate mating (Arnqvist 1997).

Another interesting mating behavior in these and most other waterstriders is for the male to “guard” his mate by riding on her back after his genitalia have been retracted (Arnqvist 1989). Of the 30 species examined by Arnqvist (1997), only four did not exhibit mate guarding. Guarding males appear to increase a female’s risk of predation (Arnqvist 1989, 1997; Fairbairn 1993; Rowe 1994), and their riding behavior may only be superficially “passive.”

*Gerris remigis* males (third-instar nymph through adult) from North America produce a high frequency (HF: 80–90 waves/s) and a low frequency (LF: 3–10 waves/s) ripple signal, while females (third-instar nymph through adult) produce only LF signals. In controlled experiments, males were able to discriminate sex of conspecifics on approach by whether or not they produced HF signals. Although visual and chemical cues are also present, the production of the HF signal was sufficient to discriminate sex of the approaching individual. Even a female with whom a male had recently mated was treated like a male when she was manipulated to produce the HF signal. “Males appear
not to remember the sex of individuals involved in previous encounters once close contact is broken" (Wilcox 1979, 1326).

The HP signals produced by Gerris remigis (or Aquarius remigis) males repel unmated males. Single males produce these ripple signals as they stand on the water surface, but mated males send vibrations through the body of the female upon whom they are riding. These male-induced ripple vibrations were suggested as a benefit to the female because they reduced harassment that would interfere with female foraging, just as male body contact signals did when single males actually touched a mating pair (Wilcox and Di Stefano 1991). However, these ripple signals are also in the range of those produced by backswimmer prey (Lang 1980). When mating Gerris odontogaster were attacked by Notonecta lutea, 75% of the successful attempts took the female, and never were both of the pair taken. The probability that the female of the pair would be taken was almost three times higher than if she were in a female-female pair (Arnqvist 1989). The same situation exists in Notonecta kirkii predation on Gerris buenoi. Female susceptibility to predation was more than double when she carried a male, and the backswimmers were "about three times more successful in attacks on mating pairs than on single gerrids and about five times more successful in attacks on wrestling pairs than on singles" (Rowe 1994, 1052).

Female Aquarius remigis carry mates for several hours, and even though they do not experience reduced foraging success due to weight bearing, their mobility is impaired and they are more susceptible to predation than single females. In a controlled experiment a female with a dead male affixed to her back was four times more likely to be eaten than controls or females with a comparable weight attached. However, after the tandems were gone, the weighted females were seven times more likely to be eaten than controls, suggesting that both loss of mobility and some visual cues were important to prey choice of green frogs, Rana clamitans (Fairbairn 1993).

Water surface waves are also important in communicating during mating. Males of the waterstrider genus Rhagadotarsus in Australia produce as many as four different signals (calling, courtship-calling, courtship, and aggressive). The calling (17–29 waves/s) and courtship-calling vibrations are produced as relatively large amplitude waves by stroking the surface with pairs of mid-legs (and possibly hind-legs) like oars, whereas the lower-amplitude waves of the closer courtship signal
are produced by paired foreleg movements along with the waterborne courtship-calling signals when females have moved to within 5–10 cm. Females also produce these foreleg courtship signals when males are within 2–3 cm. The male copulatory signal may be entirely tactile, or it may also involve production of surface waves. Aggressive signals are produced with the mid-legs, mostly in interactions with other males regarding signaling sites (Wilcox 1972).

Three types of ripple (vibration) signals are produced by the waterstrider Limnoporus rufoscitellatus from Finland: high frequency (25 Hz), low frequency (11–15 Hz), and courtship (2 Hz). The high-frequency and courtship signals are similar in structure and function to wave signals produced by L. dissortis and L. notabilis, which are Nearctic. Sexually mature L. rufoscitellatus males and old fifth-instar males produced the high-frequency signal, while only adult males produced the courtship signal, and both signals could be produced while the male was riding on the female's back. The low-frequency signal is of unknown function and is mostly observed being produced by either males or females in direct, or otherwise close, contact. This low-frequency signal was not significantly different than waves produced by waterstrider movement and likely is not a true ripple signal (Nummelin 1987).

The whirligig beetle, Dineutes discolor, may use visual and chemical signals in premating behavior, but the surface wave vibrations produced during premating are essential to mate attraction and copulation. When the Johnston's organs that detect surface vibrations were surgically removed, no mating took place in a population that had been actively mating prior to the surgery. Predatory behavior is not impaired by the removal of Johnston's organs, and tactile hairs near the antennal pedicel are proposed as the receivers for information required in predation (Kolmes 1985).

The fishing spider, Dolomedes triton, is also able to orient toward and capture prey at distances up to 40 cm using the surface waves the prey produce. The spider rests on the water surface with its legs in a typical circular arrangement of nearly constant position (Bleckmann and Barth 1984), reminiscent of the stance of alert scorpions foraging on sand (Brown and Farley 1979b). D. triton can determine both direction and distance to the source of vibration up to 20–25 cm using unknown sensory mechanisms. It appears that the vibration-sensitive metatarsal
lyriform organs are used, as well as the sensory hairs of the trichobothria, and even vision (Bleckmann and Barth 1984).

Honeycomb

As is seen in comparisons of attenuation and damping effects of signal transmission in soils of different textures, the circumstances defining the construction of the honeycomb in a honeybee nest predict the efficiency with which vibrations are propagated across a comb face. Natural honeycombs with free edges are much better at transmitting vibration frequencies than combs constructed on the frames provided in commercial beehives. Further, honeybees living in hives will remove wax to separate the comb from the frame wall on combs where their sisters dance, thus providing substrate conditions more like that of a natural comb (Sandeman, Tautz, and Lindauer 1996). There is a great deal of variation even in natural combs; however, the bandpass profiles were the same in three distinct types of combs tested by Sandeman, Tautz, and Lindauer (1996). Transmission tests showed that some frequencies were damped as vibrations were propagated across cells of open combs but that those around 250 Hz were actually amplified.

Spider Webs

The spider web represents a special class of substrates through which animals send and receive vibrations. Although we have long understood the web to be a mechanism for ensnaring prey, it also provides details about the position and characteristics of disturbance events (Masters and Markl 1981). Many web-building spiders have reduced vision, and the web is the primary communication channel used to supply information about prey caught in the web, as well as to keep track of young and to send and receive courtship signals between potential mates. The web of orb-weaving spiders consists of a hub of rather dense threads, radii that project away from the hub to attach to frame threads around the outer edge, guy threads that anchor the web to supporting objects, and spiral threads that run from one radial to another (Masters 1984). Auxiliary spiral threads provide structural support to the web, but they are typically removed when a web has been completed. Sticky spiral threads, which are laid down between auxiliary spirals, are
mechanically weaker and serve more to entangle prey (Landolfa and Barth 1996).

Although vibrations produced by airborne prey will stimulate some jumping spiders to attack, orb-weaving spiders never jump in the air to attack flying prey. Further, even though prey struggling in a web produce both airborne and substrate vibrations, the orb-weavers use the information contained in the vibrations traveling through the web (Klärner and Barth 1982).

"In a silken thread we expect longitudinal, transverse, and torsional vibrations simultaneously" (Barth 1982, 84–85), and transverse waves are the "most significant type of wave traveling in stretched fibers" (Frohlich and Buskirk 1982, 16). Longitudinal waves travel through the radii in the direction of the thread axis. Transverse wave particle oscillations are perpendicular to the plane of the web, and lateral wave oscillations (essentially transverse waves traveling within the "side-to-side" Y-axis plane, instead of the "up-and-down" Z-axis) are parallel to the plane of the web. Torsional waves could be transmitted through radii, but the small diameter threads would provide minimal torque (Masters and Markl 1981; Masters 1984). In the range of 1 to 1,000 Hz, longitudinal waves lose only 1–2 dB through attenuation, whereas transverse waves lose about 16 dB at 1 Hz. Loss is rather linear for transverse waves in the range of about 20 Hz to 500 Hz, where attenuation is about 28 dB. Lateral waves propagate with even more attenuation, dropping about 23 dB in the range of 1 to 200 Hz, and then increasing to about a 40 dB loss at 1,000 Hz (Masters 1984). For typical web materials and tensions, longitudinal waves travel the fastest, with velocity of about 2,182 m/sec, and torsional waves travel about 1,580 m/sec, while transverse waves travel at 787 m/sec in webs of moderately sized spiders and 373 m/sec in webs of large spiders (Frohlich and Buskirk 1982). Members of the orb-weaving genus Zygiaella are more sensitive to longitudinal vibration. The threshold displacement required to release a predator response is 3–4 dB lower for longitudinal than for transverse waves (Klärner and Barth 1982).

One interesting and confounding aspect is that vibrations traveling along one thread may be transformed at junctions and will propagate as waveforms down the three new arterial paths, in addition to being reflected back along the original pathway (Masters 1984). Further, "[F]or a 90° crossing (approximately correct), the incoming longitudinal vibration is completely converted to lateral vibration on the
cross-strands, and vice versa" (Masters 1984, 213). This conversion to another waveform at junctions helps to explain the finding that longitudinal vibration is more directional than transverse or lateral since it "tends to pass web junctions without being attenuated, whereas the other two types lose more energy and so tend to spread out in the web" (Masters 1984, 213). Thus, longitudinal vibration, because of its directionality, could be important to a spider's success in locating prey after it has been detected (Masters and Markl 1981; Masters 1984).

The issue is more complicated when spider species construct the web with a greater number of auxiliary and sticky threads, which provide additional paths for signal "leak off." Most web-builders remove auxiliary spiral threads after construction is complete, but the neotropical golden web spider, *Nephila clavipes*, retains them, apparently trading off signal transmission efficiency for an increase in structural support in the web (Landolfa and Barth 1996).

Spiders rely on the mechanical properties of the radial threads to receive vibrational information (Barth 1982). Spiders orient themselves along radial threads when seeking the source of a vibration (Masters and Markl 1981), but they appear to use the spiral threads exclusively for capturing prey. Orb-weavers typically sit in the hub of the web, and all radial threads connect with this mesh of threads. If spiders have been disturbed, they may move to a less conspicuous position at the edge of the web, but they leave the tarsus of one leg in contact with a radial thread. If vibrations are detected, they move back to the hub to orient themselves and to identify the source of the vibrations (Barth 1982).

**Talking to Plants**

The definition of signaling provided at the beginning of this chapter also allows for inclusion of a form of vibrational communication that is inter-kingdom in nature. This plant-animal communication is "buzz" pollination by members of as many as seven families of wild bees of pollen-only flowers that exhibit apical dehiscence, or release of pollen from their anthers via slits or apical pores. Co-evolution of these pollen producers and pollen gatherers has led to an interesting mutualism where plants appear to actually require a vibration stimulus to release pollen, and bees provide that stimulus through vibration of their flight muscles while clinging to the plant's stamens.
For example, the bloodwort *Xiphidium caeruleum* in Panama rapidly expels pollen from the apices of its anthers whenever directly vibrated by the euglossine bee *Euglossa imperialis*. The bee contracts indirect flight muscles as she grips the entire flower with her mandibles and all six legs. Vibration of the anthers in this way results in active expulsion of pollen onto the bee's body. Even though other bee foragers are likely also capable of extracting pollen by buzz pollination, there are no known examples of pollen being released spontaneously by the plant in the absence of the vibrational stimulus from a bee. Both pollinator and plant thus benefit from the co-evolution of this relationship (Buchmann 1980). In another example, plants of the genus *Solanum* in Surinam may be pollinated only by the buzz pollination of stingless bees. "By hanging over to pores and vibrating the pollen is loosened and shoots out of the pore onto the body of the bee" (Engel and Dingesman-Bakels 1980, 348).

Members of the flowering genus *Rhododendron* are pollinated in an interesting way by bumblebees (*Bombus terrestris* and *B. hortorum*) in New Zealand. Stamens are widely spaced and filaments are slender, so that the bee's weight is too great to buzz an anther by holding onto a single filament, while adjacent filaments are too far apart for her to support herself on several. Bumblebees rarely attempt to elicit pollen release by buzz vibration, choosing instead to gather nectar only. Vibrations are produced in the anthers as bees land on flowers and pass by while collecting nectar. These vibrations will cause mature anthers to release pollen on viscin threads from apical pores, and bees must pass through these pollen threads on their nectar-collecting trips. A special benefit for the plant is that the pollen ends up on the bee's back in a position that is difficult for her to harvest by self-grooming but in a very good position for deposition on the stigma of the next *Rhododendron* flower she visits (King and Buchmann 1995). Humans now exploit this communication system in greenhouse settings by inducing bumblebee pollination of tomato plants (Kirchner 1997).

Markl's (1983) definition for a signal allows us to include systems such as buzz pollinators and plants, or animal predators and prey, that would not be considered in everyone's treatments of vibration communication in animals. Markl's definition, however, also allows the inclusion of systems where we have incomplete evidence that intentional
behaviors result in signals between conspecifics and that a sender's encoded message is decoded by the receiver with minimal loss of detail. Some of the systems described in subsequent pages are taken from reports of experiments where no attempts were even made to measure substrate-borne vibration. However, behaviors or accompanying airborne sounds are similar to those in systems where the hypothesis of vibrational communication has been confirmed through empirical testing to be the only nonfalsifiable option. Substrates, and thus transfer media, vary with the species that exploit the substrate vibration channel, but patterns do emerge when we start to look at the bigger picture.
FOR AN INDIVIDUAL to act on information contained in a signal, the encoded message must be transferred from the medium through which it is sent to the animal’s central nervous system (CNS) for decoding. Some sort of receptor apparatus that acts as both a filter and a transducer mediates this transfer. A transducer could be defined as a mechanism for “transferring information from energy in one physical realm (e.g., acoustic energy) to energy in another realm (e.g., electrical energy)” (Lewis 1992, 165). In the case of vibration signals, the receiver transfers information from energy in one physical realm (the signal from substrate-borne vibrations traveling through the medium) to energy in another realm (an action potential coursing through the animal’s nervous system). The structure of transducers has taken almost as many forms as have the organisms that possess them, especially in invertebrates. Their ontogeny, or development, is rarely understood, and even within related taxa, the transducers may not reflect homology—they may not have developed from the same embryologic blueprint or from a common ancestral form. We can, however, arbitrarily assign vertebrate vibration receivers to two major categories: auditory-vestibular adaptations and somatosensory adaptations.

Auditory-Vestibular Adaptations

The generalized structure and function of vertebrate ears is fairly well understood, especially if we do not look at the exceptions to the rule
(Figure 3.1). In humans and other terrestrial mammals, for example, sound waves travel through the gaseous atmosphere and are channeled down the auditory canal of the external ear, where they impact and set up vibrations in the tympanic membrane. Vibrations in this ear drumhead are transferred to a solid medium via direct contact with the first of the middle ear's three small auditory ossicles: malleus (hammer), incus (anvil), and stapes (stirrup). After the vibrations travel down the chain of three bones, the stapes transfers these vibrations through the membrane of the oval window to the fluids and the basilar membrane of the cochlea of the inner ear. The tympanic membrane, ossicles, and oval window compose a transformer. Thus, sound is transferred through all three of our earthly physical states of matter before the bending of the stereovilli of the hair cells in the organ of Corti of the cochlea acts to

Figure 3.1. Human ear, showing components of the external, middle, and inner ears.
transfer the encoded message to neurons of the VIIIth cranial nerve (vestibulocochlear), which carry the message to the brain for analysis and decoding.

In this way airborne sound is detected in humans, and the general plan works the same way for other terrestrial vertebrates that possess a tympanic membrane, whether it is recessed or on the body surface, if we stop short of the inner ear. The vestibular senses of balance, motion of the head, and body position in humans and therian mammals are concentrated outside the cochlea, whereas in nonmammalian vertebrates there is a great deal of plasticity in the inner ear that renders the division of vestibular and auditory senses into "noncochlear" and "cochlear" inappropriate, even with organs that bear the same name (Lewis 1992). This book does not focus on the hearing pathway as such, but enough fuzzy areas exist in our understanding of the detection and processing of substrate vibration signals across animal taxa that a general discussion to serve as a baseline is included here.

Further, in the infrasound range of frequencies that are not detectable by humans, other animals may acquire useful information via the auditory-vestibular pathway. For example, the homing pigeon (Columba livia) has an estimated detection threshold (50% response) of receptors in the inner ear of about 80 dB at 1.5 Hz, 60 dB at 5 Hz, and 50 dB at 10 Hz, which is about half that measured in humans. Since many natural phenomena like thunderstorms generate infrasound, it is speculated that homing pigeons might use some sort of triangulation method based on the home and release sites and a distant source of infrasound (Yodlowski, Kreither, and Keeton 1977).

Vertebrate animals can also process signals that they detect from substrate-borne vibration through this auditory-vestibular pathway. If vibration signals are transferred to the vestibulocochlear nerve by something like vibrating skeletal components, vibrations can be "heard" just as airborne sound can be heard. It is the interaction between this extratympanic pathway and the tympanic membrane–ossicle path that gives humans the well-known sense of their own voice (Wilczynski, Resler, and Capranica 1987) and causes us to say when we hear our recorded voices, "That doesn’t sound like me!" From the point of stimulation of the VIIIth cranial nerve, however, we assume these signals are processed in the same way as other auditory information. Yet we do not
know how inputs funneled from various sources are actually sorted out in the CNS (Christensen-Dalsgaard and Jørgensen 1996).

We also do not know how important the auditory-vestibular pathway is for interpreting natural vibration signals in vertebrate animals. Even though homology of morphological elements is assumed, there is variation within and across taxa in the mechanism of signal transduction, and differences of interpretation exist while research continues to reveal details. For example, the common use of diagnostic bone conductivity tests on humans in a clinical setting to determine the source of hearing loss led Sohmer et al. (2000) to test the potential pathways from the mechanical vibration source applied to the skull to the receptors in the inner ear. They concluded that vibrations are transferred from the skull bones to the contents of the skull and that the cerebrospinal fluid within the meninges and inside the ventricles of the brain ultimately transfers the vibrations to the cochlea without first being conducted to the middle ear. Although a middle ear pathway may not be functioning in this scenario, or perhaps not at all in humans, documented evidence of vibration perception via this extratympanic channel has been found for other vertebrates. Special adaptations for transferring substrate-borne vibration information are sometimes more obvious to us in animals that live in a watery medium, those that live in close contact with the substrate, or that have some other sort of environmental constraint, such as in fossorial (burrowing) animals. It is also possible that we recognize these structures because we expect to find something special in these "aberrant" forms.

Other Mammals

The dolphin’s (*Tursiops truncatus*) lower jaw is hollow, and a mandibular fat body extends from the lateral jaw to the auditory bulla. Norris suggested as early as 1964 (cited in Brill et al. 1988) that this pathway was the primary channel used by echolocating dolphins to carry signals to the middle and inner ear. Brill et al. (1988) conducted behavioral tests that showed significant interference in reception of signals in the range of 30–50 kHz when a trained dolphin’s eyes were covered and the lower jaw was covered with a rubber hood device. This fat body and its analogs are sometimes referred to as “acoustic fat.”
Elephants have dense accumulations of fat in their feet that may play a role in vibrational communication. Even though the fat stored around the kidney and other internal organs in elephants is depleted during the winter months, the fat in the foot is not used for metabolic activity. "Elephants at times lean forward on their front feet, which are directly in line with the ear due to the unique graviportal structure of their forelimbs" (O'Connell-Rodwell, Hart, and Arnason 2001, 1166), thus they appear to be utilizing the fat in their feet to promote "hearing" substrate-borne vibrations, even though the direct mechanism involved is not understood.

The blind mole-rat, *Spalax ehrenbergii* (but also known as *Namnospalax*, or *Nanospalax*: see Mason and Narins 2001), of Israel has a specialized articulation that creates a bony bridge between the lower jaw and the middle ear. Individuals, who live solitary lives other than during mating and maternal care, have a specialized behavior of laying their jaws against the walls of their burrows at the same time that neighbors thump by hanging their flattened foreheads against the roofs of their own burrows. This pressing of the lower jaw against the burrow wall would promote the conduction of signals via the ear (Rado et al. 1989; Rado, Terkel, and Wollberg 1998). When the mandible is in contact with the soil in a "listening" mode, the mole-rat's jaw is "out of joint." The typical mammalian condition is for the condyle (the smooth articulating surface on a projection of the lower jaw bone) to fit into the mandibular fossa (depression in the temporal bone) to form the T-M (temporo-mandibular) joint. *S. ehrenbergii* has a pseudofossa just posterior (caudal) to the mandibular fossa, and when its jaw is pressed against the soil, the condyle of the mandible fits into this "false" depression, which has not been described for any other species. In addition, the second middle ear ossicle, or incus, is held in place by a ligament within a depression in the periotic bone that lies adjacent to this pseudofossa (Rado et al. 1989). Thus, when the mole-rat is "listening" with its jaw pressed to the substrate, vibrations can be transferred directly to the incus from the jaw, bypassing the tympanic membrane and malleus (Rado et al. 1989; Rado, Terkel, and Wollberg 1998). The malleus is simple and not attached to the tympanic membrane. As a matter of interest, in most of the 50 ears of *Spalax ehrenbergii* examined by Burda, Bruns, and Nevo (1989), the entire outer ear canal was filled with ceruminous (ear waxy) material that would surely interfere with transmission of airborne signals to the eardrum.
Other mammals have ear ossicles that are massive in comparison to other bones of the body. They do not reflect the proportionality of scale that we expect to see across taxa. We find these disproportionately large middle-ear bones in mammals that have relatively decreased auditory acuity at higher frequencies and enhanced acuity at lower frequencies. For example, the Indian elephant, which has been reported to use information gained from substrate vibrations, has ossicles that weigh as much as 650 mg, whereas a horse, which is not known to use information from substrate vibration, has ossicles that weigh about 74 mg (Reuter, Nummela, and Hemiä 1998). Human ossicles, of course, are the smallest bones in the body, with the incus and malleus combined accounting for only 0.00008% of the total body mass (see Mason 2001; Lewis et al. 2006).

Golden moles (family Chrysochloridae) are blind insectivores endemic to Africa south of the Sahara Desert, primarily to South Africa. Individuals forage at night, apparently using only vibrational cues from their prey (Narins et al. 1997). Golden moles have specialized structures for hearing low-frequency sounds that correspond to the range emitted by their prey. Having no muscles or ligaments in the middle ear, which allows greater elasticity of the ossicles, decreases high-frequency discrimination and enhances reception of low frequencies. A complex hyoid apparatus that contacts the tympanic bulla (thin-walled ball-shaped portion of the temporal bone that surrounds the middle ear and its ossicles) could also be an adaptation for low-frequency conduction, but its function is still unclear. Regardless, the hyoid is not commonly in contact with the tympanic bulla in other mammals. Many, but not all, golden moles have a massive malleus (see Forster Cooper 1928), which can be 96.9% of the total mass of ear ossicles (Figure 3.2). The size of the malleus and other structures in the ears of golden moles appears to be related to whether or not they forage on the surface (von Mayer, O'Brien, and Sarniento 1995). In Eremitalpa the incus and malleus represent 0.1% of the total body mass (see Mason 2001; Lewis et al. 2006). Members of the genus Georychus, like Spalax, do not have hypertrophied ossicles, which suggests that more than one mechanism for seismic sensitivity is probable in fossorial mammals (Mason and Narins 2001).

Members of the Namib Desert golden mole, Eremitalpa granti namibensis, are unusual among golden moles in not having a permanent burrow
system. Instead they submerge themselves in the sandy substrate during the heat of the day, but emerge at night to forage on the surface, where they "sand swim" and dip their heads into the sand as they search for prey (Narins et al. 1997; Mason and Narins 2002). These golden moles have no external ear, but the malleus is greatly enlarged and the center of mass of the ossicles is displaced relative to the rotary axis in such a way as to enhance, rather than reduce, inertial bone conduction. In most mammals studied, the stapes is oriented in the horizontal plane, which would reduce the noise from bone conduction of vibrations from such things as vocalizations. This is not the case for golden moles that display sensitivity to substrate-borne vibrations. The massive ossicles appear to serve as inertial sensing masses, rather than as links in the chain from tympanic membrane to oval window: they do not move in phase with the

Figure 3.2. Left auditory ossicles of the desert golden mole, Eremitalpa granti. Note the hypertrophied head of the malleus. The stapes is shown disarticulated from the incus and is shown reconstructed from a damaged specimen.

motion of the rest of the skull. If exposed to vibrations in the vertical plane, the ossicles would bounce in such a way as to push and pull the stapes against the oval window (Mason 2003). When E. g. namibensis dip their heads in the sand, they more efficiently couple their skull with the substrate, and the combination of the enlarged malleus with the orientation and elasticity of ossicles should allow them to be especially sensitive to Rayleigh waves (with particle motion perpendicular to the surface, and thus vibrations that are vertically oriented) created by their prey's disturbance of the substrate (Mason and Narins 2002; Mason 2003). There are no known studies of intraspecific communication in the golden moles, and indeed, head drumming would likely injure individuals with such a hypertrophied malleus (Mason and Narins 2002).

However, members of the Chrysochloridae with similar low-frequency sensitivity could detect prey in much the same way as Eremitalpa (Mason 2003).

The Cape golden mole, Chrysochloris asiatica, has a different shape to the malleus head than that seen in the Namib Desert golden mole, and it appears to exhibit flexibility in the rotational axis of the chain of ossicles based on frequency of the vibrational stimulus. This condition would allow the Cape golden mole to be adapted for bimodal hearing, or detection of substrate-borne vibrations as well as airborne sound waves (Willi, Bronner, and Narins 2006).

Kangaroo rats of the southwestern United States appear to exploit the vibration channel in a different way. Dipodomys deserti, D. spectabilis, and D. ingens are mound dwellers found in different habitats (sand dunes, desert scrub, and grasslands, respectively), but when detecting vibrations from footdrumming, all three species first stand alert and then enter their burrow (Randall 1997). If the banner-tailed kangaroo rat, D. spectabilis, spends any time within the burrow it typically seals the entrance with soil. When this rat is in its sealed burrow, almost all of the power in the footdrumming signal perceived from an outside source is transmitted through the substrate as a vibration and then is radiated into the air of the chamber as airborne sound. This species has no specialized adaptations for detecting the substrate vibration directly, but its members do have "excellent low-frequency hearing with a threshold of 50 Hz at 55 dB SPL . . . and probably hear even lower frequencies at 60 dB" (Randall and Lewis 1997, 530). Most fossorial mammals have some sort of sensory hairs, and even the otherwise-naked
mole-rat (*Heteroecephalus*) has vibrissae that could sense substrate vibrations radiated into the burrow in the same way that *D. spectabilis* does (Mason and Narins 2001).

Footdrumming and very large middle-ear cavities are known in gerbiline desert dwellers, some of which also have an accessory tympanum and modified malleus (Lay 1972); although, vibration communication has not been studied in all of these rodents and clear responses of neighbors to footdrumming has not been observed (Daly and Daly 1975). "The smallest middle ear cavities are found in species living in the least arid environments, and the largest middle ear cavities are found in species that live in the most extreme desert regions" (Randall 1994a, 421). Of interest, however, is the absence of footdrumming, sensitivity to low frequencies, and enlarged middle-ear cavities in the genera *Notomys* and *Pseudomys* of Australia (Randall 1994a).

**Amphibians and Reptiles**

Modification of ear ossicles also occurs in amphibians and reptiles that are in direct contact with the substrate over much of their body surface. In caecilians (Order Apoda), salamanders (Order Urodela), and frogs or toads (Order Anura) of the Class Amphibia, as well as in snakes, amphibiaenians, and some lizards in the Class Reptilia, the stapes (stirrup), or columella, of the middle ear may be in contact with the shoulder girdle or skin (Hildebrand and Goslow 2001). This contact provides a connection between the substrate and the inner ear that would allow for detection of vibrations to be processed through the auditory-vestibular pathway. In salamanders a range of amplitude and vibration frequencies produced motion in inner ear fluids when the test animals were in contact with the vibration source over most of their ventral surface (Ross and Smith 1978). Amphibiaenians, which are burrowing squamate reptiles without external ears, could hear airborne sounds conducted from receptors in the labial skin via an extracolumella to the inner ear, but this labial system could also carry substrate vibrations if the individual held its face to the tunnel wall as *Spalax* does (Gans and Wever 1972). Chameleons in the genus *Chamaeleo* have a rather low sensitivity to airborne sound in comparison to other lizards, and within the genus there are significant differences in ear anatomy. Transfer of vibrations through the jaw to the stapes would be possible,
though not practical, in the arboreal *C. senegalensis* and *C. quilensis* (Wever 1968), as would transfer from other bones of the skull through the quadrate bone in *C. hohenii* and *C. jacksonii*, in which vibration transfer was more effective than the airborne pathway in the frequency range of 100–1000 Hz (Wever 1969).

The ear of the snake is actually quite different from that of lizards, and even though the two are often grouped together in discussions of neuroanatomy, the discerning reader will note that the literature cited is often exclusive to lizards. For example, the basilar papillae of the inner ear are fewer in number in snakes than those found in lizards or mammals, but the supportive cells are better represented in snakes than in lizards. There is no external ear in snakes, and the Eustachian tube is absent, as is the round window. Thus, the extratympanic pathway is the primary route to channel sound and vibration frequencies to the inner ear (Wilczynski, Resler, and Capranica 1987). Snakes can hear, but they rarely can hear frequencies above 500 Hz. A single ear ossicle, the stapes (columella), articulates with the quadrate bone via a small cartilage (Young 2003), and “the quadrate articulates with the mandible which is in contact with the ground” (Hartline 1971, 349). Thus, any vibrations of the bones of the lower jaw are directly transported to the inner ear via the columella/stapes (Figure 3.3).

Modern amphibians, the lissamphibia, appear to be the terrestrial vertebrates most sensitive to substrate vibration, at least based on the current empirical data. Salamanders and anurans without tympanic ears have a unique extratympanic adaptation, the opercularis system (Jaslow, Hetherington, and Lombard 1988), which consists of an opercularis muscle that originates on the suprascapula of the pectoral girdle and inserts on the operculum, a relatively large structure in the oval window of the otic capsule (Hetherington 1988). Thus, when individuals rest with their forelimbs on the substrate, the opercularis is held in a vertical position well suited to transfer information carried in Rayleigh waves, which have a largely vertical component (Hetherington 1988). Kingsbury and Reed suggested as early as 1909 (cited in Hetherington 1988) that the opercularis muscle carried vibrations from the substrate to the inner ear. Hetherington tested the opercularis system (OPS) in bullfrogs (*Rana catesbeiana*) by measuring reception of substrate vibrations while individuals were placed in a variety of postures before and after the opercularis muscle was removed. The
OPS is most effective as a vibration receiver of frequencies in the range of 50–75 Hz. Most of the energy carried as Rayleigh waves is at frequencies below the 100 Hz level, and this was the range most affected when the opercularis was removed. Although direct contact with the substrate obviously provides a pathway to the inner ear for some substrate-borne vibrations, those animals that typically hold themselves above the ground, resting on their forelimbs, are able to receive vertically oriented substrate vibrations, such as Rayleigh waves, via the OPS as the operculum is linked to the vibrating pectoral girdle (Hetherington 1988). However, it is possible that increased sensitivity to substrate vibration might not be as important to these animals as an improved potential to obtain directional information from substrate vibration by integration of signals from the right and left sides of the body, via the opercularis system (Hetherington 1985).

The vestibulocochlear, or auditory-vestibular, nerve also transmits signals to the brain from “nonhearing” organs of the vertebrate inner ear, and amphibians appear to have exploited these components in ways not known in other vertebrates (Jaslow, Hetherington, and Lombard 1988). The membraneous labyrinth of frogs (Jørgensen and Christensen-Dalsgaard 1991) and of salamanders (Salamandra or

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**Figure 3.3.** Generalized view of a dissected boomslang, Dispholidus typus, showing the spatial relationships of the stapes (S), quadrate (Q), and lower jaw (C).

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Triturus) and newts (Smith 1968) contain eight sensory surfaces: three semicircular canals, three otolith organs (the utriculus, saccus, and lagena), and the smaller basilar and amphibian papillae. The origins of the basilar and amphibian papillae are obscure, and these may actually be auditory specializations new to the Amphibia. The basilar papilla is not found in all amphibians, being restricted to all anurans but only to the primitive urodeles and apodans. The fossil record indicates the inner ear was present in the oldest-known vertebrates, the ostracoderms, and inner ear reception of high-frequency vibration has been documented in the lamprey. We have no information from functional studies of early bony fish, especially the living Sarcopterygii, and this seems to be a missing key before further progress can be made on this point. The homology of some of the inner ear organs, especially with respect to amphibians, is still under debate, and it is possible that some have dual functions. Even amniotes (reptiles, birds, mammals) may have a saccule that is sensitive to high-intensity sound or substrate vibration (McCormick 1988).

The saccule of the vertebrate inner ear's "nonhearing" apparatus is actually thought to be the hearing organ in teleost fish, but in humans and most higher vertebrates it is a linear-acceleration and head-orientation sensor that helps to maintain balance (Narins and Lewis 1984; Lewis and Lombard 1988). The saccule was confirmed as a substrate vibration sensor in a direct test that combined physiology and morphology of Rana catesbeiana (Lewis et al. 1982). It is thought to be the primary vibration signal receiver in the ear of frogs (Lewis et al. 1982; Narins and Lewis 1984), showing greatest sensitivity in the range of 10–250 Hz in Rana catesbeiana (Lewis and Lombard 1988) and also in sandfish lizards (Hetherington 1989), which show an elevated sensitivity to vibration. The saccule is the common element in amphibian pathways for channeling airborne and substrate-borne information to the brain, and "the volume occupied by it is approximately equal to that occupied by all of the anuran inner ear's seven other sensory organs taken together" (Lewis et al. 2001, 1186). The VIIIth cranial nerve in the white-lipped frog, Leptodactylus albilabris, shows acute sensitivity to vibration frequencies (Narins and Lewis 1984; Lewis and Narins 1985); however, all frog species probably show similar sensitivities (Christensen-Dalsgaard and Narins 1993). This sensitivity supports the hypothesis that the saccule of the ear is a sensor for seismic signals.
in these animals (Ashcroft and Hallpike 1934; Narins and Lewis 1984; Hetherington 1988) in the range of 10 to 80 Hz, whereas the amphibian papilla is responsible for sensitivity to vibration up to about 300 Hz (Christensen-Dalsgaard and Narins 1993).

In the grassfrog, *Rana temporaria*, 97% of the afferent saccular fibers are vibration sensitive (Christensen-Dalsgaard and Jørgensen 1988). However, vibration-sensitive fibers are present in both anterior and posterior branches of the VIIIth cranial nerve of the species (Jørgensen and Christensen-Dalsgaard 1991). These fibers in the anterior branch apparently innervate the saccule and possibly the utriculus. Those in the posterior branch probably innervate the amphibian papilla. The lagena, semicircular canals, and basilar papilla of the grassfrog do not appear to be vibration sensitive. In contrast, the saccule and lagena appear to be the vibration-sensitive regions of the inner ear in the bullfrog, *Rana catesbeiana*, and not the amphibian papilla or utriculus (Koyama et al. 1982). Thus, sensitivity to vibration frequencies up to 150 Hz appears to be important to anurans, but the mechanism employed to receive this information varies even among species in the same genus (Jørgensen and Christensen-Dalsgaard 1991). The amphibian papilla and saccule are sensitive to both airborne sound and substrate-borne vibration in *Rana catesbeiana* (Yu, Lewis, and Feld 1991), as is the lagena (Cortopassi and Lewis 1998). It appears likely that the amphibian papilla in *Rana pipiens* processes information from both tympanic and extr tympanic pathways (Wilczynski, Resler, and Capranica 1987), and perhaps “low frequency sound and vibrations do not appear to be distinct modalities in the frog. This enables the frog’s auditory system to receive sound-induced vibrations from the substrate or to respond to substrate-borne vibrations, and, conversely, enables the saccule to respond to (intense) airborne sound” (Christensen-Dalsgaard and Narins 1993, 661). *R. catesbeiana*’s saccular axons are mostly broadly tuned but are insensitive to frequencies below about 5 Hz, where noise in substrate-borne vibrations from the Earth is most concentrated (Lewis et al. 2001). The story of vibration reception in amphibians is thus a complex one, and we may find that at the lowest frequencies, it is the perception of a disturbance that is key, rather than whether it is processed through auditory-vestibular or somatosensory pathways.
Fish

When we speak of vibration signals, we are almost exclusively concerned with a solid substrate of soil or plant stems, and indeed, our knowledge of vibration signal reception in the auditory pathway is a study of organisms that live in intimate contact with soil or plants. Animals in a watery medium, however, may also have specialized ways of receiving vibration signals from the environment. Because the gas (or swim) bladder contains gases, it can act as a pressure receiver and thus is often considered to be a "hearing" organ. One of the most interesting morphological adaptations is the bridge of bony elements that connects the gas bladder of some fishes to the inner ear. These Weberian ossicles are derived from bone of the vertebral column, and they serve to transfer vibrations in the membrane of the gas bladder through a chain of solid bone to the ear, much as the ossicles of the terrestrial vertebrate ear do. Weberian ossicles are found in minnows, catfishes, and carp, and they vary in number from three to four. There appears to be no homology between these bones and the middle ear ossicles used in other classes of vertebrates. They represent a unique solution to the problem of acquiring information from the environment for those animals with no "substrate" on which to perch—animals that are surrounded by a watery medium with a density almost the same as their body tissues. Cods and herrings have a different solution, which is a pair of extensions of the gas bladder that reach forward to the skull, and thus they use a soft tissue pathway for conduction of vibrations from the gas bladder to the ear (Hildebrand and Goslow 2001). Connections between the gas bladder and the sacculus of the ear are seen in some fish. Gas bladders may be directly connected to the auditory bulla, spaced very near the ear, or at some distance from the ear (Hawkins and Myrberg 1983).

Not all fish possess gas bladders, however, and some appear to produce and receive substrate vibrations in much the same way as the subterranean blind mole-rat. In the mottled sculpin, Cottus bairdi, males actually hold their mandible to the substrate as they approach a signaling male. Females of the Lake Baikal sculpin have been observed to take the same posture as they approach a nest-building male (Whang and Janssen 1994).

The gas bladder of fishes is homologous with the lung of terrestrial vertebrates, and the pneumatic duct that connects the gas bladder to
the gut is likewise homologous with the trachea in air-breathing animals. An interesting connection has been found in the Puerto Rican frog, *Eleutherodactylus coqui*, between vibration of the body wall adjacent to the lungs and routing of signals to the inner ear from the lung (Figure 3.4; Narins, Ehret, and Tautz 1988). Lower frequencies (1 kHz) of sound associated with the “co” note of the Coqui call can enter the auditory pathway from the lung and will vibrate the inner surface of the tympanum, thus providing a mechanism to receive the advertisement call and locate the source (Ehret, Tautz, and Schmitz 1990). Hartline (1971) also proposed the lung as a potential receiver to channel vibrational frequencies to the brain in snakes.

The story grows more bizarre with recent research on the African clawed frog, *Xenopus laevis*, and its ability to receive vibrational signals underwater, including receiving and accurately orienting to a mating call in the frequency range of 1.5 to 2.5 kHz. This amphibian equivalent of the laboratory rat is rarely studied in a natural context, but we must

![Diagram](image_url)

**Figure 3.4.** Schematic diagram showing existing and proposed pathways for sound transfer to the inner ear in the “coqui frog,” *Eleutherodactylus coqui*. buc = buccal cavity, et = Eustachian tube, etp = extratympanic pathway (putative), la = larynx, lu = lung, n = nares, oc = otic capsule, tym = tympanum. The buccal cavity receives acoustic input from the contralateral ear as well as from the lungs via the larynx.

Adapted and reprinted with kind permission of the authors from Narins, Ehret, and Tautz (1988, 1511).
recall that it does have a natural habitat and niche, where the ability to send and receive signals underwater would be advantageous. The ear mechanism in *X. laevis* is unique among all other vertebrate ears described in the literature. Members of this species have a cartilaginous tympanic disk, instead of a tympanic membrane, and instead of deforming like a flexible drumhead, the disk responds more like a rigid plate. The columella/stapes is rigid and embedded in the tympanic disk. A key point, though, is that the middle ear cavities and Eustachian tubes leading from them are air-filled, even when the mouth is filled with water and the external head is surrounded by water. Further, the Eustachian tubes from either side meet in the median dorsal mouth in a recess that also fits to the larynx when the mouth is closed (Figure 3.5). A direct air-filled pathway between the lungs and the tympanic disk was not found because the coupling of the larynx to the joined Eustachian tubes could not be demonstrated, even though a physical

![Diagram](image)

Figure 3.5. Schematic diagram showing the air cavities in a submerged African clawed frog, *Xenopus laevis*, including the middle ear cavities drawn from a dental cement cast. L = lung, LAR = opening of larynx, MEC = middle ear cavities, R = recess.

connection is made. Nonetheless, water-borne vibrations are transferred to the lung and ultimately to the middle ear, probably in the pathway, environment to lung to middle ear, as seen in the Coqui. This pathway would probably not be useful for orienting to the mating call, but it would serve for other, as yet unknown, low-frequency (<1 kHz) receptions of signals. Regardless, the connecting, air-filled Eustachian tubes would allow the ear to act as a pressure difference receiver. Life in shallow, muddy ponds, where the cut-off frequency for transmission through the medium would be at least 1.0 kHz, would rule out use of the lateral line system for distance communication. Higher-frequency communication developed by *X. laevis* would be required, and these interesting adaptations in receivers make that possible (Christensen-Dalsgaard and Eleftheriou 1995).

**Somatosensory Adaptations in Vertebrate Animals**

A different sort of pathway for processing information from vibration involves our sense of “touch” rather than the sense of “hearing.” In this case frequencies propagated through the substrate, or the surrounding medium of air or water, are converted to action potentials by transducers in the integument or joints and carried to the brain via somatosensory pathways through spinal nerves, rather than via the vestibulocochlear nerve.

This pathway is a dark zone in our quest to understand how vibration is used in communication. We have teased apart the roles of mechanoreceptors in skin and joints in only a few taxonomic groups. The integument can distinguish sensations of touch, pressure, heat, and cold. Pain may merely be due to an overstimulation of a neuron pathway that would otherwise carry these other sensations. We do not know if the receivers for integumentary sensations are naked or encapsulated nerve endings for most vertebrates, and we do not understand the phylogenetic relationships among the encapsulated nerve endings of land dwellers, or even if they are exclusive in transmitting one type of information (Hildebrand and Goslow 2001). A firm idea of which receiver is most appropriate for decoding vibration signals still awaits the prodding impetus from the scientific community to seek out these answers. If we do not have strong inference about a receiver’s role, or even know how widely it is distributed in animal taxa, how can we expect to explain how it
accomplishes that role? In this case, the tools are available, but the questions have not been asked.

Humans

Humans, *Homo sapiens sapiens*, possess four anatomically and physiologically distinct kinds of cutaneous “touch” receptors that are sensitive to mechanical stimuli and not associated with hairs (Figure 3.6). These are in addition to nociceptors that allow sensation of heat or pain and musculoskeletal proprioceptors that provide us with information on limb and joint position. Meissner’s corpuscles (giving a sensation of flutter) and Merkel’s receptor (sensitive to a steady indentation of the skin) are both superficial sensors with well-defined receptive fields. Meissner’s corpuscles are found in the dermal ridges, or papillae, that give us our fingerprints, and Merkel’s receptors lie at the base of the epidermis. In the palm side of the hand, both these receptors are more localized and concentrated in the tips of the index, or forefingers,
middle fingers, and the palm. Additionally, Meissner’s corpuscles are rapidly adapting, which means that they respond to the beginning of a stimulus and perhaps also the end, as when someone is first touched and then the touch is ended. Meissner’s corpuscles do not continuously respond throughout the duration of a stimulus. Merkel’s receptors are slowly adapting receptors that continue to respond to a continuous stimulus. Deeper in the dermis are found Ruffini’s corpuscles (also sensitive to a steady indentation of the skin) and Pacinian corpuscles, which give us the sensation of vibration. These deeper sensors both have broader receptive fields for each neuron than the two more superficial ones, and thus localization of the stimulus is less precise. Pacinian corpuscles are rapidly adapting sensors and most sensitive on the palm side of the hand in the entire middle finger and the lateral half of the palm and base of the smallest finger. Ruffini’s corpuscles are slowly adapting sensors with greatest sensitivity in the palm side of the hand along the base of the thumb, the outer segment of the third finger, the base of the middle finger, and the entire index finger. Thus, the slowly adapting sensors would supply continuous information on touch (Merkel’s) and pressure (Ruffini’s) as the hand grasps an object. The rapidly adapting fibers would provide a fluttering sensation (Meissner’s) or a sense of vibration (Pacinian) when a surface was initially touched, and perhaps when the hand is withdrawn. In addition, the superficial Meissner’s corpuscles are most sensitive to low-frequency input between 5 and 40 Hz, whereas the deeper Pacinian corpuscles are more sensitive to a higher frequency stimulus in the range of 100 to 300 Hz (Johansson and Vallbo 1983). An experiment to compare stimulation of the skin with heat, cold, and vibration showed little overlap in processing signals for these different phenomena. Further, “[T]he sense of touch shows the most stable perceptions both with respect to spatial resolution and frequency bandwidth” (Eijkman 1989, 169).

Nonhuman Placental Mammals and Pacinian Corpuscles

Pacinian corpuscles (Figure 3.7) are apparently unique among mammalian touch receptors in that usually only one of these transducers leads to a single axon, instead of multiple end organs leading to one axon and then to the CNS. These receivers were first suggested as vibration receptors by Tait in 1932 (cited in Calne and Pallis 1966) based
on their distribution in the skin (especially in the palms and soles of the hands and feet), around joints, in the pancreas, and along blood vessels, nipples, external genitalia, and so on. Although earlier arguments were made that vibration reception represents a separate sensory modality, it may better be viewed as a "temporal modulation of tactile sense: the relationship is analogous to that between flicker and vision" (Calne and Pallis 1966, 742). From this perspective, cycle-by-

Figure 3.7. Simplified Pacinian corpuscle in longitudinal section, showing the single, unmyelinated terminal and layers of lamellae. Actual numbers of the more widely separated outer lamellae may be 39-40, whereas the inner lamellae are closely packed.
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cycle perception is lost as a perceptual image, whether it be visual or vibrational, is formed.

However, interpretation of substrate vibration in the cerebral cortex may be a complicated story. Similar to hearing subjects used as controls, a congenitally deaf subject responded to vibrotactile stimuli of the left hand in the range of 180–250 Hz by activation of the right primary somatosensory cortex (Levänen, Jousmäki, and Hari 1998). This same individual also showed activation of the left and right supratemporal auditory cortices, a pattern not seen in the hearing controls. Furthermore, the auditory cortex of the deaf subject responded to a deviant signal in much the same way that hearing individuals would respond to variations in audible tones. He was able to discriminate between two vibration frequencies via pathways in the auditory cortex. Further work by the same laboratory showed that sensitivity to touch was enhanced in congenitally deaf individuals, but the significant enhancement was in the ability to detect changes, or infrequent stimuli, in the context of a series of vibrations of constant frequency (Levänen and Hamdorf 2001). This ability to sense sudden tactile events, such as a loud noise that could not be heard, would perhaps alert one to danger in the environment.

This neural plasticity allows us to hypothesize that humans once communicated via substrate vibration when the Earth was quieter and there were no cell phones or televisions to provide us with 24 hours of news each day (O’Connell-Rodwell, Hart, and Arnason 2001). After the 2004 tsunami when thousands and thousands of humans died, the indigenous people living in traditional communities did not. The Andaman and Nicobar islands, which are home to five small tribal groups (the Shompens, Sentinelese, Onges, Jjarawas, and Great Andamanese), lie so close to the earthquake’s epicenter that the tsunami hit them almost immediately. We can only speculate on the mechanisms used by these people to respond to environmental cues because they tend to resist contact with the outside (Parker 2004). Members of the Jarawa tribe made contact with news agencies through an interpreter a few days after the tsunami to say that all 250 of their people were safe (Kenneally 2005). However, whether they used cultural knowledge or cues from withdrawal of the ocean, or even Rayleigh waves generated by the earthquake, we do not know. Members of the Moken people on the Andaman Sea coast of Thailand recognized the receded sea from culturally transmitted traditional
knowledge about tsunamis, while a ten-year-old British girl recognized
cues from a BBC film she had recently watched on the 1946 tsunami in
Hawaii (Gregg et al. 2006). Luther Standing Bear (1933) told us that el-
derly Native Americans choose to sit or recline on the Earth instead of
being separated from it, so that they can think and feel more deeply and
communicate with the life around them. It is fairly well accepted that
Native Americans were able to detect bison herds via the vibrations that
they produced and used this information in hunting (O’Connell-
Rodwell, Hart, and Arnason 2001). Whether the plasticity of the Homo
sapiens brain investigated in other contexts for the past 40 years (see
Bliss 1962; Bach-y-Rita et al. 1969; Bach-y-Rita 2004) allows for differen-
tial allocation of cortical space for interpreting vibration stimuli during
development, based on whether or not we use that sense in our daily ac-
tivities, is not known. Neither do we know whether modern humans pos-
sess the ability to tap the vibration channel if they ever find themselves
without other communications devices.

A phylogenetic context for this neural processing has yet to be firmly
established, even though in macaque monkeys (Schroeder et al. 2001)
and humans (Foxe et al. 2002) it has been shown that sound (auditory)
and vibration (somatosensory) events are projected to a multisensory
subregion of the auditory cortex of the cerebrum. Likewise, stimula-
tion of the interosseous nerve that carries impulses from Pacinian cor-
puscles in the legs of cats yielded action potentials in the cerebral cortex
that also tended to spread from the primary receiving area to adjacent
regions that received “projections from vestibular or auditory recep-
tors” (McIntyre 1962, 59). Central segregation for processing of infor-
mation from inner ear and mechanoreceptors is likely a primitive verte-
brate condition, and all jawed and jawless fish studied project signals
to separate regions of the brain. The pattern of projection in studied
cartilaginous and bony fishes is quite similar (McCormick 1988). This
area of research promises to uncover potential vibration communica-
tion pathways, including speculation on whether or not humans and
other primates are, or ever have been, capable of signaling in this way.

Pacinian corpuscles of mammals are 0.5–1.0 mm long, multilamel-
lated vesicles that might call to mind the layered appearance of an
onion when they are viewed under a microscope. These packets have
30–40 outer, cellular layers separated by fluid-filled spaces and tightly
spaced inner layers that surround a single, unmyelinated terminal of a
sensory neuron. The lamellae and fluid in between act as a high-pass filter that may serve to screen out mechanical "noise" from the environment. Because of this, Pacinian corpuscles are considered fast adapting and do not respond to steady pressure, as such. However, they help to play a tactile role in hands and feet (and tails of prehensile primates) as they respond to the beginning and ending of a stimulus. Pacinian corpuscles respond to frequencies in the range of 60–1,000 Hz, but the threshold for neural response is lowest for 200–300 Hz frequencies (McIntyre 1980). These receivers are found in joints and ligaments and in the interosseous membranes between forearm and lower leg bones, but also in muscle, in the abdominal cavity, and in skin. In addition, they have been found associated with the periosteum (the membrane covering bone) of the tibia in cats, where they are sensitive to vibration in the range of 50–800 Hz (Hunt 1961; Calne and Pallis 1966). Corpuscles from the abdominal mesentery of cats had a similar frequency response and were anatomically identical to those in cat limbs (Sato 1961). Cutaneous Pacinian corpuscles are often associated with footpads and have been found in the feet of most mammals, even in claws and hooves (Calne and Pallis 1966). Both Pacinian and Meissner's corpuscles have been found in large numbers in the elephant trunk (O'Connell-Rodwell, Hart, and Arnason 2001; O'Connell-Rodwell et al. 2006). Recently, Pacinian corpuscles in large clusters have been found in the dermis of the periphery of Indian elephant feet, with the greatest number in the anterior region of the forefoot and the posterior region of the hindfoot (Bouley et al. 2007). Pacinian corpuscles in the cat hindlimb were able to detect a low-amplitude vibration stimulus applied within an estimated distance of 5 cm (Hunt 1961). If the lamellae are removed from the terminus, the receptor ceases to be rapidly adapting. It responds to the same stimulus, but continuously, as a slowly adapting fiber (Loewenstein and Mendelson 1965).

The blind subterranean mole-rat, Spalax ehrenbergi, which has the auditory and behavioral specializations mentioned previously for detection of vibration signals, also processes information from conspecific vibrations independently of the ear via a somatosensory channel (Nevo 1990; Nevo, Heth, and Pratt 1991; Klauer, Burda, and Nevo 1997). Which is the primary channel, or whether both systems operate simultaneously, is not well understood and still under debate (Nevo, Heth, and Pratt 1991; Rado, Terkel, and Wollberg 1998). These individuals
possess unusual simple lamellated, or simple Meissner's, corpuscles in the skin of the flattened region, or rhinarium, of the head. These structures at the border between epidermis and dermis, in the papillae of the dermis, are thought to perhaps provide “a feedback control of rhythm, amplitude and frequency of head thumping” (Klauer, Burda, and Nevo 1997, 65). Thus, these mole-rats appear to be able not only to send and receive vibration signals but also to gather sensory input to monitor their own vibration signals. In addition, individuals have similar lamellated corpuscles, which might be Pacinian corpuscles, near the toes of all four feet that appear to allow them to detect self-generated seismic waves that reflect back to them from obstacles in their tunnel paths. The information gained in this way allows them to detour more efficiently around an obstacle and perhaps to maintain a consistent tunnel depth below the surface. This proposed “echolocation” mechanism utilizes vibrations created by head thumping, but percussions were single, repeated thumps (separated by 1–13 s intervals) in the frequency range of 250–300 Hz, in contrast to the rapid head drumming at an average rate of 4/s at 150–250 Hz of the social signal (Kimchi, Reshef, and Terkel 2005).

Vibration communication, or the use of vibration in any context, has not been confirmed in the star-nosed mole (Condylura cristata), but its interesting adaptation for tactile sensation (the star of its nose) at least opens the door to some speculation. This species lives in extensive tunnel systems in the wetlands of the eastern United States and Canada, and individuals have small eyes and reduced optic nerves. Surrounding its nostrils are 22 tentacle-like fleshy appendages (the star) that are in constant motion, touching the substrate and other objects, as the mole searches for prey. This star has been proposed as the most sensitive touch organ in mammals. Two and perhaps three complete copies of an electrophysiological map of the star were seen in prepared sections of the cortex of the brain in the primary and secondary somatosensory areas. The fleshy rays of the star are densely innervated. They are covered with over 25,000 mechanosensory structures, called Eimer’s organs, each with a number of primary afferent neurons. Eimer’s organs have been found on the snouts of every examined species in family Talpidae, but the difference is that most moles have no more than a few thousand Eimer’s organs around their nostrils. These specialized structures contain superficial free nerve endings, a
Merkel cell-neurite complex, and a basal encapsulated corpuscle. The encapsulated corpuscle does not appear to have the high number of lamellae seen in Pacinian corpuscles, but its presence at the base of the Eimer's organs appears to make the star-nosed mole a good candidate for investigation of vibration sensitivity, if not communication (see review in Mason and Narins 2001).

Marsupials and Lamellated Corpuscles

Lamellated corpuscles similar to Pacinian corpuscles have been found in the interosseous tissue between the hindlimb bones of a marsupial mammal, the wallaby (Gregory, McIntyre, and Prosk 1986). These have fewer lamellae but are otherwise quite similar to those found in eutherian mammals. These corpuscles are thought to function to alert individuals, and they would be especially useful to warn of approaching predators while the wallaby has its head down during grazing (Gregory, McIntyre, and Prosk 1986). Similar vibration receivers are found in the snout and bill of individuals of the remaining mammal group, the monotremes. The spiny anteater, *Echidna*, and the duck-billed platypus, *Ornithorhynchus*, might use vibration detectors to locate prey (McIntyre 1980).

Birds and Herbst Corpuscles

Birds have special Herbst corpuscles (Figure 3.8), named for the scientist who first described them in 1849, which are lamellated structures similar in structure, function, and location in the body to the mammalian Pacinian corpuscles. Herbst corpuscles are found in between the tibia and fibula in pigeons and fowl in strings of hundreds of corpuscles, and these strings have been described as more developed than the comparable Pacinian corpuscle aggregations in the cat leg (Skoglund 1960). A single nerve terminal is surrounded by lamellae, but the packets have fewer lamellae than Pacinian corpuscles and are much smaller: 150–250μm long, as opposed to 0.5–1.0 mm long. Herbst corpuscles are also sensitive to a wider frequency range of 20–2,000 Hz, with best detection at frequencies of 200–1,000 Hz (McIntyre 1980). In the duck these receivers could act as a warning device by detecting substrate vibrations generated by the approach of predators (Dorward and McIntyre 1971).
Figure 3.8. Simplified Herbst corpuscle in longitudinal section, showing lamellae (actually not more than 12) and twin rows of "sentinel" nuclei flanking the central, unmyelinated nerve terminal. Adapted and reprinted with kind permission of Elsevier and *Trends in Neuroscience* from McIntyre (1980, 203).

Like the wallaby, ducks have an aggregation of these corpuscles in between the tibia and fibula of the hindlimb, but they are also present in the wing (Dorward and McIntyre 1971) and in the bill, including "the dorsal skin, the palate and its bony tip" (Gregory 1973, 153). They are also found in the tongue and beak of woodpeckers (McIntyre 1980). In addition to their detection of vibration through the ground or the branch on which a bird is perched or of disturbances in air movements made by an approaching predator, McIntyre proposed a role for Herbst corpuscles as stall indicators because some are found at the base of flight feathers and could detect changes in air flow (1980). They could also function as proprioceptors useful in muscle reflexes (Skoglund 1960).

Reptiles and Nerve End Organs

Black snakes, *Pseudechis porphyriacus*, possess nerve endings that are coiled or encapsulated by a single layer... not lamellated like Pacin-
ian or Herbst corpuscles, but also not free nerve endings described in early work on other reptile groups (Prosk 1969a). Reports that Pacinian corpuscles first appeared in reptiles has been disputed, but even with no specialized nerve endings in the skin of the snake belly, frequency response of receptors was very similar to that documented for Pacinian corpuscles (Prosk 1969b). The most common end organs found in skin of the trunk of the black snake were “buttons” that appeared either hollow or solid, and sometimes highly coiled. Two specialized endings, called “touch corpuscle” and “club corpuscle,” were found on the skin of the head (Prosk 1969a). Snakes are known to respond to substrate vibration in the absence of airborne sound, but the detection mechanisms have not been worked out (Young 2003). Vibration receptors in the snake body wall are capable of responding to individual stimuli in the range of 30–500 Hz and perhaps to even higher frequencies, though not in a cycle-to-cycle fashion. Reptiles with legs have fewer of these receptors in the body wall, but they are numerous in the limbs in much the same distribution pattern as seen in birds and mammals (McIntyre 1980). The veiled chameleon, Chamaeleo calyptraeus, appears to detect vibrations from the substrate via receptors in the legs or body, but it is not known whether there is a link with the auditory pathway (Barnett, Cocroft, and Fleishman 1999).

Hardline’s (1971) work with the Boidae, Colubridae, and Crotalidae supports the evidence that snakes transfer vibrations from the substratge through the lower jaw and into the auditory-vestibular pathway. He found that vibrations under the head only led through the somatosensory channel if the amplitudes were unnaturally high. He further suggested that the somatosensory and auditory-vestibular systems in the snake “gather information about overlapping sets of stimuli, but neither of which seems to signal whether the stimulus arrived through air or through substrate” (Hartline 1971, 350). The auditory-vestibular system is more sensitive to substrate vibration than the somatosensory system. “It is remarkably sensitive to head vibration: at the best frequency, 1 Å peak-to-peak amplitude is suprathreshold” (Hartline 1971, 370). However, it is about 20 dB less sensitive than the human ear to airborne sound in the range of 200–400 Hz. The somatosensory system has a broader range of frequency sensitivity than the auditory-vestibular system. However, just as has been seen with cerebral-cortical projections in mammals, Hartline found that neural signals delivered
from both pathways led to the same region of the mid-brain, with projections from the auditory-vestibular system of these snakes leading to a region totally contained within that to which projections of the somatosensory system led (1971).

**Somatosensory Adaptations in the Phylum Arthropoda**

The somatosensory pathways of arthropods receive vibrational information channeled through a variety of receivers. In insects, all of these receivers are classified in the large group of mechanoreceptors, and sometimes our understanding of function does not allow us to clearly discriminate among the types of vibrational information being processed. Receivers can be classified as proprioceptors for processing information from body joints (scolopale joint receptors and campaniform sensilla), touch receptors for direct contact (surface hair sensilla), motion receptors to detect fluid flow around the body (hair sensilla or Johnston's organ of antennae), or vibration receptors (subgenual organs inside insect legs, campaniform sensilla, etc.) (Kalmring 1985).

Arachnids have their own peculiar array of vibration receptors, but spiders have no chordotonal organs such as those found in insects and crustaceans, and internal joint receptors do not function as subgenual organs. Trichobothria "are thin hairs (Gr. trichos, hair) articulated within and emerging from a conspicuous cup-like socket (Gr. botrium, cup") (Barth 1982, 85) similar in function to hair sensilla. "Slit sensilla may be thought of as biological strain gauges" (Barth 1982, 92) that are analogous to campaniform sensilla. Specialized arrangements of slits are found in the basitarsal compound slit sensilla (BCSS), the specialized vibration receptors of scorpions (Brownell 1977; Brownell and Farley 1979a,b,c), and the metatarsal lyriform organ, which serves as the primary vibration receptor in spiders (Barth 1982, 1997).

Hutchings and Lewis (1983) organized mechanoreceptor types based on morphology. The simplest, the trichoid sensillum, is "a hair-like projection of the cuticle situated in a membraneous socket which allows the hair to articulate with the body surface. The hair is associated with one or more neurons whose dendrites are inserted into the cuticle at one edge of the base of the hair. Movement of the hair causes deformation of the dendrites and the production of receptor potentials" (1983, 183). These sensilla can be sensitive to touch, particle flow
in the medium, high-amplitude airborne sounds, and substrate vibrations. Sensilla are found at high densities, for example, in cricket cerci (Hutchings and Lewis 1983), which are sensitive to low-amplitude, low-frequency fluid motion. These sensilla would be the contact or motion receptors of Kalmring (1985).

Campaniform sensilla are thin ovals of cuticle found in joints and at the base of wings, which are served by a single neuron that may have the dendrite covered by a cap, or scolopale (Hutchings and Lewis 1983). These are the proprioceptors of Kalmring (1985) and may have no role in detection of substrate vibration signals.

Chordotonal organs are complex receptors that exist singly or in groups of scolopidia. These organs are found throughout the body surface and are entirely subcutaneous. They can play a role in proprioception but may also detect airborne sound and motion (Hutchings and Lewis 1983). Subgenual organs (Devetak, Pabst, and Delakorda 2004), Barth's organs (Popper, Salmon, and Horch 2001), and Johnston's organs (Jeram and Pabst 1996) may be considered as specialized types of chordotonal organs.

Tarsal scolopidial organs are vibration receptors found in the waterboatman, or backswimmer, Notonecta glauca, whereas other mechanoreceptors in the tibiotarsal and tibiofemoral joints have not been characterized. This predatory aquatic insect rests on its back on the water surface and two legs are modified as hairy oars. Greatest sensitivity is to vibrations between 100 and 150 Hz, but they are able to detect surface waves in the range of 5 to 300 Hz. A receptor system at the tip of the abdomen contains sensory hairs in contact with the water that are most sensitive to wave vibration frequencies from 60 to 300 Hz (Lang 1980).

Subgenual organs are the primary vibration receptors of insects and are found in the cavity of the proximal tibia of each leg. The organ contains scolopidia and accessory cells and can be complex, with components variously arranged (Hutchings and Lewis 1983).

Comparisons of the suitability of all available potential receivers for communication using vibration as the signal channel are rare for any species. However, recent work with two species of green lacewings, Chrysoperla carnea and C. lucasina from Slovenia, used standard electrophysiology, histology, and gross morphology techniques to study all leg mechanoreceptors (Devetak and Amon 1997; Devetak, Pabst, and Delakorda 2004). Each species had campaniform sensilla and four
chordotonal organs: "the tarso-pretarsal organ, tibial distal chordotonal organ, subgenual organ and femoral chordotonal organ" (Devetak, Pabst, and Delakorda 2004, 164). The campaniform sensilla do not appear to be primary receivers for substrate vibration signals as reported for the Orthoptera. Their role is in monitoring body position and leg movements. The tarso-pretarsal organ of Chrysoperla is not sensitive to substrate vibration, as it is in Notonecta, and thus acts as a proprioceptor. The tibial distal chordotonal organ is also a proprioceptor not sensitive to substrate vibration, but full definition of its role warrants additional study. The femoral chordotonal organ in Chrysoperla appears to have a complex functional role. It is capable of detecting substrate vibration at close range but is less sensitive to substrate vibration than the subgenual organ, which appears to be the primary receptor for vibrational cues that hold biological significance in this genus. “The threshold values for the subgenual receptor cells occurred in the frequency range 1.5–2 kHz at a displacement near 0.2 nm and acceleration near 0.03 ms⁻²” (Devetak and Amon 1997, 435). The broader-tuned subgenual organ in Chrysoperla may act not only as the receiver for mating signals but also for vibrations from nearby predators (Devetak and Amon 1997; Devetak, Pabst, and Delakorda 2004).

Subgenual Organ

The subgenual organ was a focus of anatomical and physiological studies in the first half of the twentieth century and has been described for a number of insect species. This organ has been clearly identified as a transducer sensitive to substrate vibration, but also to high-amplitude airborne sounds below the frequency of 1,000 Hz (Howse 1964a). Two species of bugs in the Cydnidae (Hemiptera) with very low–amplitude airborne calls were shown as early as 1974 to respond primarily, if not exclusively, to substrate vibration signals, and the vibration receptors were experimentally isolated to a location in the legs above the tarsi (Gogala, Drašlar, and Blažević 1974). In bushcrickets, intermediate and subgenual organs of all six legs detect vibrations in the frequency range of 100 to greater than 5,000 Hz (Kalmring et al. 1997); however, the entire bushcricket body may serve as the sensing mass.

The structure of the subgenual organ varies across taxa, as does its sensitivity to substrate vibration (Figure 3.9). Not surprisingly, the cock-
roach, *Periplaneta*, showed the greatest sensitivity to 100–800 Hz vibrations of any of 16 representatives tested from six orders of insects. In fact the Orthoptera as a group were a couple of orders of magnitude more sensitive to low-frequency vibration than members of the Hemiptera, Hymenoptera, Coleoptera, and Diptera, even though a couple of taxa in the Lepidoptera showed responses similar to the least-sensitive Orthoptera (Autrum and Schneider 1948). Although more direct measurements of the cockroach subgenual organ's super-sensitivity do not support the conclusions of earlier work that thresholds were as low as “1/50 the diameter of a hydrogen atom” (Shaw 1994b, 1169), the SGO is still considered capable of detecting signals “similar to the displacement at auditory threshold of the basilar membrane of a guinea pig” (Shaw 1994b, 1180).

Howse (1962, 1964a) argued that the subgenual organ responds to rapid changes, or transients, in the intensity of a stimulus, or to “amplitude modulation of a harmonic stimulus” (Howse 1964a, 422) rather than to the steady state of hemolymph pressure within the leg that follows a stimulus. Its function is thus analogous to that of the Pacinian

![Diagram](image)

**Figure 3.9.** Schematic diagram of three proposed steps in the evolutionary transformation of a vibration-sensitive subgenual organ (SGO) into an auditory organ (AO). A = auditory stimuli, cm = covering membrane, α = chordotonal sensilla, s = spiracles, t = trachea, T = tympana, te = tracheal expansion, V = vibrations.

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corpuscle in vertebrates. The subgenual organ responds "not to steady-state conditions, but to phenomena that precede or interfere with the steady state" (Howse 1962, 457). In this way, the subgenual organ responds to vibration transients much as the insect tympanal organs do to pulses of sound (Howse 1964a) and supports the interpretation that "[T]he separation of a vibration sense from hearing is less justified in insects than it is in vertebrates" (Schwartzkopff 1974, 308).

More recent investigations into the sensitivity of the cockroach (*Periplaneta americana*) subgenual organ led to the interpretation that the same cells in the SGO respond directly to both substrate vibration and airborne sound. "It is suggested that the SGO may have arisen as a

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**Figure 3.10.** Subgenual organ (SGO) in the left metathoracic leg of the cockroach, *Periplaneta americana* (a) looking distally, and a scolopidium (b) showing one bipolar neuron encased in sheath cells (not to scale). The axons of the bipolar neurons enter branch 5r8e of leg nerve 5. Adapted and reprinted with kind permission of John Wiley & Sons, Inc., and *The Journal of Neurobiology* from Shaw (1994b, 1168).
vibration-detecting system that underwent later modification for enhanced sensitivity through its coupling to an expansion of the air-filled trachea of the leg (Figure 3.10), analogous to the auditory organs and swimbladder of some fish, and that access to this air pathway provided the crucial modification that pre-adapted the organ to detect airborne sound” (Shaw 1994a, 14).

The subgenual organ in the genus *Crysopeirida* has only three scolopidia, units composed of a bipolar sensory cell and two accessory cells: the scolopale cell and the cap cell (Devetak and Pabst 1994). The subgenual organ of the southern green stink bug, *Nezara viridula*, contains two scolopidia, each having one sensory cell (Čokl 1983; Čokl and Virant-Doberlet 2003). Extracellular recordings of vibrationally evoked spike potentials made from the leg nerve revealed the presence of a middle-frequency (MFR) and a high-frequency (HFR) receptor neuron, probably from the subgenual organ. However, these two receptor cells were not actually confirmed as being the two scolopidial cells from the subgenual organ. Both receptor neurons show best frequency responses in the range representing the dominant and basic frequency peak of conspecific vibration signals (Čokl 1983). The best frequency response of the MFR neuron also corresponds to the dominant resonance peak of vibrations induced in stink bug host plants, such as bean (Čokl et al. 2005).

In contrast the subgenual organs described for Orders Orthoptera, Lepidoptera, and Hymenoptera have many more cells, even if arranged distinctively (Autrum and Schneider 1948). *Crysopeira*, however, has a structure not found in the other taxa, called a velum (Figure 3.11), which is “composed of cell bodies of three cap cells, surrounded by the extracellular material” (Devetak and Pabst 1994, 255). The velum appears to be a loose diaphragm in contact with the inner wall of the leg and its trachea, and when the hemolymph filling that space vibrates, it likely sets up vibrations in the velum as well (Devetak and Pabst 1994; Devetak 1998). A similar velum has been found in five other genera of the Neuropteroidea: *Dichrostigma*, *Hemeroptus*, *Osmylus*, *Semidalis*, and *Sisyra* (Devetak 1998).

Parasitoid wasp females from two families, all of those tested from the Orussidae and five of 39 subfamilies of the Ichneumonidae, drum on substrates with their antennae to locate immobile prey in a form of echolocation called “sounding.” These females also have enlarged
subgenual organs to receive returning vibrations. As many as 400 scolopale cells are seen in each subgenual organ, which are so hypertrophied that the tibiae in which they are located are obviously swollen (Broad and Quicke 2000).

The organization of vibration sensors is not identical in all insect legs. For example, in the bushcricket, *Polysarces denticauda*, "the midleg receptor cells of the crista acustica, the intermediate and subgenual organs, have significantly lower-threshold values to vibratory stimulation than the foreleg receptors. This is especially pronounced in the case of receptor cells with tuning frequencies higher than 1,000 Hz" (Kalmring et al. 1996, 328). In this instance, the mid- and hindlegs lack the

![Diagram](image)

Figure 3.11. Subgenual organ in the mesothoracic leg of the green lacewing, *Chrysoperla*, composed of three scolopidia (S1–3) originating from the velum (V). SE = sensory cell, SC = scolopale cell, C = cap, CC = cap cell, DIST = distal, PROX = proximal, TR = trachea. Adapted and reprinted with kind permission of the Finnish Zoological and Botanical Publishing Board and *Acta Zoologica Fennica* from Devetak (.998, 90).
acoustic trachea and tympana that are found on the foreleg, which is more sensitive to airborne sound and less sensitive to substrate vibration (Kalmar et al. 1996). However, in the leaf-cutting ant, *Atta cephalotes*, it is the receptors in the forelegs that are 4–5 times more sensitive to substrate vibration than those in the mid- and hindlegs (Markl 1970).

The subgenual organ of the carpenter ant, *Camponotus ligniperda*, is representative of the Order Hymenoptera. The one feature distinguishing Hymenopteran subgenual organs “from all other scolopidial organs described so far, is the large extracellular cavity enclosed by the sensory units, the attachment cells and the non-cellular membrane surrounding the whole organ. The cavity is filled with filament-like structures, which are stained by a specific marker for hyaluronic acid, an acid mucopolysaccharide” (Menzel and Tautz 1994, 741) that is also “an important component of the receptor lymph space of insect cuticular sensilla” (741). The subgenual organ is separated from the haemolymph by a noncellular membrane, which may be porous but otherwise acts as a barrier (Menzel and Tautz 1994).

Video recordings made through the transparent cuticle of honeybees less than one day old revealed that the subgenual organ is “oscillating with and not in the haemolymph” (Kilpinen and Storm 1997, 315). The subgenual organ in honeybees is shaped like a hollow cone and suspended in a hemolymph channel, almost blocking it, between the cuticle and two tracheae. Instead of damping the oscillations of the subgenual organ, the haemolymph may actually enhance them (Kilpinen and Storm 1997).

In honeybees the subgenual organ is most sensitive to frequencies in the range of 300–600 Hz and is located in the proximal part of the tibia of all six legs. The subgenual organ is likely best suited to receive vertical vibrations, or those parallel to the long axis of the leg (Rohrseitz and Kilpinen 1997). Honeybees do respond to horizontal vibrations, but the stimulus threshold for horizontal vibrations is about 10 dB higher than that for vertical vibrations. This difference suggests that leg position of honeybees standing on the comb face is very important in predicting sensitivity to vibration signals (Rohrseitz and Kilpinen 1997), which is also true for scorpions (Brownell and Farley 1979b; Brownell and van Hemmen 2001) and fiddler crabs (Aicher et al. 1983).

The typical vibrations produced by honeybees on the comb face, however, are at frequencies and amplitudes that may not match the
sensitivity range of the subgenual organ: 15 Hz by waggling, 250 Hz from the thoracic muscles of dancers that vibrate their wings, and 320 Hz for begging hivemates soliciting from dancing returning foragers. Possible receptors for these lower frequencies might be found in other chordotonal organs in the proximal or distal joints of the tibia (Saudek, Tautz, and Lindauer 1996). However, Nieh and Tautz (2000) found that the 200–300 Hz vibration produced by dancers was "just at the detection threshold of the subgenual organ" (1579). They suggested that integration of signal reception among the subgenual organs of all six legs might allow for a cancellation of some comb noise but also that the signal need only be local in scope to effectively transfer information from a dancer to her hivemates.

Endemic tenebrionid beetles in the species Onymacris plana plana, Zophosis orbicularis, and Lepidochora discoidalis of the Nами Desert in Africa are highly sensitive to substrate vibrations produced by surface winds and conspecifics. These species live isolated in sand dunes, apparently burying themselves up to 10 cm below the surface to avoid harsh daytime conditions. Individuals buried 5 cm below the surface are able to detect conspecifics running along the surface. Individuals on the surface were able to locate buried male and female conspecifics, even though researchers detected no tapping vibrational signals such as those used by Kenyan tenebrionids (Zachariassen 1977; Kristensen and Zachariassen 1980) or those from North America (Tschinkel and Doyen 1976; Slobodchikoff and Spangler 1979; Pearson and Allen 1996) to communicate with mates on a nonsandy substrate. Onymacris plana males responded to frequencies in the range of 100 Hz to 5 kHz, with highest sensitivity between 500 and 1,000 Hz. Males of Z. orbicularis and L. discoidalis were even more sensitive, but female O. plana were 2.5 times less sensitive than conspecific males. When Onymacris rugaipennis and Physodemia globosa from the Kuiseb River bed were tested similarly for sensitivity to substrate vibration, they were less sensitive than the dune dwellers to a statistically significant degree (Hannah and Kirchner 1994).

Johnston's Organ

Johnston's organ is a specialized chordotonal organ in insects, discovered in 1855 in the second segment (pedicel) of the mosquito antenna.
and proposed as a potential receiver of airborne sound. Later work confirmed that males are able to detect near-field particle oscillations from the female song with the Johnston’s organ and use the decoded information from the signal to locate conspecifics for mating (see Göpfert, Briegel, and Robert 1999). The scolopidia in this organ are composed of three (or two in the Diptera) sensory and three enveloping cells. Different insect groups have between 30 and 5,000 scolopidia in the Johnston’s organ. “It has been shown to function variously, as a proprioceptor, hearing organ, gravity detector, air current detector or, as a detector of water currents in aquatic insects” (Jeram and Pabst 1996, 228). In the leafhopper Oncopsis flavicollis (Hemiptera: Cicadellidae), which produces airborne sounds but has no tympanal organs, the Johnston’s organ has been proposed as the airborne sound receiver (Howse and Claridge 1970).

The green stink bug, Nezara viridula (Hemiptera: Pentatomidae), has 45 single scolopidia in the Johnston’s organ and 7 scolopidia, three single and four located in pairs in scoloparia, in a “central organ” that lies within the Johnston’s organ (Jeram and Pabst 1996). This bug communicates with mates via substrate vibration signals while perched on plants, and the subgenual organs in all six legs are known to be sensitive to substrate vibration displacement velocities as low as $10^{-6}$ m/s. Campaniform sensilla and other chordotonal organs are also involved. However, when males are moving upwards on a plant stem in search of signaling females, they antennate both branches of a fork in the path (Jeram and Čokl 1996). They are known to straddle the forked branches and to receive vibration signals traveling down either as they determine which path leads to the female. However, the touching of the branches with the antennae led Ota and Čokl (1991) to hypothesize that Johnston’s organ might be sensitive to substrate vibration, as well as to near-field particle displacement. Electrophysiological experiments revealed that sensory cells in the antenna’s pedicel respond to vibration stimuli delivered by tungsten electrodes in the range of 60 to 200 Hz, which is the same as for Johnston’s organ sensory cells. Even though the responding cells were not positively identified as Johnston’s organ cells, most of the mechanoreceptors in the region of stimulus application did belong to the Johnston’s organ. These cells had a lower threshold when stimuli were applied parallel to the long axis of the flagellum, rather than perpendicular to it. The highest sensitivity was
seen at a stimulus frequency of 100 Hz when vibration displacement velocities were as low as $10^{-4}$ m/s, or much less sensitive than the subgenual organ in these individuals (Jeram and Čokl 1996).

Johnston's organ in the whirligig beetle (Coleoptera: Gyrinidae) is the receiver for surface wave vibrations. When the antennae are removed, and the Johnston's organs along with them, precopulatory production of wave vibrations does not result in mating, even in a population that had been actively mating before the manipulation (Kolmes 1985).

Slit Sense Organs

Slit sense organs are one group of a class of proprioceptors designed to measure displacement in arthropod exoskeletons, and they are analogous to campaniform sensilla that also play this role in crustaceans and insects. Slit sensilla, specifically, are only found in arachnids, but all the sensors in this class consist of a membrane covering a hole in the cuticle of the exoskeleton and a dendrite connected to the internal surface of the membrane. Any displacement of the membrane initiates depolarization of the dendrite and subsequent processing of information in the animal's nervous system. In the slit sensilla, the opening covered by the membrane is slit-like instead of rounded, and displacement perpendicular to the long axis of the slit provides the stimulus. Slits are found in the cuticle, mostly in the extremities, and they may be single or found in organized groups. The wandering spider, _Cupiennius salei_, has as many as 3,300 slits, most of which are not sensitive to vibration. However, the pair of single slits found on either side of the tarsus just behind the claw does respond to substrate vibration, and another slit is sensitive to far-field airborne sound (Barth 1982). In complete darkness, this spider is also known to walk on six legs while holding the front pair out to gather sensory information much like a blindfolded human would hold out his hands to keep from running into a wall (Schmidt 1997). Whether these legs pick up vibrations from tactile hairs or slit sense organs is not known.

_Basitarsal Compound Slit Sensilla (BCSS)_

The BCSS on each of eight legs allows the scorpion _Paruroctonus mesaeitis_ to detect Rayleigh waves caused by moving prey as the scorpion stands on the surface of sand. This array of eight slits, found at the anterior,
distal end of the basitarsus just before its joint with the tarsus, is especially well designed to detect the vertical displacement of Rayleigh waves. The two longest BCSS slits are oriented approximately perpendicular to the plane of displacement when the scorpion is in a hunting stance, and a pulse stimulus amplitude of 1 Å will excite the BCSS in 50% of the trials (Brownell and Farley 1979a). Each slit in the BCSS has two afferent neurons, and the six slits of each BCSS together have a total of 12 neurons "but only one or a few of these respond reliably to threshold levels of stimulation" (Brownell and van Hemmen 2001, 1231). Other single and grouped slit sensilla that are located on more proximal leg segments are morphologically similar to those in the BCSS, but these are not known to be sensitive to substrate vibrations from prey. Neither do the variety of mechanoreceptors in the scorpion's distal leg segments, such as "hairs, bristles, pedal spurs and pretarsal claws" (Brownell and Farley 1979a, 24) respond to vibrations or provide information on source direction. When these tarsal elements were experimentally removed, there was no change in the ability of a scorpion to orient to a substrate vibration stimulus; however, damage to the BCSS in any given leg blocked the sensory channel for substrate-borne vibration source information on direction for that leg without any loss of mobility or ability to respond to direct touch (Brownell 1977; Brownell and Farley 1979a, b).

Scorpions integrate the information contained in prey vibrations to determine direction of the source when they assume a hunting stance (Figure 3.12). The eight legs of Paruroctonus mayoensis are arranged in a circle of about 5 cm in diameter (in adults) with each tarsus perpendicular to the soil. Input from more than four adjacent legs is required to accurately determine direction of the prey (Brownell and Farley 1979b). The fishing spider, Dolomides triton, maintains a similar posture as it rests on the water surface awaiting detection of vibrations from its prey (Bleckmann and Barth 1984). In contrast, the stance of the wandering spider, Cupiennius salei, is similar, but the legs are not arranged in an equidistant pattern. A much greater angle is seen between the third and fourth pair of legs when individuals assume an “alert” posture. Even though this spider turns toward a stimulus source in the direction of the stimulated legs sooner or at higher amplitude, "[T]he individual legs evidently do not contribute equally to the induction of this response. The turn tends to be in the direction of the most anterior legs stimulated" (Hergenröder and Barth 1983b, 364). Sensory
inputs from different legs have predictably different weightings, with the forelegs having heavier weighting, and inhibition is only directed toward the posterior of the individual (Hergenröder and Barth 1983b).

**Lyriform Organs**

Slit sense organs may be grouped together in the extremities of arachnids in parallel bundles of up to 30 slits called lyriform organs (Barth 1982). In the wandering spider, *Cupiennius salei*, the metatarsal lyriform organ is located dorsally on the distal metatarsal leg segment, in contrast to the placement of other lyriform organs (Barth 1997). About

![Figure 3.12](image)

*Figure 3.12. Arrangement of basitarsal compound slit sensilla (BCSS) receptors (outer circle) on the eight legs of the sand scorpion, *Paruroctonus mengensis*, in its alert stance and at angle $\gamma$ relative to the sensory field center. These eight BCSS innervate eight command neurons (inner circle), each of which has inhibitory neurons (only those for R3 and L2 are shown). This inhibitory triad model accounts for vibration source localization.*

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half of the 21 slits of this organ were tested for frequency sensitivity. Even though the organ is composed of slits roughly arrayed from long to short, from the most distal to the most proximal, they do not serve in frequency discrimination in the same way as the graded basilar membrane does in the organ of Corti of the vertebrate ear. Differences in sensitivity among slits may be up to 1.5 times at a given frequency, but only crude frequency discrimination is possible from the whole organ, and this is apparently due to CNS processing (Barth and Geethabali 1982). In some way the C. salei lyriform organs on the tibiae and femora are required for directional orientation. When a blinded spider with intact lyriform organs is chased away from its prey, it can successfully return 95% of the time. If the lyriform organs are damaged through ablation, C. salei cannot find the prey again and pass more than 10 cm away from it more than 67% of the time. What kinesthetic cues are received and transmitted by the lyriform organs are not known (Seyfarth and Barth 1972).

The slits of the metatarsal lyriform organ in spiders are homologous to the scorpion BCSS. They are located in a similar position and are also sensitive to vibration of the tarsus (Brownell and Farley 1979a). Slits are oriented perpendicular to the leg's long axis and are sensitive to lateral displacement, as well as to compression in the dorso-ventral plane. This means that the organ can detect vibrations traveling as either longitudinal or transverse waves (Barth 1982), and their sensitivity to displacement is in the range of 10–100 Å (Barth 2002). At least in Cupiennius salei, the metatarsal lyriform organ appears to function in proprioception, in addition to vibration detection (Barth and Geethabali 1982). The patellar lyriform organ described by Finck from the orb-weaver Araneus sericatus (1981) was raised in a papilla above the surface of the exoskeleton and resembled "a harp or marimba" (231).

Position of the legs is critical for efficient conducting of vibrations to the lyriform organs (Finck 1981), and the alert, or hunting, stance we see in scorpions (Brownell and Farley 1979b) and the fishing spider, Dolomedes triton (Bleckmann and Barth 1984), is reflective of this position effect. The displacement threshold for patellar lyriform organs in female Araneus sericatus differs by 224:1, depending on whether the leg is held close to the body or extended. This position-based threshold difference provides the spider with a mechanism to increase sensitivity or avoid noise just by changing the position of her legs. “A 100-Hz tuning
fork applied near a spider will cause her to pull the legs tight into the body. In this position the animal is remarkably insensitive to further stimulation. If, however, the fork is applied some distance from the spider (at the periphery of the web or some nearby leaves) she will extend her front legs as if to optimize the reception of silk-conducted vibrations” (Finck 1981, 292).

Male Cupiennius salei produce a substrate-borne courtship signal through abdominal (opisthosomal) vibrations that are grouped as syllables, and another through drumming or scratching with the pedipalps (a pair of leg-like appendages that lie between the first pair of walking legs and the jaws). The pedipalps produce broad-frequency substrate-borne vibration signals, which are always produced in between two opisthosomal vibrations. Natural drumming signals were detected by all tested slits of the metatarsal lyriform organ, even though the long and short slits were sensitive to different (and specific) frequencies and temporal components. However, no single slit was found to be narrowly tuned to frequency. It is thought that the pedipalpal drumming conveys information to the female on distance to the male. The opisthosomal vibrations, which have a narrower frequency range (60–100 Hz) than those from the pedipalps, preferentially stimulated long slits 1–3. These substrate vibrations provide the female with information necessary to recognize conspecific males, even from a distance, and only slits 1–3 respond to both low- and high-amplitude syllables (Baurecht and Barth 1992). Sensitivity to a broad amplitude range is at the expense of discrimination of differences in amplitude; however, absolute amplitude of the male signal is one of the least important of the vibration parameters in eliciting a female response (Barth 1997).

Female C. salei respond, even to synthetic signals, with substrate vibrations of their own, and the metatarsal lyriform organ “is narrowly tuned to both temporal and spectral characteristics of the male call” (Schüch and Barth 1990, 823). Even though with natural signals no sharp frequency tuning of any slit was found, when synthetic signal parameters were tested by varying only one parameter at a time, slit 11 (a short proximal slit) was found to be sharply tuned to a 500 Hz signal, but only when the signal was present at a suprathreshold level (Baurecht and Barth 1993). Likewise, when the relative importance of the pauses between syllable trains in the opisthosomal signal was examined, natural and synthetic signals elicited very different responses. If only
synthetic stimuli had been used, the responding group would not have been representative of the population as a whole, and data would be heavily biased (Schmitt, Friedel, and Barth 1993). This difference in response to natural and synthetic stimuli reinforces the necessity of using synthetic signals that fall within the range of behaviorally significant natural values for all parameters tested and of rigorously testing the synthetic signals before they are approved for any experimental design.

However, sharp tuning of each slit is not necessary for successful signaling between male and female *C. salei*. The opisthosomal component of the male courtship signal is narrow in frequency but does not decay much during propagation due to the leaf structure of the monocotyledonous plants on which individuals live. Animals that signal from dicotyledonous plants, which have netted veins, tend to produce a more broad-frequency courtship signal and may be found to have broadly tuned receivers. *C. salei* live and court only on monocotyledonous plants; therefore, narrow tuning to a narrowband signal that is propagated on a leaf with parallel veins should be highly adaptive.

The metatarsal lyriform organ is less sensitive to low-frequency vibrations in the range and at amplitudes typical of natural signals. However, its slits are highly sensitive acceleration detectors for events occurring within these frequency ranges (Barth 1982; Barth and Geethabali 1982). Thus, they (along with subgenual organs) act much like the rapidly adapting Pacinian corpuscles of eutherian mammals in being most sensitive to transients, or to the beginning and ending of longer signals. Higher frequencies are likely to carry information important to prey identification (Barth and Geethabali 1982).

*Barth’s Organ*

Members of the fiddler crab genus *Uca*, which live in sheltered intertidal zones, and ghost crabs, *Ocypode*, of open sandy beaches, both have specialized chordotonal organs called Barth’s myochordotonal organs. These receptors on each walking leg have a thin window in the exoskeleton, and vibrations in the window set up action potentials in bipolar neurons housed in soft tissues (muscle and ligament) that attach to the inner surface of the window (Popper, Salmon, and Horch 2001). It is possible that the window acts as a tympanum for airborne sound detection, but more likely the vibrations are carried through the exoskeleton for both genera, even though the window structure is rela-
tively larger in *Ocyopode* and some other decapods than in *Uca pugilator* and *U. minax* (Salmon, Horch, and Hyatt 1977).

Although the sensitivity range of the Barth's organ is above 300 Hz, the fiddler crab still primarily uses substrate vibrations to receive signals from conspecifics, which can be detected above background noise at a distance of 1 m. Ghost crabs, in contrast, are probably also sensitive to airborne sounds. Further, unlike scorpions, ghost crabs lose little vibrational sensitivity with loss of appendages (Popper, Salmon, and Horch 2001). Experiments that destroyed Barth's organ did not block all reception of substrate vibrations, and so other receptors are likely secondarily important in this communication channel in both genera of crabs (Salmon, Horch, and Hyatt 1977). However, the body position does play a key role in sensitivity to substrate vibration in *Uca pugilator*. Signals with frequencies in the range of 25–250 Hz are amplified through the legs when individuals (male or female) are in the upright stance that they typically take in response to a neighbor's rapping, but much less so, and over a broader range, in individuals resting with the body in contact with the substrate (Aicher et al. 1983).

*Sensilla (Hairs)*

Compressional (P) waves excite mechanosensory tarsal hairs of the scorpion and may allow an individual to estimate distance to the vibrational source. Ability to distinguish the distance of prey decreases with distance from the source, supporting the idea that distance cues are carried by the faster attenuating P-waves (Brownell 1977; Brownell and Farley 1979b,c). Vibration-sensitive hairs on the thorax of the noctuid caterpillar of *Barathra brassicae* can detect airborne vibrations in the range of 100–150 Hz and could detect a flying wasp predator more than 0.5 m away (Tautz 1977). However, hairs are less sensitive to substrate vibration than the BCSS in scorpions, with a stimulus of about 10 Å required to excite them in 50% of the trials (Brownell and Farley 1979a).

Decapod crustaceans have a large number of structures that act as mechanoreceptors: sensitive hairs on the body surface that detect low-frequency disturbances in the surrounding air or water, "hair fans" in a macruran decapod that are sensitive to substrate vibration and flowing water, recessed hairs on the chelipeds that are sensitive to acceleration of water-borne vibrations, and chordotonal organs in the joints and appendages that are sensitive to movement and stress as well as
substrate-borne and water-borne vibrations. Satocysts are not known to act similarly to those in vertebrates as particle motion detectors, but sensilla associated with the statolith appear to respond to vibrations in the statolith and are directionally sensitive. The Norway lobster, *Nephrops norvegicus*, responds in a predictable way to close range (up to about 90 mm) particle displacement in water-borne vibrations with thresholds near 0.9 μm in the frequency range of 20–180 Hz. This sensitivity to close particle motion is comparable to that of the fish lateral line system (Popper, Salmon, and Horch 2001). The semi-terrestrial fiddler crab, *Uca pugilator*, is sensitive to substrate vibrations with frequency components produced by rapping in three ranges: 30–60 Hz, 600 Hz, and 1.5 kHz. Salmon and Horch (1972) hypothesize that these three sensitivity peaks provide individuals with a long-range detection mechanism, as well as methods for estimating distance and direction, because of the differences in propagation of signals at these frequencies.

Some spiders have nondirectional hairs, called trichobothria, on pedipalps and on the tarsus, metatarsus, and tibia of all of the walking legs, which serve as particle motion detectors. The wandering spider, *Cupiennius salei*, can detect flies buzzing in the air at a distance of 7 cm with trichobothria. Two to four dendrites lead from the base of each hair, so that displacement of a single hair can provide information on stimulus direction. Trichobothria may occur in straight rows or groups with a gradation in length of hairs; however, frequency discrimination is not simply a matter of different lengths being tuned to different frequencies (Barth 1982). A difference in the importance of trichobothria may exist between spiders that live on a more solid substrate, such as soil or leaves, and web-dwellers. Whereas members of the genera *Cupiennius, Agelena, Sericopelma*, and *Pisaura* all have trichobothria distributed along the appendages as described above, the orb-weavers *Nephila, Zygia*, and *Araneus* have trichobothria "mainly found on the dorsal side on the proximal tibia, whereas the metatarsus carries only one trichobothrium" (Klärner and Barth 1982, 453).

Experiments exploring the roles of trichobothria and slit sense organs in *Cupiennius salei* revealed a complex CNS-level interaction between signal information transmitted from the two distinct receivers. Trichobothria are well known for their detection of slight air movements, whereas slit sense organs such as the metatarsal lyriform organ are substrate vibration receivers. When *C. salei* detects low-frequency vibrations
(3–4 Hz) that are typical of prey, predatory behavior is released, while higher-frequency vibrations (350–460 Hz) elicit withdrawal or escape behavior. Experiments with intact C. salet and others with the trichobothria surgically removed showed that input from the trichobothria can inhibit the release of predatory behavior in response to some substrate vibrations: “when both of the two receptor systems receive either a ‘prey-like’ stimulus or a stimulus eliciting withdrawal their effects add, but when the trichobothria receive stimuli ‘unlike prey’ they inhibit the approach reaction that would otherwise be triggered by substrate vibration” (Hergenröder and Barth 1983a, 347).

Mid-coxal Protuberance

Preliminary investigations of vibration communication in the fly genus Lipara have revealed a mechanoreceptor on the middle leg (2nd coxa) of both adult males and females. When female L. japonica perched on a reed stem were subjected to high-amplitude synthetic substrate vibrations, they actually raised their middle legs away from the substrate. If the mid-leg was cut between the coxa and trochanter, females failed to respond to the male’s calling song. No other substrate-borne vibration receptors have been described for members of the Diptera, where subgenual organs are not found (Kanmiya 2006a).

We thus see that even in vertebrates the senses of hearing and vibration may be truly distinct only at the perception level. Even when airborne information is carried via cranial nerves to the brain and substrate-borne information is carried via spinal nerves and the spinal cord to the brain, processing and analysis of the signals may be accomplished in the same or adjacent brain regions. “Moreover, the excellent agreement between predictions of theory and behavioral observations suggest that the neuronal mechanisms for perception of vibrational space will to some extent be similar to those used for localization in auditory space” (Brownell and van Hemmen 2001, 1239). At this time we do not have enough empirical data to support broad generalizations, and extrapolation is full of risk, but what we do know is intriguing. Further, even across widely divergent taxa, the primary vibration receivers appear to be fast-adapting sensors (in the sense of a differentiator) that provide information on transient events, or the beginning and ending of a stimulus. Pacinian corpuscles, subgenual organs, and the metatarsal lyriform
slit organs—in fact all the specialized substrate-borne vibration sensors for which empirical data exist—are fast adapting. Perhaps the conventional wisdom up through the 1980s, which held that vibrations were essentially just an alerting mechanism, was narrow in focus but not so far off the right path after all.
Sending Signals

Vibrations are initiated as an artifact, or incidental consequence, of almost any intentional motion by animals. Even the lightest impact of a body part with another structure, including another life form, will set up a wave of vibrations. We have only begun to examine how these incidental contacts came to be used as true communication signals, but the range of possibilities employed by animals and the relationship these actions have to other functions performed by individuals are intriguing. The hunting sand scorpion that was shown in the late 1970s to respond to Rayleigh waves produced by their prey has since shown evidence of intraspecific communication as individuals thrust the body forward, thump the tail, and wipe the tail across the sand. “In this way an evolutionary connection may be drawn between passive detection of vibrational information for purposes of orientation to food and the more evolved process of active signal generation for purposes of communication between conspecifics” (Brownell and van Hemmen 2001, 1229).

Vertebrate Signaling

Vertebrate animals with appendages use them to signal. They impact soil, or water, or other organisms with hands, feet, tails, and heads. Humans “knock on the door” before entering someone’s home, and the airborne frequencies alert others to their presence outside. At closer quarters we tap on someone’s shoulder, touch an arm, or lightly tap with our fingers on a surface that they are also touching, to privately
attract attention without making an audible noise. These vibration signals are typically not our primary mode of communication unless other channels are blocked to us, but they are an alerting mechanism to attract attention so that a visual or audible signal can be transmitted. Furthermore, very high-amplitude airborne sounds produced by vertebrate animals (such as lions, elephants, and the black rhinoceros), or even thunder, can impact the soil and initiate vibrations there that are propagated through the substrate (Ewing 1989; O’Connell-Rodwell, Hart, and Arnason 2001). In many cases it is difficult to determine which pathway the signals are traveling, or even whether they follow multiple pathways. Vibration-producing behaviors are familiar to us from observing all sorts of vertebrate animals, but documented cases of vertebrate signaling by substrate-borne vibrations are rare.

The first confirmed instance of vibration signal production by terrestrial mammals was in a rodent: the blind mole-rat, *Spalax ehrenbergi* (or *Nannospalax*, or *Nanospalax*) of Israel (Heth et al. 1987; Rado et al. 1987). Solitary, blind individuals have a flattened forehead that they bang against the ceiling of their burrow in the context of territorial display or mate location and advertisement. When individuals in the laboratory were placed in tubes separated by a 1 mm gap, so that they could receive airborne sound and olfactory cues but not substrate vibrational ones, they did not respond to neighbors by drumming with their heads. However, after the tubes were brought into contact, head drumming was initiated, including dueting in 72% of the pairs tested (Rado et al. 1987). Of interest is that even when territories are as close as 0.5 m in the field, tunnels never intersect, and thus head drumming may play a major role in maintenance of spacing in territories. These mole-rats appear to be aware of neighbors, and abandoned territories are occupied almost immediately (Heth et al. 1991).

Other incidences of vertebrate signaling have yielded additional empirical data. Drumming behavior of mammals using feet, head, and teeth has been studied in at least 32 species in 11 families, including foot-drumming in rabbits and “at least five species of elephant shrew” (Randall 2001, 1144). Although drumming appears to be more common in solitary than social species, it is seen in contexts including spacing and territory maintenance, coordination of mating, sexual and agonistic interactions, male competition, alarm signaling, and predator defense (Randall 1993, 1994a). Solitary Cape mole-rats, *Georychus capensis*, from
the Cape region of South Africa signal to conspecifics by drumming with their hindlegs from within their evenly spaced burrows. Both males and females footdrum and sometimes duet, but the male always initiates drumming (Bennett and Jarvis 1988). The substrate-borne vibrations produced by this drumming that are used in intraspecific communication appear to travel as Rayleigh waves, and it is hypothesized that drumming serves as a cue in maintenance of spacing and advertisement of territories. However, during the mating season, drumming is sexually dimorphic (Narins et al. 1992).

Drumming of the hindfeet on the ground has been described in Mongolian and Israeli gerbils and in woodrats, even if these behaviors are not known to produce functional substrate-borne vibration signals (Randall 1989). This footdrumming is a well-studied phenomenon in kangaroo rats in the genus *Dipodomys* and may have independent origins among allopatric species in North America. "Kangaroo rats produce footdrums in at least three ways. They hit one foot on the ground while standing on the other foot, alternate feet, or hit the tips of the hind feet simultaneously while balancing on the front feet and tail" (Randall 1994a, 418). Patterns can be simple or complex and appear to provide information important in spacing and avoidance of conflict with conspecifics. *Dipodomys deserti*, *D. spectabilis*, and *D. ingens* all footdrum in the presence of conspecifics and when entering or leaving their own burrows; however, *D. ingens* footdrums in the burrow in response to playbacks from all three species, whereas *D. deserti* does not footdrum in response to even conspecific playback signals, and *D. spectabilis* responds only to signals characteristic of its own species. The drumming patterns of all three *Dipodomys* appear to be species specific, but *D. spectabilis* exhibits individually distinct variation, while *D. deserti* shows no individual or sex-related signatures (Randall 1997).

A study of *Dipodomys hermanni* revealed an interesting social context to drumming. When an experimental pair included an adult male and female, only females drummed, and this was from within the burrow. The drumming was initiated when the male approached the female’s burrow, and he responded to her drumming by moving away. Four of the six males in this test had previously been observed to footdrum, but males are typically socially dominant to females. When an adult male was paired with a juvenile male, the juvenile drummed from within the burrow similarly to the females. However, when a female was paired
with a juvenile male, the juvenile was the only drummer. Again, drumming was from within the burrow upon approach by the female. Thus, a hierarchy of social dominance appears to trigger drumming behavior in this species, and the signal means something like "Leave me alone!" or "Get away from my home!" (Shier and Yoerg 1999).

The prairie spotted skunk, *Spilogale interrumpa*, in Iowa in the United States, also footdrums, but with the front limbs. This foot stamping is audible for distances of meters and is exhibited by disturbed animals prior to the better-known spraying of liquid musk (Crabb 1948). This behavior is perhaps an agonistic display, or "bluffing," used to deter predators or in other disturbing encounters.

White-tailed deer, *Odocoileus virginianus*, repeatedly stamp one front hoof, effectively drumming on the substrate with the forelimb, in response to disturbance or presence of a potential predator. Individuals appeared not to be signaling to the predator, but their behavior did alert nearby conspecifics that had been unaware of encroachment. Foot stamping was more often elicited in open areas, isolated individuals stamped as often as those in groups, and both males and females stamped. Although conspecifics did not flee in response to the stamping, preliminary conclusions are that foot stamping serves as an alarm call that alerts conspecifics to the presence of an intruder (Caro et al. 1995).

One of the most provocative lines of research has gathered data from elephants, where Rayleigh waves that appear to have been set off by vocalizations and other movements of individuals (O’Connell, Arnason, and Hart 1997) have been measured with geophones up to 120 m from the source (Arnason, O’Connell, and Hart 1998). Elephants are known to move toward distant thunder and thus find water after a rain. The working hypothesis from this research is that vibration signals are used in long-range signaling in elephants, where groups merge and then separate, to re-form after a period of time during which smaller groups are separated by great distances. Reuter, Nummelä, and Hemilä (1998) argue that their morphology could support this, and that perhaps “[L]ow-frequency surface waves could act as arousal signals over long distances” (1998, 1129). Asian (Elephas maximus) and African (Loxodonta africana) elephants emit a very low-frequency (20 Hz), high-amplitude (90–103 dB) “rumble” vocalization that is carried separately as airborne and substrate-borne vibrations. Both the vocalizations and “stomps” produced with locomotion travel through the
ground at a velocity consistent with their traveling in the form of Rayleigh waves (O’Connell-Rodwell, Arnason, and Hart 2000; Günther, O’Connell-Rodwell, and Klemperrer 2004; O’Connell-Rodwell et al. 2006).

Asian elephants bang their trunk on the ground in a number of contexts: following the birth of a calf, when a musth bull joins the herd, to threaten an intruder, or to test a pathway. This trunk banging produces an airborne component that can be heard at a great distance, possibly as air is expelled by the percussion event, but it would also produce substrate-borne waves (O’Connell-Rodwell, Hart, and Arnason 2001).

In controlled experiments with African elephants in their natural habitat in Namibia, O’Connell-Rodwell et al. (2006) played vibration signals to 11 different breeding herds while documenting their behavior. Airborne and substrate-borne vibrations inevitably occur together, and the airborne component must be masked in some way to ensure that the focal animal is not responding to an airborne signal. Yet one of the benefits of experiments with substrate vibration in the absence of airborne sound detectable by humans is that you can more confidently assert that the behavioral observations in real time were made without prejudice, because the human observers cannot detect the stimuli. However, it is very difficult to ensure that the animals being tested are not detecting and responding to an airborne cue. Herds responded by moving closer together in aggregations, orienting their bodies perpendicular to the direction of the stimulus, and exhibiting more vigilance. They also spent less time at the watering holes than did herds that were not manipulated (O’Connell-Rodwell et al. 2006). When wild family groups of African elephants were played familiar and unfamiliar substrate-borne alarm calls at a water hole, they responded to the familiar alarm with increased vigilance and decreased spacing. However, they did not respond to the unfamiliar alarm calls or controlled vibration stimuli (O’Connell-Rodwell et al. 2007).

Can elephants communicate with others via vibration over distances of miles so that they can rejoin their herd following a separation? Can they recognize their own family groups based on cues found in substrate-borne vibrations? Could vibration also account for anomalies in herding in other large grazing mammals, such as bison? This research is opening the door to answers to these questions and others. At this point, it has been demonstrated that elephants can detect and
respond to substrate-borne stimuli and that their vocalizations do propagate as substrate-borne vibrations, but whether they actually send and translate signals is still under study, as is the mechanism by which they are able to detect the stimuli (O’Connell-Rodwell et al. 2006).

The eastern grey kangaroo (Macropus giganteus) at Yan Yean, Victoria, Australia, produces signals by foot thumping. A typical thump consists of two pulses, the first at a frequency of about 650 Hz and the second at about 900 Hz (Bender 2006). These compare with substrate vibrations produced during locomotion, where feet impacting the ground in a hop produced a 2 Hz wave in the substrate with remarkably small variation seen in 465 recordings of individuals of different age, sex, and mass (Stewart and Setchell 1974). Only adults in the Yan Yean study produced thumps, and females were more likely than males to produce them before they attempted to escape from an intruder. Solitary individuals were more likely to produce thumps than those in groups of two, which were most often a female and her offspring. Multiple foot thumping was more likely at low-light levels than was fleeing without producing thumps. These observations support the conclusion that foot thumping in eastern grey kangaroos is directed toward the predator and not an alarm call to benefit conspecifics (Bender 2006).

Drumming, or foot thumps, in tammar wallabies (Macropus eugenii) in Australia is considered the most intense level of antipredator display (Blumstein et al. 2000). Individuals thumped in the presence of a variety of predator models but did not respond with thumps to playbacks of sounds of predator vocalizations. However, sounds of conspecific thumping did elicit an increase in vigilance and a decrease in foraging. This suggests that foot thumping serves at least as an antipredator, or alarm, signal to conspecifics, even though it may play additional roles, as well (Blumstein et al. 2000).

Our present understanding of social organization in marsupials, in general, is very limited, but the rule appears to be that association is most usual between members of a mating pair, and then only for a brief time. Herbivorous females manage to feed themselves and their young without help from the male, and only the kangaroos (of all studied marsupials) appear to be passively gregarious. Marsupial vocalizations are typically of low intensity, and described mostly from animals in captivity (Russell 1984). Anecdotal reports of drumming in many species, including the Tasmanian devil, Sarcophilus harrisii, and members of the
genus *Macropus* (Eisenberg, Collins, and Wemmer 1975), leave room for a potential role for vibrational communication in this understudied group.

- A brief note from England suggests that the coot, *Fulica atra*, slaps one foot in a drumming fashion on patches of vegetation near the water in an apparent alarm call that can be heard at least 100 m away by humans. Richardson (1982) observed this behavior when an individual was approached by a human, and even saw one swimming coot leave the water to foot-slap on land.

Signal production by reptiles has been studied less than the ability of lizards or snakes to locate prey through incidental vibrations. One preliminary study of the veiled chameleon, *Chamaeleo calyptratus*, however, revealed plant-borne vibrations that were produced when each of three males was presented with a receptive female. During typical courtship motions, males tilted or moved their heads in such a way that vibrations were produced in the stems on which they perched. Variation in these vibrations hinted at a potential repertoire of signals, but two particular groups had dominant frequencies at 156 Hz and 49 Hz. Males and a female also produced substrate vibrations when touched at the base of the tail, but females did not produce vibrations while being courted by a male. Chameleons appear to be particularly suited for communication via substrate-borne vibration; other members of the family have been reported to vibrate in response to touch, and head movement during courtship is also known (Barnett, Cocroft, and Fleishman 1999).

Snakes are not known to communicate at all via airborne sounds. Substrate-borne communication cannot be ruled out, however, because their major impediment to airborne communication is not a factor in vibrational communication: airborne sounds produced by snakes are at higher frequencies than the extreme of the range of the snake ear's sensitivity. Behavioral observations that snakes thrash and vibrate during agonistic displays leave open the possibility that they do communicate something like an alarm call via a substrate vibration channel (Young 2003).

One of the first reports of vertebrate signaling also convincingly linked the mechanism to context. The male white-lipped frog, *Leptodactylus albiflaris*, in Puerto Rico produces substrate-borne vibrations as he sings an airborne sexual advertisement song (in the frequency range of 1.0 to 2.3 kHz) to attract a mate. The male sings from the soil
surface, but instead of supporting himself in an upright position as many other frogs do as they inflate their vocal sacs, this frog partially buries himself in the soft soil and sings from a position in direct contact with the ground. As he sings, his gular pouch is thumped against the soil and sets up Rayleigh waves (at frequencies mostly between 20 and 70 Hz) that can be propagated at an amplitude detectable by conspecifics at distances of 3–6 m. Males in this population tend to cluster at nearest neighbor distances of 1–2 m, and thus are capable of receiving vibration signals from their calling neighbors. Some males in the population do not produce thumps as they sing, and these appear to be those that are calling from grass or loose gravel (Lewis and Nairns 1985). Likewise, during a prolonged dry spell no males produced thumps, but immediately after a rain, thumping males were once again common (Lewis et al. 2001).

Sending airborne signals to females and substrate-borne ones to males represents a bimodal form of communication that may be more common than fits our current worldview. The same action signals a distant female through frequencies that are received by her hearing channel, but nearby males receive and process vibration signals. Male _L. albifrons_ are known to be highly sensitive to substrate-borne vibration, and when simulated thumps were introduced near them, they responded with sounds associated with male-male interactions. Further, the vibrations detected during their advertisement calling are not just an artifact produced as the airborne sound waves impact the soil, but they actually appear to be caused by the rapidly inflating gular pouch (Lewis and Nairns 1985). When the airborne components of the calling signal are effectively masked, and that channel is unavailable for male assessment, the substrate vibration channel alone is sufficient to deliver a stimulus that elicits a response from a competing male (Lewis et al. 2001).

Another _Leptodactylus, L. syphax_ from Brazil, produces substrate-borne vibrations by drumming its forelimbs on the substrate. This drumming also produces weak airborne sounds audible to humans. The species does not drum in the process of either advertisement or aggressive calling, but it was stimulated to drum its forelimbs by playback of conspecific aggressive sounds. This species was found in dry areas of granitic outcroppings: boulders, sheets of rock, and a rock face where calling like the white-lipped frog would not be possible (Cardoso and Heyer 1995).
A provocative description of Andean frogs from Chile in the genus *Telmatobius* of the Leptodactylidae reports that individuals have a reduced vocal repertoire; however, the detection of substrate vibration signals was not part of the investigation of these relatives of the *Leptodactylus* species known to signal via vibration. Five species (*T. marmoratus, T. halli, T. pefluri, T. zapahuirensis*, and *T. peruviarius*) are found in northern Chile, while *T. montanus* is found in central Chile. In the high-altitude streams in which these frogs were found in the field, no vocalizations were ever heard. However, in the laboratory, individuals of the northern Chilean species could be induced to produce a low-intensity “contact” sound (dominant frequency about 600 Hz) and a higher-intensity alarm, or distress, sound (500–10,000 Hz with dominant frequency about 600–1,500 Hz). The greatest relative amplitude of the distress/alarm sounds was for 5–8 kHz frequencies. Two of the species, *T. peruviarius* and *T. pefluri*, also have a reduction in components of the middle ear that should render them incapable of detecting the higher frequency (above 1 kHz) alarm calls that they produce (Penna and Veloso 1987). Airborne signals would likely be less effective in the noisy stream environment in which these species are found; however, streams would be expected to produce a great deal of substrate-borne noise, as well. It would be interesting to determine whether individuals signal via substrate vibration, as their relatives in the genus *Leptodactylus* do, or whether they have overcome the constraints of their signaling environment in some other way. Because substrate-borne signals have evolved in other species of this family, it would not be grossly speculative to hypothesize that these quiet *Telmatobius* species signal similarly.

Signaling can also occur where the sender and the receiver are surrounded by water. We know very little about how nonmammals signal from underwater, and this represents a fuzzy area in our dichotomy of sound versus vibration signaling. One interesting, though understudied, area has to do with use of the gas, or swim, bladder in bony fish (Class Osteichthyes) to both send and receive signals. There are a variety of adaptations, assumed to be independently derived, to accomplish signal production through “drumming” of the gas bladder, and we know of more than 50 families of teleost fishes that use this channel. For example, the oyster toadfish *Opsanus tau* produces sounds as intrinsic muscles contract to rapidly change the bladder volume (Fine 1983). Harris is cited as recognizing in 1964 that “[S]ince it can
undergo volume changes, the organ can act as an efficient radiator of sound, acting in the simplest case as a monopole source” (Hawkins and Myrberg 1983, 365). Pearlfish in the Carapidae have muscular and skeletal modifications that allow them to drum the gas bladder, which they do when they encounter conspecifics. The first abdominal vertebrae have epipleural ribs that are in some way connected with the gas bladder: by ligaments or fibers or, in the case of the third pair, which is modified as a plate of bone, by actually merging with the tissue of the gas bladder. The bladder is also modified at the point of contact with the vertebral plate. Extrinsic muscles lead from the skull to the bladder, and they contract to pull the anterior portion of the bladder much like we might stretch an inflated balloon. Signals produced by the three species studied were distinct in frequency, with most of the energy emitted in the ranges of 80–440 Hz, 90–280 Hz, and below 600 Hz (Parmentier, Vandewalle, and Lagardère 2003). Production of gas bladder signals has been observed in the contexts of alarm calling, mating (where males typically signal to entice gravid females to spawn), and territory defense. As is the case with substrate-borne vibration signals of a number of the better-studied arthropods, gas bladder drumming signals of fish are discriminated more on their temporal qualities than on their spectral ones by conspecifics and mostly at close range (Hawkins and Myrberg 1983).

The mottled sculpin, Cottus bairdi, which has no gas bladder, uses a different approach to signaling under water. These fish produce substrate vibrations, mostly when a female approaches the nest that a male has constructed under large rocks in running water. Males produce three separate substrate-vibration signals that are associated with nest defense or sexual advertisement or both. Head nods are performed with their pectoral fins in contact with the substrate, but they also slap their heads against the sand of the bottom of the stream. Frequencies produced are below 200 Hz (Whang and Janssen 1994).

Arthropod Signaling

The great wealth of empirical evidence for vibration signal production comes from Phylum Arthropoda, which makes sense because more than 80% of all described animal species actually are arthropods (Greenfield 2002). Whether or not members of any other invertebrate phyla are able
to signal via the vibration channel awaits further investigation. Within the Arthropoda, vibration signaling is known from the Crustacea (fiddler and ghost crabs), the Arachnida (spiders), the Diplopoda (millipedes), and several orders of the Insecta: Plecoptera (stoneflies), Orthoptera (grasshoppers, crickets, katydids, etc.), Isoptera (termites), Psocoptera (book lice), Coleoptera (beetles), Hymenoptera (bees, wasps, ants), and Diptera (flies) (Markl 1969). The recent discovery of vibrational signaling via a tymbal mechanism in Hackeriella veitchi (Hemiptera: Cercorrhyncha), a Gondwanan relict lineage, suggests that vibrational communication is ancient in the Hemiptera (cicadas and hoppers, true bugs). This study provides evidence that tymbal vibration, as well as percussion and stridulation, had evolved by 230 million years ago in insects (Hoch, Deckert, and Wessel 2006). Spiders use a number of diverse vibration signals in broad ecological contexts (Uetz and Stratton 1982), employing mechanisms such as “by drumming with the palps and the abdomen, by stridulating, or by plucking threads of their own or other spiders’ webs” (Barth 1982, 67).

One of the earliest accounts of substrate drumming, or tapping with the abdomen, came from observations of book lice in the Order Psocoptera. Sounds audible to humans were associated with the tapping, which was exclusive to females and assumed to be a sexual advertisement signal (Pearman 1928). About the same time, termite (Reticulitermes flavipes) soldiers were noted to drum the substrate with their heads when disturbed. Although this action produces airborne sound that can be detected by humans with amplification, experiments indicate that termites are highly sensitive to substrate vibrations but do not hear airborne sounds well (Emerson and Simpson 1929). Ossiannilsson (1949) referred to the mating signals produced by tymbals of the cicada relatives (Hemiptera: Auchenorrhynca) in Sweden as “drumming,” but the substrate vibrations he described were not due to percussive events. Miranda (2006) uses the same terminology in describing a female signal, but throughout this book, unless otherwise noted, drumming refers to a behavior that produces vibrations by striking the substrate with some body part (i.e., footdrumming, rapping with appendages, tapping the abdomen or head, etc.).

One of the earliest empirical tests of substrate vibration resulting from stridulation as a potential channel for communication was with the grasshopper Chorthippus parallelus. Males were tested on hard-
packed soil and substrate vibrations were hard to detect, but within 6 cm of the sensor vibrations at 400–500 Hz were obvious. Previous observations had shown that females whose tympanal organs had been destroyed still responded to stridulating males (Haskell 1955). The stridulatory apparatus was described in predatory bugs in the Reduviidae as early as 1710, and by 1974 the laboratory group of Gogala knew that bugs in the Cydnidae could produce airborne sounds and substrate vibration, but it was the vibration that they used for communication. The Gogala group also noted that the vibration signals included frequency modulations, when previously only the temporal pattern and amplitude had been considered as important parameters in substrate signaling (Gogala et al. 1974). Within four years this group had published descriptions of male courtship and female acceptance songs, disturbance sounds from both sexes, and aggressive songs from all investigated groups (Gogala 1985b). Another rather early description of substrate vibration communication was in the terrestrial crab, *Gecarcinus lateralis*, which was reported to have distinct sexual signals, as well as aggressive and appeasing signals (Klaaßen 1973). In other words, the groups being investigated were using a repertoire of vibration signals, and sometimes substrate vibration was the primary channel for communication, even when airborne sound was produced as an artifact. Further, just as has been noted with airborne sound (Masters 1980), aggressive or disturbance signals are similar across taxa, but other substrate signals are species-specific, and mating mistakes are rare even in congeneric species living on the same plant (Gogala 1985b).

**Drumming (Percussion)**

Spontaneous sound production in decapod crustaceans is known only from the subfamily Ocypodinae, which includes ghost crabs in the genus *Ocypode* and fiddler crabs in the genus *Uca* (Clayton 2001), but the airborne components are probably artifacts of the production of vibrational signals (Clayton 2005). The male fiddler crab, *Uca pugilator*, has claws (chelae) of unequal sizes that are borne on an anterior pair of appendages called chelipeds. Males are known to wave the larger chela in courtship signaling to attract females. In addition, they set up substrate vibrations by drumming the large chela against the ground after waving it when a female is nearby. In the dark, when waving the
chela would be an inefficient mechanism for mate attraction, vibrations are produced from drumming the large chela, even in the absence of waving (Aicher and Tautz 1990). Rapping the substrate in ghost crabs appears to signal an individual's location, and thus could be used in both mate attraction and burrow spacing (Clayton 2005). Rapping occurs both outside and inside burrows, and is thus obvious to human observers, but female *U. pugilator* also produce substrate vibrations through body thumping, where they raise and lower the body and impact the substrate within their burrows after a nearby disturbance (Salmon and Horch 1972).

Drumming is a mechanism for producing substrate vibrations in a number of insect orders and is used in a variety of functional contexts. Alderflies in the genus *Stalis* drum with both abdomen and wings (Rupprecht 1975). Ants, especially in arboreal species in the genera *Camponotus* and *Polyrhachis*, drum (Kirchner 1997). Carpenter ants in the genus *Camponotus* produce a drumming signal by banging their mandibles (mouth parts) and their gaster (abdomen) on the substrate, usually in an alternating pattern. The signals produced by the drumming are much more effective inside the nest than outside, where the soil or tree trunk would act as substrate. Nests are constructed inside trees by hollowing out the spring wood to form thin sheets, or lamellae. Drumming on the thin lamellae produces signals with acceleration amplitudes as much as ten times higher than drumming outside the nest. Signals produced by drumming in the nest could theoretically be carried as far as 90 cm, whereas leaf-cutting ants on the soil surface can only signal up to 8 cm (Fuchs 1976).

Substratal drumming in North American Jerusalem crickets, which is diverse and species specific, has been the basis for studying systematic relationships in an extensive group that was once thought to be composed of a small number of widely distributed species. Species north of Mexico have no auditory tympana and are wingless. They drum on the substrate with the abdomen or thorax-abdomen unit, and signals are detected with subgenual organs. "Calling" drums are mostly species specific, are spontaneously produced by both males and females, and can be produced in duets. "Sex clarification" drums are nonspecies-specific signals produced only by males in species where the male and female calling drums are the same. The sex clarification drum is thought to signal male identity when the calling drum does not
specify the sex of the drummer, and it follows male detection of a conspecific drummer. “Courtship” drums are produced when two adults are within 6 cm of each other and are nonspecies-specific signals. Individuals may also tremulate or produce thoraco-abdominal stridulations. “Nymphal” drums are signals sometimes produced in duets by subadults. They are not always heard in both sexes, but these drums have the same pattern as adult calling drums, even though they do not elicit sexual responses from adults (Weissman 2001).

Wasp queens in the genus Polistes also appear to produce vibration signals by drumming, but they drum with their antennae, and the drumming is directed toward the rims of nest cells just before the queen delivers a liquid meal to larvae in the cell. In response, larvae lower the rate of their salivary secretions as they ready themselves to be fed (Pratte and Jeanne 1984).

Two undescribed species of Ametrus and Hadrogrylla in the Orthopteran family Gryllacrididae produce a defensive airborne sound by rubbing the femur across the abdomen, but a substrate vibration component of this sound was not detected. However, in these species with no airborne sexual advertisement call, both males and females produced vibration signals by drumming both hindlegs against the substrate. Rather than impacting the file and scraper used in defensive calls, individuals hold their legs away from the abdomen during drumming (Field and Bailey 1997).

The oak bush cricket, Meconema thalassinum, drums the substrate with one leg in a social context, but a vibrational component to the airborne sound has not been reported. This mode of signaling is unusual in the Tettigoniidae, where tegminal stridulation using a file and scraper is common (Sismondo 1980).

Spiders produce substrate vibrations by drumming with front legs, pedipalps (the pair of leg-like appendages between the front pair of legs and the jaws) and the abdomen (opisthoma), by stridulating and through tremulation (Barth 1982; Uetz and Stratton 1982). Male wolf spiders, Hygrocybosa rubrofasciata, in Finland signal to females during courtship by drumming their abdomen (Figure 4.1) against dry leaves on the ground (Rivero et al. 2000). However, Rovner (1975) was able to show that the drumming of pedipalps in the wolf spiders Lycosa and Schizocosa was not percussive at all. Rather, a well-hidden stridulatory device in the tibio-tarsal joint produced airborne sounds that could be
transferred through the palps to the substrate via stout spines that act as "holdfasts." This file-and-scraper mechanism was confirmed in an additional sibling species pair of *Schizocosa*, where almost identical devices are used to make signals different enough to reproductively isolate the species (Stratton and Uetz 1983). Anchoring of the palps may

![Diagram of signal length (ms) and pulse](image)

**Figure 4.1.** Oscillogram (a) and spectrogram (b) of a drumming signal of the wolf spider, *Hygrotycosa rubrofasciata*. Each vertical line in (a) corresponds to one pulse, which is produced by a single percussive event of the male's abdomen on the substrate.

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be required before sufficient pressure can be applied to the file and scraper of the tibio-tarsal joint. Regardless, females better orient to the substrate component than to the airborne sound produced during stridulation (Rovner 1975).

Male burrowing Uruguayan tarantulas in the species *Eupalaestrus weigenberghi* and *Acanthoscurria suina* also produce substrate vibrations during mating via body vibrations (with tarsal claws gripping the ground) and palpal drumming. Females of both species tap the substrate from within burrows after males signal. Experiments definitively demonstrated that substrate-borne signals alone elicit a female response, while airborne sounds alone will not. Use of an airborne communication channel could not be ruled out for *A. suina*, even though it appears to be less important than the substrate vibration channel. Based on observations and experimentation, substrate vibration signals in courtship appear to be the main communication mechanism for burrowing tarantulas (Quirici and Costa 2005).

Antennal drumming by wasps is also seen in an interesting behavior known as “sounding,” where the wasp female uses something like echolocation to locate deeply placed and immobile pupal prey (Broad and Quicke 2000). This was first reported in the parasitoid ichneumonid, *Pimpla instigator*, which specializes on pupae of the Lepidoptera. In this case, *P. instigator* females were tested with a lure made of a cigarette filter placed inside a thin paper sheath. They were always able to locate the filter by drumming on the paper surface regardless of its position in the sheath, irrespective of whether two filters were used instead of one, and without first seeing or touching the filter. However, use of thicker paper effectively blocked their ability to locate the lure (Henaut and Guerdoux 1982).

In the related species *Pimpla turionellae* (also known as *P. examinator*), which is a solitary parasitoid, there is a 15-fold variation in body size. Larger females can produce louder, or higher-amplitude, signals by antennal drumming, but the signal frequencies across three size classes were not significantly different. Larger females are more successful in locating prey, possibly because the resonating signal from the substrate is also of higher amplitude. Controlled experiments with this species helped to validate the findings of the Henaut and Guerdoux (1982) study because larger females were able to locate prey housed in the
heaviest gauged paper, whereas the medium-sized and smallest females were not. This finding suggests that larger females would be more successful at locating prey in a broad range of substrates, including thicker or denser substrates, than the smaller-bodied wasps (Otten et al. 2001).

Female wasps that use vibrational sounding as a mechanism for prey location have modified antennae with a variety of hardened structures that would enhance their drumming. They also have enlarged subgenual organs in their legs, seen externally as swollen tibiae, to receive the feedback from sounding; however, in some wasp species the hind tibiae are also enlarged in males, and a few wasps have females with enlarged tibiae without modified antennae. Vibrational sounding was only assumed for species where females had both modified antennae and hypertrophied subgenual organs (Broad and Quicke 2000).

Stridulation

Stridulation relies on friction for production of vibrations as body parts are moved against each other, and a variety of mechanisms are known from the Arthropoda. These vibrations of the body are simultaneously transferred to both the air and the substrate, but whether conspecifics use airborne or substrate-borne signal information, or cues from both, is often still not known. Spiders have as many as eight different types of file-and-scraper mechanisms, depending on the body parts involved, including abdomen-prosoma, appendage-appendage, appendage-abdomen, and adjacent surfaces in joints of a single appendage. These types of stridulation are used to produce airborne sound, which spiders can hear, but they also most likely produce substrate vibrations that may evoke stronger responses from females (Uetz and Stratton 1982).

Ghost crabs of the genus Ocypode in Onan stridulate as they move a file (pars stridens) on the inner surface of the larger cheliped across a scraper (pectrum) on the ischium of the same appendage to produce a rasping sound that typically terminates in a rap of the cheliped on the substrate. A ghost crab almost always produces rasping from within a burrow as another crab approaches (Clayton 2005). This stridulation is thus most likely produced in burrow defense to signal nearby intruders, and its airborne component may be more important than the vibrational one. The rasping is usually followed by rapping of the cheliped
on the substrate, which signals location of the individual over longer distances (Clayton 2005).

The file-and-scraper mechanisms vary across the five species of *Ocypode* that Clayton studies in Oman and contribute to species-specific vibration spectra. *O. sinensis* has no file apparatus and was not observed to produce rasps. In *O. platytaurus* the scraper is greatly reduced. Dominant frequencies are typically in the range of 250–270 Hz for *O. jousseaumei*, 400–500 Hz for *O. saratan*, and 570–580 Hz for *O. rotundata*. Rasps in *O. jousseaumei* and *O. saratan* include harmonic overtones, with up to 10 harmonic bands other than the dominant in *O. jousseaumei* (Clayton 2001).

A number of species of ants are able to produce both airborne sound and substrate-borne vibration through stridulation of a file-and-scraper mechanism located on the abdomen. Structures used for stridulation “occur mostly in species that nest in the soil and tend to be absent in species that nest in plants, rotten logs and leaf-litter” (Kirchner 1997, 274). In the leaf-cutting ant, *Atta sexdens*, vibrations of the exoskeleton are initiated as the “scraper attached to the posterior edge of the postpetiole moves across a striated file plate located on the first segment of the gaster” (Masters et al. 1983, 240, but see also Markl 1968). The ant abdomen is composed of the petiole, which attaches the abdomen to the thorax, and the gaster, which is the terminal portion of the abdomen. Each toothstrike of the file on the gaster creates a vibration event, and the gaster appears to be the primary radiator of the system. Energy in the radiated sound through air can be grouped into three regions: about 1 kHz, about 10 kHz, and above about 20–30 kHz (Masters et al. 1983). However, the soil is a different conduction medium where radiation of the low-frequency component of the stridulation sound would be emphasized over the higher frequencies (Michelsen et al. 1982, Masters et al. 1983). Further, one of the best-known contexts in which stridulation occurs in *A. sexdens* is when a worker buried by a nest cave-in recruits nestmates through stridulating. An individual signaling while surrounded by a solid substrate always produces a substrate-borne component when an airborne component is produced. In these circumstances, the nestmates do not respond to the airborne component. They rescue buried relatives in response to the alarm signal carried by substrate vibration (Markl 1967). Since *A. sexdens* is most sensitive to frequencies in the range of 50 Hz to 4 kHz, it is possible that an ant
stridulating underground would produce damped vibrations more within this range of greatest sensitivity, rather than within the range of the higher frequencies predicted in air (Masters et al. 1983). Frequencies carried as substrate vibrations do not exceed 6–8 kHz, and the intensity maximum is 1–3 kHz. "A soldier ant, covered by 1 cm of sand, can produce a peak-to-peak signal amplitude of 18 cm/sec^2 at the surface" (Markl 1968, 103).

The stridulatory apparatus of many dung beetles in the genus *Aphodius* (Scarabacidae) is an abdomen-alar organ, where the file is on the underside of the hindwing and the scraper (pectrum) is on the first abdominal segment. The substrate-borne vibrational songs of four species (*Aphodius pectoralis*, *A. sigmoides* and *A. rainieri*, native to North America, and *A. granarius*, introduced to North America) collected near Seattle, Washington, were species specific, as were the stridulatory organs. Substrate-borne songs were in the frequency range of 0.4–4 kHz for the four species. Both males and females apparently produce a disturbance vibration signal by stretching and contracting the abdomen, but only the male produces a substrate-borne courtship signal when he encounters a female on dung. The female does not reply to the courtship with a vibration signal (Kasper and Hirschberger 2005). Likewise, males of five populations of *A. ater* in Denmark, the Netherlands, and Germany produce a complex substrate-borne courtship song when they encounter females on dung. There is no long-range calling song, and females rarely stridulate, even though members of both sexes produce substrate-borne disturbance vibrations. Courtship songs of the members of all five populations contain the same structure and patterns, but a great deal of individual variation is present that could hold information useful to females in mate choice (Hirschberger 2001).

Hindwing-abdomen stridulation is also known from the platypodid beetle, *Platypteryx quercivorus*, which is a major pest of oak trees in Japan. Scrapers on the elytra differ between sexes, but males and females produce very similar stress chirps and spontaneous chirps. Thus, females produce three kinds of sounds, and males three, but only the preening buzz of the female and the in-gallery sound of the male are considered unique. Signals are audible to humans, but whether they are propagated to the receiver through air or substrate is not clear. The female’s buzz is produced with her forehead (frons) in contact with the male’s elytral declivity (Ohya and Kinuura 2001).
Psyllid bugs from Russia (Hemiptera: Psylloidea) stridulate via an abdomino-alar organ. File teeth are found on both pairs of wings and a scraper of teeth, or corrugations, is found on the meso- and metascutellum of the thorax. These morphological features were first described in the 1960s as "possible stridulatory organs" (Tishechkin 2006, 357), but no suggestion was made that they might be used in production of substrate-borne mating signals. Calling is accomplished with the wings held in a resting position against the body, but they are rapidly moved up and down. As with the European Aphodius species previously discussed, temporal patterning of the calling song can be variable within species but rather similar across species (Tishechkin 2006).

Triatomin bugs (Hemiptera: Reduviidae), which are haematophagous (blood-sucking) bugs of medical importance in South America as vectors for the trypanosome that causes Chagas disease, stridulate by rubbing the proboscis against a prosternal organ made of transverse ridges along a cuticular groove. Females of Triatoma infestans and Rhodnius prolixus produce copulation-rejection stridulations (Roces and Manrique 1996; Manrique and Schilman 2000; Schilman, Lazzari, and Manrique 2001), and both males and females produce disturbance stridulations. When the disturbance signals of these and three other triatomin species (T. sordida, T. guasoyana, and Dipetalogaster maxima) were compared, it was determined that "the vibrational signals of all species have similar frequency spectra and repetition rate, in spite of these species having different sizes and inter-ridge distances of their stridulatory grooves" (Schilman, Lazzari, and Manrique 2001. 174). It is suggested that these substrate-borne vibrations serve as a generalized signal to frighten or confuse predators, or to advertise their lack of palatability (Schilman, Lazzari, and Manrique 2001). The mate-rejection stridulations of both T. infestans (Roces and Manrique 1996: 20 attempts) and R. prolixus (Manrique and Schilman 2000: 61 attempts) are 100% effective in preventing copulation. How either of these signals is received is still unclear since triatomin bugs have neither tympanal nor subgenual organs. They do, however, have tibial scoloparia and campaniform sensilla, as well as trichobothria and Johnston's organs in the antennae (Roces and Manrique 1996; Manrique and Schilman 2000).

Male and female cerambic beetle (Hyletripes bajulus) produce vibrations by rubbing multiple parallel files on the mesoscutum (dorsal
plate of the middle thoracic segment) against a pectrum on the prothorax (anterior portion of the thorax that bears the first pair of legs). Vibrations are transferred from the prothorax to the prothoracic legs, which are straightened and stretched during stridulation, to the substrate. Stridulation has both an airborne and a substrate-borne component, but substrate vibration alone is sufficient to evoke responses in both aggressive and courtship behavior. In aggressive encounters, vibration from stridulation made the opponent retreat prior to contact in 70% of the trials. In courtship, a male transfers vibrations while in direct contact with a female to entice her to allow mating (Breidbach 1986).

Waterbugs, such as *Corixa dentipes* and *C. punctata* from Germany (Hemiptera: Corisidae), stridulate underwater by moving a file of pegs on the femur across a pectrum on the side of the head. The fundamental frequency of what is assumed to be a species-specific calling song used in mate attraction and location is in the range of 1.5–2.8 kHz. These animals spend most of their time underwater but are air-breathing. They are known for collecting a bubble of air from the surface and exchanging gases between their bodies and the air bubble as they respire after diving. Besides that held in their tracheae, the air available to a submerged corisid is “mainly distributed over the water-repellent ventral surface and between the elytra and the dorsal surface of the abdomen” (Theiß 1982, 227). Stridulation introduces transient pulses, or pressure changes, into the air bubble with each tooth strike of the file, and these pulses are radiated to the surrounding water from the air bubble. The air bubble “actually is the predominant oscillator” (Theiß 1982, 232), but it is more strongly damped than a typical free air bubble because it is bounded on half its surface by the animal’s body instead of the more easily displaced water. The pulses traveling through the water set up vibrations in the air bubble of a “listening” animal where damping properties are essentially the same because male and female corisids are approximately the same size and shape. The signal receiving organs would also lie within the air bubble and are thought to be the mesothoracic tympanal organs, which in *C. punctata* are sensitive to 2 kHz frequencies (Theiß 1982). Female *C. punctata* answer a male and duet with him by using the same stridulatory mechanism (Theiß 1983).

Stridulation in the Orthoptera is also known to produce both airborne and substrate-borne signals used in mating (i.e., Keuper and
Kühne 1983; Latimer and Schratl 1983); however, the bushcricket, *Ephippiger ephippiger*, produces this combined signal through stridulation and a completely separate vibration signal from movements described as drumming (Keuper et al. 1985), tremulation by drumming (Stiedl and Kalmar 1989), or tremulation, which is used in the same context as other nonpercussive substrate vibrations traveling as transverse waves that are produced by the Orthoptera (Morris 1980).

**Tremulation**

Katydid produce vibrations in plant stems through tremulations (Figure 4.2), or complex “silent” body oscillations that are intense enough to visibly shake plants and which propagate through plants as a signal (Belwood and Morris 1987, 65). “Insects are small animals and their tremulation is more likely to influence than woody plants. The relative mass of insect and plant organ and the muscular capacity of the insect and deformability of the plant must allow an efficient application of forces” (Morris 1980, 48). The neotropical katydid *Copiphora rhinoceros* of Costa Rica produces a sexual advertisement call that includes tremulation and stridulation in an alternating fashion. Rate of tremulation is affected by competition from nearby conspecific singers, but males advertise via the calling song even in the absence of females (Morris 1980). Tremulation is known from at least one species of false-leaf katydid, a group known for its “universal occurrence of file and scraper organs on male forewings” (Morris, Klimas, and Nickle 1988, 915).

Tremulation can be complex in some species, such as the pseudophylline katydid *Myopophyllum speciosum*, which is known from only one valley in the Andes of Ecuador. In the signaling of this species, a short and a long tremulation have different functional roles in courtship: short for distant (up to 1 m) and long for close courtship. Further, long tremulations are produced through two distinct actions: bobbing and rocking. The bobbing involves motion only in the vertical plane, like very rapid pushups, while rocking is more of a lunging, with the head downward, which also involves vertical displacement in an ovoid motion (Morris et al. 1994). Tremulation has also been observed under laboratory conditions in the false-leaf katydids *Melanomatus powellorum* (Morris and Beier 1982) and *Dociocercus chlorops* (Morris, Klimas, and Nickle 1988), even though any corresponding substrate vibrations were not measured.
Figure 4.2. Tremulation pulse from a *Conocephalus nigropileum* male: (a) oscillograph of two pulses, (b) one enlarged pulse from (a) showing the sinusoidal waveform of four oscillations (i–iv), (c) power spectrum of pulse from (a) 1=peak positive amplitude, 2=pulse duration, 3=inter-pulse interval.

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Vibrational signaling is known from a number of taxa of the Neuropteroidea, which is an older taxonomic grouping that included the related species of snake-flies, alderflies, dobsonflies, and net-winged insects such as lacewings and ant-lions (Devetak 1998). An early description of mating in the Coniopterygidae suggested an unknown pheromone might be involved in precopulatory behavior of both sexes, which was marked by elevating the abdomen and fluttering the wings (Johnson and Morrison 1979). Devetak (1998) lists this as a report of vibrational signaling, and Johnson and Morrison are very likely describing a sort of tremulation. Green lacewings in the Chrysopidae tremulate, and most energy in their songs is in the frequency range below 200 Hz (Devetak 1998). Stridulation is not common in green lacewings, and stridulatory structures for Meleoma, Brinchochrysa, and Chrysocera were described only from preserved specimens, so their function in airborne sound or substrate vibration production is not known (Brooks 1987).

Spiders also tremulate through low-amplitude oscillations of the legs and abdomen. A humming airborne component of the signal in the long-legged wandering spider, Heteropoda venatoria, lead Rovner (1980) to suspect that the behavior was analogous to the buzzing of winged insects. These spiders were collected either on the lower leaves of avocado, or on dried leaves on the ground immediately beneath. A male made downward jerks of his body while he stood with legs extended and body raised above the substrate, and while hair tufts on his claws anchored his legs to the substrate. A primary signal was accompanied by scrapes of the palps, but neither the abdomen nor the palps seemed to make any contribution to this essentially leg oscillation-induced vibration signal. Although this was the first report of a tremulation-like behavior in spiders, an earlier description of violent tremors in the body of the courting Australian huntsman spider, Isopoda immannis, was referenced (Rovner 1980).

The wandering spiders in the genus Cupiennius produce substrate-borne vibrations through dorso-ventral abdominal vibrations, or opisthosomal oscillations, that do not impact the substrate, as well as scratching or drumming by males with their pedipalps in a percussive signaling (Rovner and Barth 1981; Dierkes and Barth 1995). The opisthosomal vibrations alone are sufficient to elicit mating behavior from females (Schüch and Barth 1990). In male C. getazi, displacement of the abdomen varies from about 0.4 mm early in courtship to about 6 mm in the
latter part of the signal. A single muscle attached to the pedicel (Figure 4.3) was shown to function as a depressor of the opisthosoma, to contract only during courtship, and to account for both the temporal and spectral components of the vibration signal (Dierkes and Barth 1995). In *C. salei*, which like the others of its genus courts at night when ambient temperatures have dropped, parameters of both the male and female dorso-ventral vibration signals are temperature dependent. As is seen in other acoustico-vibratory signaling systems, temporal changes are seen with changes in temperature (i.e., cricket chirp rate can be used to approximate ambient temperature). Duration of series, interseries, and quiet periods decreased with an increase in temperature; therefore, the signal pace increased with temperature. However, the duty cycle, which appears to be a major cue used by females for mate recognition, varied with individuals but did not vary with temperature. Each female appeared to compensate by preferring signals from males that were produced at her current ambient temperature (Shimizu and Barth 1996).

Figure 4.3. Musculature of the pedicel (parasagittal section) of the wandering spider, *Caupiennius getazi*, with the double arrow marking the axis of the dorso-ventral opisthosomal movements. Adapted and reprinted with kind permission of Springer Science and Business Media and *The Journal of Comparative Physiology* from Dierkes and Barth (1995, 38).
Female planthoppers (Hemiptera: Delphacidae) signal on rice plants with dorso-ventral whole abdominal movements, called female abdominal vibration (FAV). These body movements do not involve any percussion, or drumming, and appear to transfer vibrations to the substrate via the tarsal elements (Ichikawa 1976; Claridge 1985). A female inserts her stylet into a rice plant stem and then bobs her abdomen. Mature virgin females perform the FAV, even when males are not present, but mated females or immature females do not (Ichikawa and Ishii 1974).

Male whiteflies (Hemiptera: Aleyrodidae) from Japan produce dorso-ventral oscillations by contracting thoracic muscles without wing movements. Substrate-borne vibrations have been recorded for 32 species in 18 genera. Males produce calling, courtship, and premating vibrations, but female response signals are known from only six species. Males have also been observed to drum their antennae, rock back and forth as in tremulating, and to produce wing flicks, but the study of vibration signaling in this group is barely ten years old (Kamniya 2006b).

Dorso-ventral abdominal movements are also seen in the wingless New Zealand tree weta, Hemideina femorata (McVean and Field 1996), H. crassidens (Field and Rind 1992; Clinit D. Kelly pers. comm.), and the rare H. ricta (Field 1993) of the Orthopteran family Anostostomatidae (formerly Stenopelmatidae). However, a clear link between this behavior and substrate vibration has not been shown for any of these species of large Orthopterans of the forests of the South Island. While H. ricta may occupy holes and crevices among rocks and fallen logs (Field 1993), both H. femorata and H. crassidens use galleries formed in hollowed out sections of tree trunks. These galleries are sites for diurnal refuge and mate location, while at night individuals are found browsing among the foliage (Kelly 2006). Males may produce a number of signals, including a defensive airborne sound by stridulation of the femur against the abdomen (Field and Rind 1992), but social signals are produced "by keeping all six legs on the substratum while rapidly oscillating the abdomen up and down against the appressed hind legs" (McVean and Field 1996, 102; Field 1993). A vibrational component was detected only for the defensive signal, even though a hypothesis was presented for the efficacy of social signaling via the dorso-ventral abdominal movements. Under experimental conditions, males could be stimulated to emit the defensive sound but not the social one (McVean and Field 1996).
Drumming of the abdomen has been confirmed as vibrational signaling in the related ground weta (\textit{Hemiandrus pallitarsis} and four undescribed species in the same genus). Males of all five species drummed to produce what appear to be premating signals, and one female \textit{H. pallitarsis} was observed to respond to the male signal with her own distinct abdominal drumming pattern. As in the tree weta, a defensive signal is produced, but in the case of \textit{Hemiandrus}, it is via stridulation, rather than dorso-ventral abdominal vibrations (Gwynne 2004).

Honeybee foragers in the multiracial species \textit{Apis mellifera} produce vibrations in the honeycomb as they dance after returning to the colony. Very low-frequency substrate-borne vibrations of about 15 Hz are produced as they waggle their abdomens, and frequencies of about 250 Hz are transmitted from their thoracic muscles as they vibrate their wings. Individuals stand on the rims of open cells of the comb and rock from side to side while sisters following their motion also stand with their tarsi on the rims, typically no more than one cell away from the dancer. Begging bees that attend dancing foragers also produce vibrations of about 320 Hz with thoracic muscles as they press them against the comb (Sandeman, Tautz, and Lindauer 1996). This vibration of flight muscles without actual wing movement is also known in bumblebees and stingless bees (Kirchner 1997) and is apparently the primary mechanism for vibration signaling in flies in the Agromyzidae and the Chloropidae, even though vibration communication is poorly studied in the Diptera and some recent reviews of the literature do not even mention vibration signaling in flies (Kamnitsa 2006a). No vibration has been documented when the East African gryllid \textit{Phaeophilacris spectrum} produces infrasound via “wing flicks” in the absence of any file-and-scaper mechanism on the forewings (Kämper and Dambach 1979), but the behavior is similar to that seen in other taxa where vibration signals have been confirmed.

**Buckling of Tymbals**

Male cicadas worldwide are best known for their loud airborne signaling using buckling tymbals, which are thin exoskeletal membranes located dorsally or dorso-laterally on the first abdominal segment and associated resonant abdominal air sacs. The abdominal air sacs can be broadly tuned in species where signals are complex, or they may be narrowly
tuned to the tymbal's natural frequency. Tymbals are also well developed in other groups, such as the non-cicada Auchenorrhyncha of the Hemiptera (Figure 4.4): leafhoppers, treehoppers, froghoppers, and planthoppers (Shaw, Vargo, and Carlson 1974; Shaw and Carlson 1979; Claridge 1985), other bugs in the Hemiptera and some tiger moths (Claridge 1985). The seminal work on signaling in cicada relatives is that of Ossiannilsson (1949), which describes tymbal anatomy for 79 species and signals produced for 96 species, as well as behavioral obser-

Figure 4.4. Adult male *Circulifer tenellus* showing location of tymbal mechanism: lab = 1st abdominal segment, da = dorsal apodeme, tb = tymbal sclerite, II–IV = abdominal segments.

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ulations for many of these. He also reviewed the pertinent literature prior to 1949, but commented that just as the tymbals and songs of the cicadas had been well studied, they had been equally poorly studied in the cicada relatives. Extensive searching for auditory organs in the Auchenorrhyncha has found none that corresponds to the cicada condition (Ossiannilsson 1949; Smith and Georgiou 1972; Mitomi, Ichikawa, and Okamoto 1984).

Two relatives of cicadas in the genus *Tettigonia*, *T. tomentosa* from Tasmania and *T. cribrata* from southeast Australia, represent relict survivors of a Mesozoic radiation that have only primitive tympanal auditory organs (Claridge, Morgan, and Moulds 1999). Male and female *T. cribrata* in New South Wales make slight dorso-ventral abdominal movements that appear to create substrate vibrations. Attempts to record vibrations from the bark on which they were collected were not successful, but low-intensity signals from one male in the laboratory were recorded. The assumption is that this primitive cicada is more closely aligned behaviorally to its much smaller leafhopper and treehopper relatives than to less primitive cicadas in the mechanisms employed in mate recognition and courtship. Thus, they appear to have retained a basic Hemipteran feature and their study could provide key information in sorting out phylogenetic relationships in their order (Claridge, Morgan, and Moulds 1999).

Males of the planthopper species *Nilaparvata lugens*, *Laodelphus striatellus*, and *Sogatella furcifera* have modified first and second abdominal segments (terga) that serve as a tymbal organ to produce substrate-borne vibrations (Ichikawa 1976). In *N. lugens* males, these two tergites are different in shape from the adjacent ones, and they are yellowish white, except for the center of the 2nd tergite, whereas all other tergites are darkly pigmented. A pair of dorsal longitudinal muscles (DLM 1) appears to play the primary role in producing vibrations via the tymbal mechanism, whereas two pairs of dorso-ventral muscles appear to be tensors, or accessory tymbal muscles. These observations suggest that the sound-producing tymbal of the cicadas and the vibration-producing tymbal of the "little cicadas" are not strictly homologous because the cicadas depend on the dorso-ventral muscles to buckle the tymbal. In the female, the comparable two abdominal segments are not different from their neighbors in color or sclerotization, and a number of muscle attachment sites present in the male are not seen. The invitation signal,
described above as a Female Abdominal Vibration, is most likely produced by contraction of the DLM 1, which is the principal tymbal-vibrating muscle in the male and a relatively large and powerful muscle in both sexes (Mitomi, Ichikawa, and Okamoto 1984).

Whereas the tymbal of the cicada features a sclerotized membrane that is much thinner than the cuticle surrounding it, the male beet leafhopper, *Circulifer tenellus*, has a thick sclerite surrounded by membrane, more like the condition in *Tettigonia tomentosa*, previously mentioned. In addition to the tymbal sclerites, dorsal apodemes are the only external evidence of the location of the tymbals. These dorsal apodemes, one of the shelf-like ingrowths of the exoskeleton of arthropods, are most likely attachment sites for the tymbal muscles or tymbal apodemes, which provide strength and support for those structures. “Contraction of the tymbal muscle causes the tymbal apodeme to pivot about its attachment at the dorsal apodeme and to produce an in-out click of the tymbal sclerite” (Smith and Georgiou 1972, 223). Females have a much reduced tymbal mechanism and associated musculature, which accounts for their much lower volume sounds (Figure 4.5). When individuals sing, contraction of the tymbal muscle causes the abdomen to jerk up and down (Smith and Georgiou 1972).

The tymbals of the potato leafhopper, *Empoasca fabae*, are also difficult to locate; however, the morphology appears to be similar to all the other *Empoasca* species that have been studied and similar to related genera studied by Ossiannilsson (1949). Shaw and Carlson (1979) noted that the logical candidate for a tymbal muscle, the dorso-ventral muscle homologous to the cicada’s principal tymbal-buckling muscle, did not insert via a tendon as has been described in cicadas and other Auchenorrhyncha. Instead, this muscle inserts on a tymbal sclerite, much as Smith and Georgiou (1972) described for the beet leafhopper. The dorso-longitudinal muscle proposed by Mitomi, Ichikawa, and Okamoto (1984) as the primary tymbal muscle was not described by either Shaw and Carlson (1979) or Smith and Georgiou (1972) in the species they studied. These observations, while not conflicting, point out that the homology and simplicity of the tymbal structures in the Auchenorrhyncha cannot be assumed and that further study is warranted. This conclusion is especially true in light of the observation that the *E. fabae* male’s courtship sound is not produced by the tymbal, but through what appears to be a sort of tremulation (Shaw and Carlson 1979).
Although the cicada, *Okanagana rimosae*, of North America does not have specialized structures for production of substrate vibrations, males produce loud airborne songs with a tymbal as they perch on woody plants. Vibrations with peak frequencies similar to the airborne song could be detected on the same branch as the male up to a distance of 60 cm. Males and females produce "wing flips" that might set up vibrations in more flexible stems, but the airborne song clearly contributes to a source-to-substrate pathway. No role in communication for these vibrations was established, but the information carried in

![Diagram of Cicada Anatomy](image)

Figure 4.5. Cross section of the 1st abdominal segment (1ab) and tymbal apparatus of an adult *Cicindela tenellus* male (A) and female (B): dlm = dorsal longitudinal muscle, fu = furca, fua = furcal arms, ta = tymbal apodeme, tb = tymbal, tem = tensor muscles, tm = tymbal muscle.

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these frequencies could be beneficial to mate location (Stötting, Moore, and Lakes-Harlan 2002).

Land bugs in the Cydnidae often use both a tymbal and a stridulatory apparatus to produce vibration signals, even simultaneously. The tymbal is formed by fusion of the first two abdominal tergites, and the edge of the first tergite can act as a scraper (plectrum, or lima) across which a file (stridulitrum) of the wing is drawn. Individuals in related taxa such as the Scutelleridae may have a file on the tibia that is drawn across the abdomen, whereas in the Reduviidae a special rostral plectrum and pectoral stridulitrum have been described. Additional signals produced while walking and head bobbing continue to be investigated in land bugs (Gogala 1985b).

Other Mechanisms

In addition to the drumming, stridulation, tremulation, and tymbal buckling through which most known arthropod vibration signals are produced (Ewing 1989), some more specialized mechanisms are used, and it is possible that additional mechanisms will yet be found to be commonly employed in vibration communication. In the cherry leaf roller caterpillar, Caloptilia serotinella, of New York in the United States, three vibrations have been documented: vibrating, which may be a form of tremulation but may also involve scraping of thoracic legs, scraping and plucking, both of which involve nondrumming contact between the mandibles and the leaf substrate. The larvae of this species construct leaf shelters on the black cherry, Prunus serotina, by attaching their spun silk to opposing portions of the leaf and curling it around them in a process that takes 4–10 hours. All three vibration events appear to be directed toward conspecifics for the purpose of spacing and territory maintenance, and staged heterospecific encounters with other caterpillars, wasps, or jumping spiders elicited no vibration signaling. Scraping is the most common signal, and plucking was seen associated with scraping. The tremulating, vibrating signal was used more at long range, whereas the scraping and plucking were seen in closer encounters (Fletcher et al. 2006).

The story is far from complete. We have mostly preliminary observations of vibration signal production for a small set of vertebrate and
arthropod taxa. However, success with revealing the use of such signals by related species, when we have ventured to look, suggests that this communication channel is widely employed and that animals incorporate a rich array of morphological and behavioral mechanisms in vibration signal production. The challenge is to explore the use of this channel more broadly to include more taxa, but also to include use of additional tools, such as the scanning electron microscope, as we examine processes. We must first identify the players, of course, before our questions can be framed within phylogenetic and ecological contexts. However, what we already know seductively promises that a gold mine of information is waiting for the right investigator, albeit a gold miner who carefully sorts and screens like a scientist.