

# Chapter 6

## Interactions Between Airborne Sound and Substrate Vibration in Animal Communication

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**Abstract** Airborne sound and substrate vibrations are communication channels inextricably linked through commonalities in signal production, propagation, and reception. Bimodal recordings of acoustic calls reveal that signal components in one modality often excite energy in the other and can thus be propagated to receivers via either channel. While studies of communication via airborne sound and substrate vibrations have proceeded largely independently of one another, the frequency at which these modalities co-occur and the number of receivers sensitive to both kinds of energy underscore the broad potential importance of interactions between the two communication channels. Nevertheless, only a handful of species are known to use bimodal acoustic signals. This chapter summarizes what is known about the interactions between airborne and substrate-borne signal components, discusses how interactions between modalities may shape the evolution of bimodal acoustic signals, and identifies outstanding issues in the field along with promising avenues for future study.

### 6.1 Introduction

Acoustic signals, such as insect and bird song, are used by a wide range of animal taxa and are recognized as key traits influencing important biological processes, such as mate choice and speciation (Bradbury and Vehrencamp 2011). Much of our understanding of the behavioral ecology of animals has come from the study of such signals. In many species, however, the function of “acoustic” calls and songs

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is likely more complex than generally assumed and may not be limited to a single communication channel.

The production of acoustic signals is a highly energetic behavior and unavoidably excites vibrations in both the fluid medium (air or water) surrounding the signaler and any substrate on which the signaler is resting (Caldwell et al. 2010; Fahy and Gardonio 2007; O'Connell-Rodwell et al. 2000; Stölting et al. 2002). No two other sensory modalities are so intertwined as audition and the perception of substrate vibrations. Airborne sound and substrate-borne vibrations are both generated by physical movement in the signaler's body, usually the vibration of specially adapted structures, both propagate as mechanical waves, and they are often transduced by the same sensory receptors. Only the paths and wave types through which they propagate differ.

The communication implications stemming from these differences and from what could be a particularly common form of bimodal communication, however, merit some special attention. While a handful of species have been shown to exploit both the airborne and substrate-borne call components (Hill and Shadley 2001; Latimer and Schatral 1983; Lewis et al. 2001; O'Connell-Rodwell and Wood 2010), the potential importance of bimodal transmission to the function and evolution of acoustic calls has generally been overlooked.

The purpose of this chapter is to make a case for further research into the interactions between airborne and substrate-borne components of acoustic signals, to provide a conceptual starting place for those studies, and to identify promising directions for this work.

Major questions regarding the interactions between airborne and substrate-borne components of acoustic signals:

- How commonly and in what contexts do airborne sounds and substrate vibrations interact during animal communication?
- Are airborne and substrate-borne components of bimodal acoustic signals largely redundant or do receivers extract different information from each component? What sorts of non-redundant information are encoded in each component?
- Do receivers of bimodal acoustic signals extract information from comparisons between the airborne and substrate-borne signal components?
- Do signalers facultatively alter the relative characteristics of airborne and substrate-borne signal components (e.g., the relative amplitude of each component) depending on behavioral context?
- What is the relative importance of acoustic energy that is coupled to either the air or a solid substrate directly via the signaler's body, and which propagates to receivers exclusively through this medium, as compared to energy which transfers from one medium to the other during signal propagation?
- What roles do the interactions between airborne and substrate-borne components play in the evolution of multimodal signals?

## 6.2 Examples of Bimodal Sound/Substrate Vibration Signals

Thus far, there have been very few studies on bimodal sound/substrate vibration communication, and only a few species have been experimentally confirmed to use such signals. These examples do, however, come from disparate taxa, and the signals they employ differ greatly in function, hinting at the hidden diversity of bimodal acoustic communication systems yet to be described.

### 6.2.1 *Katydids*

Male katydids (*Tettigonia cantans*) stridulate from low vegetation to attract mates. In addition to airborne sound, these songs produce substrate vibrations in the plant, detectable for up to 2 m (Keuper and Kuhne 1983). Male and female conspecifics approach the airborne component of this signal, but in choice trials where the source of the airborne component was difficult to localize, both sexes were more likely to walk onto branches through which the substrate component of the song was being played (Latimer and Schatral 1983). The airborne component of katydid stridulatory songs likely serves to attract mates from afar, while the substrate-borne component aids mates and rivals in localizing the signaler once they reach the plant. Results from bimodal playback to another katydid species (*Ephippiger ephippiger*) are consistent with the pattern of receivers using the substrate vibrations excited by acoustic calls to localize signalers on a plant (Stiedl and Kalmring 1989), although the latter study was not specifically designed to test this hypothesis.

### 6.2.2 *Mole Crickets*

Male prairie mole crickets (*Gryllotalpa major*) chirp from underground to attract flying females. These stimulatory songs produce a strong airborne component that is both amplified and coupled to the air with the help of an acoustically tuned burrow (Hill et al. 2006, but see also Bennet-Clark 1987). Stridulation also excites lower frequency seismic vibrations that carry to neighboring males. During playback, females responded to the airborne component of the advertisement call, but males did not (Hill and Shadley 2001, see also Walker and Figg 1990). When played a synthetic approximation of the call's substrate component, however, males responded by adjusting their call timing in a variety of ways (Hill and Shadley 2001). It appears that the two components of this stridulatory signal are used by different receivers. Females are attracted to the airborne sound, and males respond to substrate vibrations generated by their rivals.

### 6.2.3 *White-lipped frogs*

Male white-lipped frogs (*Leptodactylus albilabris*) call from moist ground to attract females. As in most frogs, these calls produce a conspicuous airborne component (1–3 kHz). When calling from a muddy substrate, however, males also produce impulsive, low-frequency seismic vibrations (‘thumps’, <150 Hz) as their vocal sacs impact the ground with each call (Lewis and Narins 1985). Bimodal playbacks reveal that in conditions of high-amplitude airborne noise, like those commonly encountered in frog choruses, males use these seismic thumps to adjust call timing, insuring that their calls do not overlap temporally with those of neighboring frogs (Lewis et al. 2001). Although it has been suggested that thump vibrations may influence spacing between signaling males, this has yet to be confirmed (Lewis and Narins 1985).

### 6.2.4 *African Elephants*

African elephants (*Loxodonta africana*) produce low-frequency alarm calls (fundamental frequency  $\sim 20$  Hz, dominant frequency  $\sim 40$  Hz) when predators are nearby. These calls excite intense airborne and substrate-borne components with similar spectral and temporal properties (O’Connell-Rodwell and Wood 2010). During playback trials, both components of the signal elicited defensive responses from other elephants. When played the airborne component, receivers became aggressive and fled the area (O’Connell-Rodwell et al. 2000). Responses to the substrate component were not as strong, but receivers did display defensive behaviors, such as grouping more tightly with troupe-mates and increased vigilance (O’Connell-Rodwell et al. 2000, 2007). For both call components, receivers appear to show a greater response to the recorded calls of familiar individuals than to the calls of elephants from other troupes, indicating that they are able to extract a considerable amount of information from both airborne and substrate-borne vibrations (O’Connell-Rodwell et al. 2000, 2007).

Both African and Asian elephants also produce intense, low-frequency “rumble” calls thought to coordinate group movements when separated by long distances (O’Connell-Rodwell and Wood 2010). Just as with alarm calls, rumbles excite strong airborne and substrate-borne components (Günther et al. 2004; O’Connell-Rodwell et al. 2000). Receivers respond to the airborne component when played alone (McComb et al. 2003), but it not known whether the seismic component functions as part of the signal.

## 6.3 A Comparison of the Airborne and Substrate-borne Acoustic Communication Channels

### 6.3.1 *The Production of Airborne Sound and Substrate Vibrations*

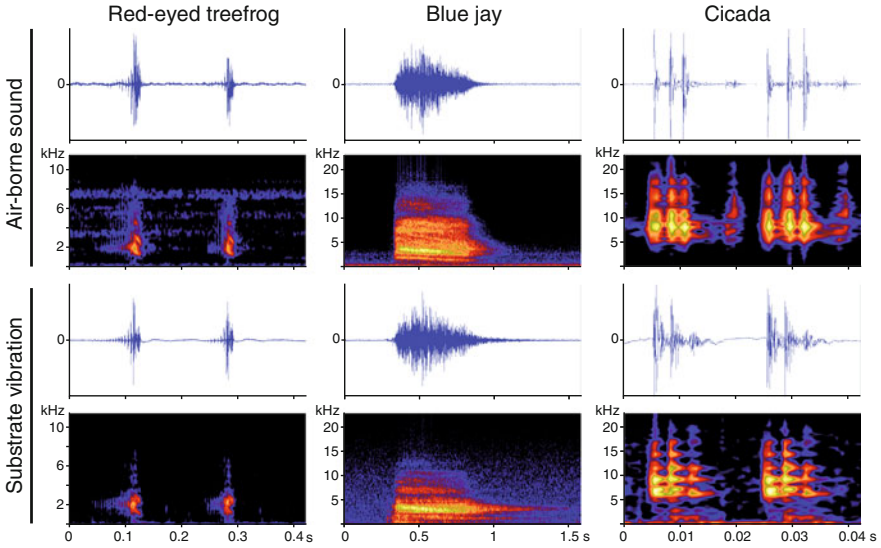
Animals have evolved a great diversity of mechanisms for the production of acoustic signals. Most arthropod species use exoskeletal stridulatory structures, tymbal organs, drumming on the substrate, or whole body tremulation to produce acoustic calls (Drosopoulos and Claridge 2005; Taylor and Patek 2010; Virant-Doberlet and Cokl 2004). Fish call either by stridulating skeletal structures, by drumming parts of their bodies against the substrate, or by muscular vibration of the swim bladder (Collin and Marshall 2003; Whang and Janssen 1994). In most terrestrial vertebrates, calls are generated by modulating the pressure of air flowing between body cavities through the vibration of a resonant vocal valve organ (syrinx or larynx) (Bradbury and Vehrencamp 2011). Drumming is also found across 15 families of fossorial and other mammals (Randall 2010).

For these vibrations to be useful acoustic signals, they must be well coupled with the air (or water), the substrate, or both signaling media (Bradbury and Vehrencamp 2011; Fahy and Gardonio 2007). While there has been considerable research on the function and structure of acoustic radiators that couple body vibrations to the air (Bradbury and Vehrencamp 2011), far less is known about how signalers effectively couple vibrations to the substrate (Hill 2008). Even less well-understood is how animals simultaneously couple energy to both modalities during the generation of bimodal acoustic signals.

#### 6.3.1.1 Schemes of Bimodal Acoustic Signal Production

Bimodal acoustic signals can be produced through three general schemes:

1. Airborne and substrate-borne signal components can be produced by the same structures and mechanisms. The bimodal acoustic stridulation signals of some katydids (Keuper and Kuhne 1983), mole crickets (Hill and Shadley 2001), some spiders (Rovner 1975), and the vocal calls of elephants (O'Connell-Rodwell and Wood 2010) are examples of this scheme. Some vocal calls produced by frogs and birds (Fig. 6.1; Caldwell et al. 2010), insect tymbal songs (Stölting et al. 2002), and drumming signals used by insects (Morris 1980), crustaceans (Taylor and Patek 2010), and mammals (Randall 2010) also employ a single mechanism to generate intense airborne and substrate-borne components. Although in many cases, it is not known whether these signals function bimodally.



**Fig. 6.1** Airborne sound and substrate vibration recordings of animal vocalizations. Shown are waveforms and spectrograms for airborne and substrate-borne vibrations excited by (1) The “double chuck” sexual advertisement call of a male *red-eyed treefrog* (*Agalychnis callidryas*) calling on a small sapling. The airborne component was recorded with a microphone at 1 m. The substrate component was recorded at 50 cm with an accelerometer attached to the plant. Noise at 4 and 8 kHz in the airborne sound recording is due to insects and other frogs calling in the same pond-side chorus, and is not present in the substrate recording. (2) The “scold” call of a *blue jay* (*Cyanocitta cristata*) perched on a thin wooden dowel. The airborne component was recorded with a microphone at 2 m. The substrate component was recorded at 30 cm with an accelerometer attached to the perch. Note the extended 4 kHz ring down in the substrate recording. (3) Excerpt of song from the *cicada* (*Okanagana rimosa*) resting on a twig elicited by electrical stimulation (adapted with permission from supplemental recordings published with Stöltgen et al. 2002). The airborne component was recorded with a microphone at 20 cm. A separate substrate component was recorded at 10 cm with a laser vibrometer focused on the twig

Tremulation may be the signal production mechanism least likely to excite an intense airborne component and thus the least common form of single mechanism bimodal acoustic signal production. Indeed, tremulatory signals are often described as producing no audible sound (Belwood and Morris 1987; Caldwell et al. 2010). Because tremulation does not benefit from the frequency multiplying structures of other signal production mechanisms, the upper limit of tremulation signal frequency is constrained by muscular physiology (Bradbury and Vehrencamp 2011; Hill 2008) and thus often limited to low-frequency ranges that for small animals are inefficiently coupled to the air (Bennet-Clark 1998).

- Airborne and substrate-borne components can be produced by the same set of structures but by different mechanisms. The seismic thumps of calling white-lipped frogs are a good example of this. Inflation of the frog’s vocal sac is

integral to the production of airborne call components, but this same structure also produces seismic thumps when it impacts the substrate (Lewis et al. 2001). Consequently, the two signal components have very different frequency and temporal properties.

3. Airborne and substrate-borne components could be produced by separate, independent structures. Multimodal signals involving components produced by separate structures are common in nature (e.g., Holldobler 1999; Narins et al. 2005; Partan and Marler 2005; Uetz and Roberts 2002). Males of the wolf spider *Schizocosa ocreata*, for example, include bimodal signals in their courtship displays, with visual components produced by the movement of decorated front legs, and acoustic components produced with stridulatory structures on the palps (Uetz et al. 2009). However, examples of this scheme for the production of purely acoustic bimodal signals are scarce (but see Stiedl and Kalmring 1989). It is possible that bimodal airborne and substrate-borne acoustic signals where both components are generated by the same structures are more likely to evolve than signals where each component is generated separately because both modalities are already inescapably excited by any single vibrating structure.

### 6.3.1.2 Asymmetry in Bimodal Acoustic Signals

While signals with conspicuous airborne components are likely to also produce intense substrate vibrations, the converse is not always true. In some situations, signals with conspicuous substrate components may not produce airborne components that are detectable at any useful range. Red-eyed treefrogs (*Agalychnis callidryas*), for example, produce several airborne calls that also excite strong substrate vibrations. Tremulatory signals produced by the same frog, however, produce only a substrate component, with no audible sound (Caldwell et al. 2010). This asymmetry is also seen more broadly among insects. As mentioned above, approximately 20 % of insects communicate with both airborne and substrate-borne acoustic signals. However, while a further 70 % of insects are thought to acoustically communicate with substrate vibrations alone, only about 5 % use airborne sound alone (Cocroft and Rodriguez 2005). At the heart of this asymmetry is the greater impedance mismatch between a signaler's body and the surrounding air than between that body and the substrate, which is often itself composed of live, or once living, tissue. Thus, many body vibrations are likely to couple more strongly with the substrate than they are to the air. Whether unimodal substrate-borne signals are less common for benthic animals in water, where the impedance of a signaler's body is more closely matched to the surrounding fluid medium, has not been fully resolved.

### 6.3.2 *The Propagation of Airborne Sound and Substrate Vibrations*

While both airborne sound and substrate vibrations propagate as mechanical waves, solid media support a greater diversity of wave types. Airborne and waterborne far-field sound signals travel as compressional (pressure) waves (Bradbury and Vehrencamp 2011; Cremer et al. 2005). By contrast, vibrational signals in solid substrates usually travel as boundary waves, with Rayleigh waves accounting for most ground-borne signals and bending waves accounting for most plant-borne signals (Markl 1983; Michelsen et al. 1982). Surface waves that propagate at the interface between air and water are used for communication by some aquatic animals. The mechanics of surface waves in water shape these signals in unique ways, but they can generally be considered a form of substrate vibration (Markl 1983).

#### 6.3.2.1 Propagation Characteristics of Each Modality

There are consistent differences in the global- and frequency-dependent attenuation characteristics of compressional waves in fluid media and those of boundary waves in solid substrates and liquids. In addition, solid substrates are often more structurally complex and spatially heterogeneous than air or water, which are each comparatively uniform in their effects on propagating signals (Markl 1983). Thus, the attenuation and degradation of substrate vibration components will be more variable than that of their airborne counterparts (Elias and Mason 2010). Each of these factors will strongly influence the function and evolution of bimodal acoustic signals (Table 6.1; Bradbury and Vehrencamp 2011; Cremer et al. 2005; Forrest 1994).

Mechanical waves traveling through solid substrates and at the air–water interface show more pronounced frequency-dependent filtering than compressional waves in fluid media (Markl 1983; Michelsen et al. 1982), with many substrates acting as low-pass filters (Cokl et al. 2007; Magal et al. 2000). The propagation of substrate vibrations can be further complicated by reflections, standing waves, changes in the axes of medium vibration, and spatial variation in the mechanical properties of the substrate. Thus, in some substrate types, most notably plants, amplitude does not always decrease monotonically with distance from the vibration source as it often does in air (Fahy and Gardonio 2007; Michelsen et al. 1982), and the transfer function of energy passing through the substrate between a signaler and receiver will depend, in complex ways, on the position of each animal.

While the speed of sound in air is fairly constant ( $\sim 340 \text{ ms}^{-1}$ ) and varies only slightly with temperature, pressure, and humidity, the propagation velocity of substrate-borne acoustic waves varies widely (phase velocities for acoustic communication signals in several substrates are reviewed in Virant-Doberlet et al. 2006) and is dependent on wave type, substrate density, substrate stiffness, and a host of



**Table 6.1** Comparison of the airborne and substrate-borne acoustic communication channels

	Airborne sound	Substrate vibration
Wave types	Longitudinal pressure waves, with minimal particle movement (far field)	Rayleigh and bending waves: particle movement is transverse with displacements normal to the surface of the substrate, and in the case of Rayleigh waves, also longitudinal
Spatial variability of transmission medium	Relatively homogeneous	Highly variable
Propagation velocity	Relatively constant within and across habitats	Highly variable: substrate vibrations used for communication generally travel more slowly than pressure waves in air, but velocities can vary greatly within a substrate and between substrate types
Active space	Large and predictable	More variable: Often smaller, with well-defined limits corresponding to the edges of the vibrating substrate
Global attenuation	Moderate and predictable: Loss due to spreading scales with the square of distance. Medium absorption is relatively low. Amplitude decreases monotonically with distance	Variable: loss due to spreading is negligible or scales in direct proportion with distance. Medium absorption is high. Amplitude often does not decrease monotonically with distance
Frequency-dependent attenuation	Weak frequency-dependent filtering	Frequency-dependent filtering can be substantial
Frequency dispersion	All wavelengths propagate at the same speed.	Propagation velocity often depends on wavelength
Energetics of production	For small animals, coupling of low frequencies to the air is inefficient	High frequencies often do not propagate efficiently through the substrate. High-frequency tremulatory signals are difficult to produce
Environmental noise	Variable, often high	Variable can be lower than noise levels for airborne sound in the same environment due to the smaller active spaces of many substrate vibration signals

other factors (Cremer et al. 2005). Unlike compressional waves, each wave type commonly used for substrate vibrational communication is dispersive, meaning that wave propagation velocity (phase velocity) varies with frequency. For Rayleigh waves, the exact nature of this frequency dispersion is dependent on how mechanical properties of the particular substrate vary with depth. For bending waves, dispersion is influenced by the thickness and mechanical properties of the vibrating structure (Fahy and Gardonio 2007). Water surface waves are also dispersive due to interactions between gravity, surface tension, and water depth, with energy at very low and very high frequencies generally propagating faster than that at intermediate frequencies (Markl 1983). It is not clear how relevant frequency dispersion is to biological signaling. It could, in theory, degrade frequency-modulated or broadband amplitude-modulated signals (Casas et al. 2007) or be used to determine range to a signal source (Elias et al. 2006; Michelsen et al. 1982). In many cases, however, dispersion of high-frequency substrate signals will be minimal (Brownell 1977; Casas et al. 2007).

The theoretical maximum effective range of substrate vibration signals is larger than that of compressional waves in air. This is because airborne sound is subject to spherical spreading, attenuating with the square of distance from the signal source, while Rayleigh waves in the earth exhibit cylindrical spreading, attenuating in direct proportion to distance, and bending waves in plants exhibit linear propagation, showing no spreading loss (Bennet-Clark 1998). In practice, damping due to material properties can rapidly attenuate substrate signals (Cocroft and Rodriguez 2005; Markl 1983). The maximum effective range for seismic vibrations excited by elephant rumbles, for example, is approximately 2 km under a best case scenario, similar to the range of the airborne component (Günther et al. 2004). The active space of substrate signals can be further limited by the physical boundaries of the vibrating medium. For instance, vibrational signals traveling through a plant will not generally propagate far beyond that plant (but see Eriksson et al. 2011; Michelsen et al. 1982). The pattern of substrate-borne vibrations having a more limited active space than their airborne counterparts is probably reversed in the case of burrowing animals such as fossorial mammals, however. Here, continuous lengths of airspace for the transmission of auditory signals are limited to burrows themselves, while a contiguous solid medium, the soil, connects even distant burrows. Indeed, several species of burrowing mammal use seismic signals for inter-burrow communication, and airborne signals appear to be limited to short-range interactions (Mason and Narins 2001; Narins et al. 1992).

Given the characteristics of wave propagation in each modality, what sorts of calls make the best bimodal acoustic signals? Generally, transmission of high frequencies is strongly attenuated in solid substrates (Markl 1983; Michelsen et al. 1982), while low frequencies are difficult for a signaler to couple to the air (Bennet-Clark 1998). Furthermore, global amplitude variation may not be informative for signals traveling in many solid media (Michelsen et al. 1982; Polajnar et al. 2012). We might, therefore, expect that effective bimodal acoustic signals have energy in intermediate frequency ranges efficiently propagated in both communication channels, or broad spectra, such that subsets of the energies

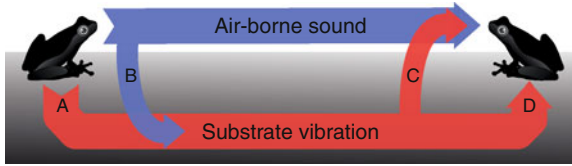
generated by the signaler will propagate well in each channel. We might also expect that much of the information is encoded in the temporal, rather than frequency or global amplitude properties of the signal. Broadband, pulsatile or drumming signals, or temporally amplitude-modulated signals restricted to a narrow range of intermediate frequencies are, therefore, promising candidates for bimodal acoustic communication.

### 6.3.2.2 Induction of Substrate Vibrations by Airborne Sound

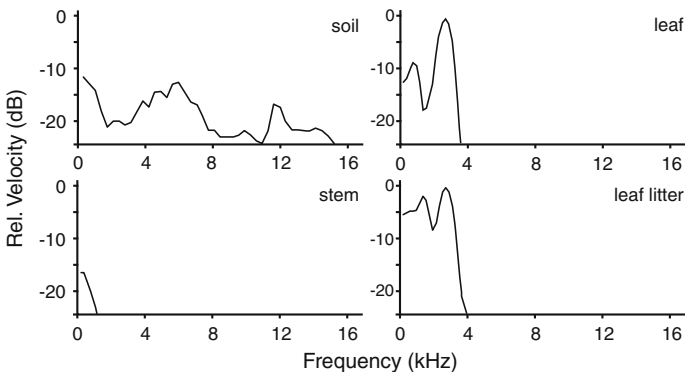
Acoustic signals excite substrate-borne vibrations in one of two ways. Either vibrations are coupled directly from the signaler's body to the substrate or vibrations radiate from the signaler as airborne waves that then induce vibrations in the substrate (Fig. 6.2). This second mechanism is a singular issue in bimodal acoustic communication, and the function and biological importance of airborne-sound-induced substrate vibrations is poorly understood.

The mechanical response of substrate to airborne pressure waves will depend on the frequency of the pressure waves, their intensity, the spatial distribution of that intensity, as well as the acoustic impedance of the substrate (Cremer et al. 2005). Animal ears and vocal systems employ a variety of impedance matching structures adapted to more efficiently couple body vibrations to the surrounding fluid media. In the case of sound waves acting directly on solid substrate, these structures do not exist and coupling is not as efficient.

Attempts to describe the transfer of acoustic energy from airborne pressure waves to substrate vibration using layered fluid/solid models predict that vibrations in the two media will be maximally coupled at frequencies where the phase velocities of dispersive substrate waves are closest to the propagation velocity of pressure waves in air (Jardetzky and Press 1952; Press and Ewing 1951). For soil, where phase velocities decrease with frequency, these frequencies of best coupling tend to be very low, in the range of airborne sound signals produced by elephants (Günther et al. 2004), but below those produced by small animals (Bennet-Clark 1998). In plants, where phase velocities increase with the square root of frequency (Cremer et al. 2005), the airborne sounds of many animals should be better coupled to the substrate. In some cases, however, modeling the ground surface as a homogenous solid may not be accurate. Ground surface layers are often made somewhat porous through the actions of weathering and biotic sources. The result is lowered wave conduction velocity in the uppermost ground layers and improved coupling between the air and substrate across sound frequencies (Arnott and Sabatier 1990; Bass et al. 1980; Sabatier et al. 1986). In nature, coupling between substrate and air can be much better than that predicted by current models (Fig. 6.3). Air-to-substrate coupling in plants is so good, in fact, that substrate vibration signals can propagate non-contiguous plant structures by radiating airborne sound waves, which in turn induce vibrations in nearby plants. Eriksson et al. (2011) demonstrated that the substrate vibration signals of leafhoppers



**Fig. 6.2** Paths of acoustic signal propagation. Vibrations generated by animal acoustic calls propagate to receivers through both substrate-borne- and airborne-communication channels. Substrate vibrations can be excited either by direct mechanical coupling between the signaler and the substrate (a), or they can be induced in the substrate through the action of airborne sound waves (b). Likewise, receivers may detect substrate vibrations by direct coupling with the substrate (d), or substrate vibrations may radiate into the air and be detected as airborne sound (c)



**Fig. 6.3** Substrate vibrations induced by airborne sound. Shown are frequency responses, as measured with a laser vibrometer, for four substrate types exposed to playback of airborne sound at 100 cm (equal amplitude tones 100 Hz–16 kHz): (1) damp soil, (2) the leaf of a small plant (*Philodendron* sp.), (3) a stem from the same plant, and (4) damp leaf litter over soil. All three plant structures strongly attenuate high frequencies. The soil has a broader frequency response, but for frequencies under 4 kHz was not as well coupled to the air as the leaf structures

(*Scaphoideus titanus*) elicit a behavioral response from conspecifics on non-contiguous plant cuttings separated by a gap of up to 6 cm.

Only a handful of studies have looked at the relative contributions of direct coupling and induction by airborne sound to the substrate components of bimodal acoustic signals. Wolf spiders (*S. ocreata*) respond defensively to airborne sound playback of predatory bird calls when on filter paper, but not on granite substrate, which is poorly coupled to air (Lohrey et al. 2009). These defensive responses ultimately lead to lower mating success when bird calls are present (Gordon and Uetz 2012). O’Connell-Rodwell et al. (2000) show a propagation velocity for the seismic component of Asian elephant rumbles that is considerably slower ( $\sim 250 \text{ ms}^{-1}$ ) than the speed of sound in air ( $\sim 340 \text{ ms}^{-1}$ ). They conclude that this seismic component is not induced in the substrate through the action of airborne sound and therefore must be the result of direct coupling via the animal’s

body. In a separate study, however, the seismic component of African Elephant (*L. africana*) rumbles was found to travel at considerably higher velocities ( $\sim 410 \text{ ms}^{-1}$ ) and to interact with the airborne component (Günther et al. 2004). The nature of airborne-sound-induced vibrations in the substrate was also examined for the stridulatory songs of katydids (*T. cantans*). Airborne song components are limited to frequencies above 6 kHz, but plant-borne substrate vibrations excited by the same signal are broadband, with additional energy between 30 Hz and 5 kHz. To determine the relative contributions of direct coupling and airborne sound induction to the observed plant-borne vibrations, Keuper and Kühne (1983) compared substrate vibrations excited by a stridulating male perched on a stick to those excited by pre-recorded sound played through a nearby speaker. They found that low frequencies were excited by direct coupling, while higher frequencies, more characteristic of the airborne component, were excited through induction. A similar study investigating the role of acoustic induction in the generation of plant-borne vibrations by cicada (*Okanagana rimosa*) songs found that direct coupling to the plant was not necessary to excite strong substrate vibrations across the frequency range of the song, but that high-frequency components of a substrate signal were eliminated if the tymbals (airborne sound radiators) were destroyed (Stölting et al. 2002).

Just as pressure waves in fluid media can impart mechanical energy to solid substrates, biological signals traveling in the substrate can radiate as pressure waves in air and water (by acoustic reciprocity)(Fig. 6.2). Near- and far-field airborne sound radiating from vibrating substrates could be a useful communication channel for some species. Small animals unable to efficiently couple low-frequency body vibrations directly to the air could, for example, vibrate the substrate, relying on substrate structures with greater surface areas, such as nearby leaves, to radiate their signals into the air. Likewise, insects and arachnids possess a number of peripheral receptors that are sensitive to near-field particle movement in the air and may be particularly likely to utilize airborne vibrations induced by substrate movements (Barth 1998; Drosopoulos and Claridge 2005; Hergenröder and Barth 1983). Parasitoid wasps (*Sympiesis sericeicornis*), for example, may use near-field sound radiating off leaves to detect their leafminer hosts (Casas et al. 1998).

### ***6.3.3 The Reception of Airborne Sound and Substrate Vibrations***

Sensitivity to both airborne and substrate-borne vibration is a prerequisite for the evolution of bimodal sound/substrate vibration signals. While this condition is not universally met, and the exact proportion of animal species sensitive to both modalities is not known, the number of potential receivers for bimodal sound/substrate vibration signals is enormous. Species from nearly every taxon examined have been found to be sensitive to substrate vibrations (Hill 2008), and a great

number of aquatic and terrestrial animals can also detect pressure waves traveling through water or air (Bradbury and Vehrencamp 2011; Drosopoulos and Claridge 2005). Importantly, there is extensive overlap between the species sensitive to each of these modalities and therefore considerable opportunity for bimodal signals to evolve. Cocroft and Rodriguez (2005) estimate that just over 7 % of acoustically communicating insect species use exclusively airborne or waterborne sound signals. By contrast, more than 20 % of insect species employ a combination of airborne and substrate-borne signals. Given that bimodal acoustic signals have not been a focus of communication research and many bimodal signals may currently be assumed to function in only a single modality, this estimate could be low.

In some taxa, input from both sensory modalities is transduced by the same peripheral sensors or processed in the same areas of the central nervous system (see Sect. 6.3.3.2 below). We might expect bimodal sound/substrate vibration signals to be particularly common in these animals. Cross-modal sensitivity of the receiver's neurology will, in the very least, affect the perception of acoustic signals.

### 6.3.3.1 Cross-Modal Sensitivity of Peripheral Sensors

Sensory receptors in many animals show cross-modal sensitivity to airborne and substrate-borne vibrations. This is not surprising given the fundamental similarities of acoustic waves in fluid and solid media and that in many cases sensors that transduce energy in one acoustic modality have evolved from predecessors tuned to the other modality. Arthropods employ a vast diversity of mechanoreceptors, with most species able to transduce acoustic waves using a variety of sensors (Drosopoulos and Claridge 2005; Hill 2008). The sensitivities of many of these receptors have not been fully mapped out, but it is clear that bimodal responsiveness to air and substrate vibration is a common occurrence throughout the taxon. One notable example is the bimodal response of insect subgenual organs. While the subgenual organ is often considered a specialized receptor for the transduction of substrate vibration, it has also been shown to respond to stimulation by far-field airborne sound in katydids and cockroaches (Drosopoulos and Claridge 2005; Shaw 1994). This pattern of cross-modal sensitivity may be, in part, due to the history of mechanoreceptor evolution. Across insects, it appears that organs sensitive to airborne sound have evolved from substrate vibration sensors (Shaw 1994). Indeed, sensitivity to substrate vibrations is phylogenetically more widespread and appears to predate the evolution of airborne sound sensitivity in several insect lineages (Cocroft 2005).

Insects are not the only group of arthropods known to possess bimodal mechanoreceptors. The three major classes of mechanoreceptors found in crustaceans capable of transducing acoustic waves (chordotonal organs, sensilla, and statocysts) are all sensitive both to waterborne or airborne vibration and to substrate vibration (Taylor and Patek 2010).

Whether bimodal mechanoreceptors are common in arachnids is unknown. Extensive research has documented the diversity and function of mechanoreceptors in arachnids, but this work has been mainly focused on the remarkable sensitivity of spiders and scorpions to substrate vibrations, and to a lesser extent near-field sound (Barth 1982; Brownell and Farley 1979). Spiders, at least, do respond behaviorally to far-field airborne sound (Barth 1982), but it is unclear whether the particular slit sensillae that transduce this energy are also sensitive to substrate vibrations.

The acoustic receptors of vertebrates also show cross-modal sensitivity. In contrast to the diversity of bimodal receptors found in arthropods, however, similar mechanisms involving bone conduction to the ear are responsible for all known cases of bimodal air and substrate vibration receptor sensitivity in vertebrates. In teleost fishes, the inner ear otoliths respond to head movements excited by acoustic wave particle motion in the water. Swim bladder pulsations excited by waterborne pressure waves are also coupled to the head through the body tissues, and in some teleost groups (e.g., Ostariophysi), this coupling is improved by a boney linkage, the Weberian ossicles (Popper et al. 2003). Thus, the inner ear responds to both the particle movement and pressure components of waterborne waves.

In frogs, a specialized structure, the opercularis muscle, connects the scapula directly to the operculum bone, which rests on the oval window of the inner ear and is responsible for exquisite sensitivity to substrate vibrations. Vibrations are then transduced by the saccule and amphibian papilla, structures that also transduce airborne sound stimuli (Narins et al. 2006).

Although snakes can use cutaneous sensors to detect ground movement, substrate vibrations are also coupled through the skull to the middle ear via bone conduction (Young 2010). Interestingly, because snakes lack the tympanic ears found in most terrestrial vertebrates, it appears that vibrations of the skull, induced by airborne sound, may be responsible for sensitivity to both acoustic modalities (Christensen et al. 2012).

It is not known whether birds can detect substrate vibrations through bone conduction to the ear or whether substrate vibration sensitivity in this group is limited to cutaneous mechanoreceptors (Dorward and McIntyre 1971). Some bird species, however, are very sensitive to extremely low-frequency airborne sound (Kreithen and Quine 1979; Warchol and Dallos 1989), increasing the likelihood that any substrate vibrations, which are typically of low frequency, that reach the ear will be transduced by the auditory receptors.

The mechanisms of substrate vibration reception in fossorial mammals are not totally resolved, but most species appear to receive this energy through bone conduction to the middle ear. The ear also shows sensitivity to airborne sound, although direct coupling of the ear to airborne vibrations is reduced in comparison to that found in other mammals (Mason and Narins 2001).

Finally, the inner ear of African elephants appears to be adapted to detect substrate vibrations through bone conduction and should be sensitive to both the airborne and substrate-borne components of elephant “rumble” vocalizations (Reuter et al. 1998).

### 6.3.3.2 Bimodal Integration in Higher Neural Structures

Even in species with separate specialized acoustic receptors that respond to excitation in a single modality, airborne and substrate-borne vibration may be processed together at higher neural levels. In katydids, which possess specialized tympanal structures for the reception of airborne sound, acoustic neurons ascending to the head ganglia are without exception bimodal, responding to both airborne and substrate-borne vibrations (Rossler et al. 2006). This pattern of extensive integration of substrate vibration and auditory input extends to locusts, where a network of interneurons mediates excitatory or inhibitory interactions between neurons ascending from modality-specific sensors (Bickmeyer et al. 1992; Drosopoulos and Claridge 2005). Furthermore, cross-modal integration is not a phenomenon limited to arthropods. In snakes, cutaneous somatosensory receptors and auditory hair cells both project to the auditory midbrain (Hartline 1971; Young 2003). Likewise, in humans and macaques, sensory input from airborne sounds detected at the ears and substrate vibrations transduced via the somatosensory system converge in the auditory cortex, and similar cross-modal integration would be expected in other primates (Foxe et al. 2002; Schroeder et al. 2001).

The perceptual consequences of cross-modal sensitivity at the receptor level and multimodal integration of sensory input at higher levels are not well understood. In theory, because the transmission properties of each communication channel differ, airborne and substrate-borne signal components are likely to carry non-redundant sets of information about the signaler or signaling environment. Some of this information will not be available to receivers who lack the ability to assess signal components in each modality separately. By contrast, neural integration of sensory input from air and substrate vibration sources allows for a greater range of potentially informative comparisons of stimuli arriving through each communication channel (Hebets and Papaj 2005; Partan and Marler 2005). Further research is needed to elucidate the ways in which receiver neurology affects the structure and function of bimodal acoustic signals.

## 6.4 Implications for the Function and Evolution of Signaling Systems

With only a handful of examples of species known to communicate with bimodal acoustic signals, it is impossible to make broad conclusions about how these signals function and evolve in nature. We can, however, assemble a collection of intriguing and untested hypotheses that may serve as fertile ground for future biovibrations research.



### 6.4.1 *The Evolution of Bimodal Acoustic Signals*

Airborne and substrate-borne vibrations may be particularly likely to evolve jointly as components of multimodal signals. With the precondition that the signaler is in contact with some substrate, only these two modalities are unavoidably excited together. Evolution of an airborne acoustic signal insures that substrate vibrations will co-occur, setting the stage for this “unintended” component to be co-opted as part of a novel bimodal acoustic signal. Although perhaps less common (see Sect. 6.3.1.2), coincidental airborne sound produced by a signal that has evolved to function through substrate vibration can, likewise, be audibly intense and thereby subject to selection imposed by receivers. Furthermore, the abundance of peripheral receptors sensitive to both modalities and cross-modal processing at higher neural levels increases the likelihood that receivers attending to a signal that initially evolved through one acoustic modality can also detect components propagating through the other.

It is valuable to identify and understand bimodal acoustic signals, not just because unexplored signal components may mediate important aspects of behavioral interactions, but because selection acting on each component can affect the evolution of the entire signaling system, including components in the other modality, through functional trade-offs and pleiotropic interactions (Cooper and Goller 2004). When, for example, white-lipped frogs thump the ground with their vocal sacs while calling, it not only produces a vibrational signal in the substrate, but also introduces amplitude modulations into the airborne component of the call (Lewis et al. 2001).

### 6.4.2 *Integration of Information Across Sensory Modalities*

In some cases, both components of bimodal acoustic signals may be informative, with components assessed either as separate information sources or assessed relative to one another (Hebets and Papaj 2005; Partan and Marler 2005; Rowe 1999). Even when the airborne and substrate-borne components of a signal are generated through the same physiological mechanism, differences between the components in coupling to the signaling media and in propagation through the environment can imbue them with informative variation.

Receivers may exploit this variation in the localization and ranging of signal sources. The use of multi-sensor, or multi-sample, comparisons for the localization and ranging of visual, acoustic, or chemical signal sources is found in most animal taxa (Bradbury and Vehrencamp 2011; Popper and Fay 2005). Sand Scorpions (*Paruroctonus mesaensis*), for example, compare arrival times across an array of vibration sensors in their legs to localize moving prey at distances of up to 20 cm (Brownell and van Hemmen 2001). The types of substrate waves used for communication generally propagate at lower velocities than airborne sound (Virant-Doberlet et al. 2006). When the substrate component is assessed alone,

this leads to greater arrival time and phase differences between spatially separated sensors than are seen with airborne sound and should facilitate localization. In addition, arrival time differences between airborne and substrate-borne components could facilitate ranging, without the constraint on sensors needing to be spread out spatially. Scorpions and spiders may use a similar unimodal strategy, comparing the arrival times of substrate-borne compressional and Rayleigh waves to determine distance to moving prey (Aicher and Tautz 1990; Brownell and Farley 1979). In theory, frequency dispersion or frequency-dependent attenuation of substrate vibrations could also be used for ranging (Elias et al. 2006; Michelsen et al. 1982), but there is currently no convincing evidence that receivers use frequency dispersion information in this way (Popper et al. 2003; Virant-Doberlet et al. 2006).

Because airborne and substrate-borne signal components can have different active spaces, the simple presence or absence of each modality may also communicate some information about a receiver's distance to a signal source. African elephants, for example, respond defensively to seismic presentation of alarm calls, but this response is reduced compared to that seen following playback of the airborne component (O'Connell-Rodwell et al. 2006). If the substrate vibrations generated by alarm calls travel further in the elephant's environment than their airborne counterparts (but see Günther et al. 2004), it is possible that receivers interpret the presence of the seismic vibrations in the absence of the airborne component as an indicator that the alarm call was issued from a distant signaler and thus corresponds to a non-imminent threat (O'Connell-Rodwell et al. 2006). This method of ranging may be particularly useful for territorial plant-dwelling animals who defend an area of contiguous substrate, where the active space of substrate vibration signals is well defined (Caldwell et al. 2010).

Differences in the propagation properties of airborne and substrate-borne vibration components could also aid receivers in the localization or assessment of signalers at different spatial scales (Hebets and Papaj 2005). Katydid (*Tettigonia cantans*) employ bimodal acoustic signals in this way. The airborne component of the male stridulatory signal attracts females from afar, and the plant-borne vibratory component aids in close range localization (Latimer and Schatral 1983). Similarly, some courting male wolf spiders in the genera *Lycosa* and *Schizocosa* couple papal stridulations to the leaf litter, producing substrate vibrations as well as airborne sound that radiates from the leaves. Rovner (1975) suggest that the airborne component of this bimodal strategy may function to communicate with distant females while the seismic vibrations become the dominant communication channel once a female is standing on contiguous substrate.

It is often suggested that substrate vibrations may be a relatively private information channel (Bell 1980; Henry 1994; Markl 1983), with a more limited active space and fewer potential eavesdroppers than visual or sound signals. With the diversity of animals sensitive to substrate vibrations, it is still very much an open question how commonly the concept of a private communication channel applies (Casas et al. 1998; Cocroft and Rodriguez 2005; Virant-Doberlet et al. 2011), but it is certainly the case that airborne and substrate-borne signal

components have different, likely overlapping, sets of potential receivers. Moreover, in some cases, the two components may have adapted for communication with separate groups of receivers. This arrangement may be particularly common in lekking species, where signalers benefit from a signal that is effective in communicating both with potential mates at a distance and with nearby competitors. White-lipped frogs and prairie mole crickets appear to use bimodal acoustic signals in this way (Hill and Shadley 2001; Lewis et al. 2001).

### 6.4.3 Backup Signals

Because both air- and substrate-borne vibrations are often generated by the same physiological mechanism, and both propagate as mechanical waves, they may be more likely to be redundant in information content than components in any other two modalities. Redundant signal components can, nevertheless, serve important communication functions by acting as backup signals and thereby improving transmission efficacy in noisy or variable signaling environments (Hebets and Papaj 2005; Partan and Marler 2005; Rowe 1999). White-lipped frogs use bimodal acoustic signals in this way. Males coordinate the timing of their sexual advertisement calls using the airborne component of calls from neighboring frogs. When this component is masked with noise, however, males instead adjust call timing based on the seismic component of neighbors' calls (Lewis et al. 2001).

Because solid substrates are variable and mechanically complex compared to fluid media (Cremer et al. 2005; Markl 1983; Michelsen et al. 1982), we might expect the unreliability of substrate components to drive the evolution of bimodally redundant acoustic calls. In some cases, however, constraints on sound propagation in air may also drive the evolution of redundant signals. Dense forest, for example, rapidly degrades airborne sound signals, and forest animals such as Asian elephants may benefit from informationally redundant seismic call components in areas where airborne signals are strongly attenuated by vegetation (O'Connell-Rodwell 2007).

Bimodal redundancy is not a foolproof strategy for mitigating the effects of environmental noise. By the same mechanisms that make simultaneous generation of airborne and substrate-borne signal components so likely, environmental noise can also be cross-modal. The receptivity of female wolf spiders (*S. ocreata*) to male substrate vibration courtship signals, for instance, is reduced in the presence of airborne synthetic noise (Gordon and Uetz 2012). As these spiders are not sensitive to airborne sound, it is vibrations induced in the substrate by the noise that are responsible for the reduced effectiveness of male signals. It is not clear whether airborne sounds mask the substrate signals of these spiders in nature. Playback of recorded cicada choruses did not have the same effect. The phenomenon of cross-modal masking might be of use to the agricultural industry, as vibrations induced in a plant substrate by airborne sound can mask the transmission of substrate-borne signals used by crop pests (Saxena and Kumar 1980).

#### 6.4.4 *Sensory Drive*

The summed input of two redundant signal components can better stimulate a receiver's sensory system (Hebets and Papaj 2005; Partan and Marler 2005; Rowe 1999), and this may have significant implications for the function and evolution of bimodal acoustic signals. Whether call intensity encodes information about signaler quality or is a cue to signaler proximity, receivers show a general preference for higher amplitude acoustic signals (Castellano et al. 2000; Latimer and Sippel 1987; Ritschard et al. 2010). Signalers benefit by maximally exciting the sensory systems of receivers, and depending on signaling context, the most effective means of doing this may involve a multimodal strategy, simultaneously stimulating both sound and substrate vibration sensors (Rowe 1999).

The cross-modal sensitivity of mechanoreceptors in several taxa leaves open the door for the intriguing possibility that some bimodal acoustic signals evolve through sensory exploitation. Physiological or environmental constraints on the amplitude of unimodal airborne sound or substrate vibration signals can enforce signal honesty (Bennet-Clark 1998, Fitch and Hauser 2003). However, novel adaptations that better couple a signaler's call to a second transmission medium, either the surrounding fluid medium or the solid substrate, could in essence hijack preexisting receiver strategies that assess signaler quality or location using unimodal amplitude cues. This idea is as yet untested and would likely require a phylogenetic analysis of acoustic call trait evolution to resolve.

#### 6.4.5 *Context-Dependent Shifts in Bimodal Signal Structure*

In some behavioral contexts, it may be dangerous or ineffective to produce intense signals in a particular sensory modality (Elias and Mason 2010; Zuk and Kolluru 1998). Signalers would, therefore, benefit from the ability to facultatively alter the relative amplitude or other characteristics of bimodal acoustic signal components. Even when both airborne and substrate-borne vibrations are generated by the same mechanism, the characteristics of each component could be independently modified by adjusting the mechanical response of a signaler's resonant structures or by altering the coupling of each component to the environment.

Unintended receivers, such as predators, parasitoids, and conspecific rivals, can exert strong selection on acoustic signals (Bernal et al. 2006; Zuk and Kolluru 1998) and may shape the evolution of facultative shifts in the structure of bimodal acoustic signals. Cicadas (*Okanagana rimosa*), for instance, undergo periods of "silent singing" where they flex their tymbal organ without producing the high-amplitude airborne component of their advertisement call. This tactic may favor the substrate call component, reducing exposure to parasitoid flies (Stölting et al. 2002). Over an evolutionary timescale, a shift from airborne calls to substrate-borne signals does appear to be an adaptive strategy for avoiding airborne-sound-oriented predators.

Katydid calls from areas with high densities of predatory bats produce airborne calls with lower duty cycles and rely more heavily on substrate-borne tremulatory signals (Belwood and Morris 1987; Morris et al. 1994). Many animals exhibit lower amplitude airborne calls when they are in close proximity to intended receivers (Caldwell et al. 2010; Dabelsteen et al. 1998). Whether signalers are relying more heavily on substrate-borne signal components in these contexts is not known.

Another potential benefit of facultative changes in a signaler's relative investment into either airborne or substrate-borne signal components comes from the fact that the quality of signaling substrate can be highly variable depending on behavioral context. At times, receivers may not be in contact with contiguous substrate, or the substrate may transmit vibrational signals poorly (Elias and Mason 2010). Signalers would benefit from the ability to assess the current efficacy of communication in each channel and respond by investing more heavily in effective signal components. Similar strategies have been described in animals using other types of multimodal signals. Wolf spiders (*S. ocreata*), for example, use more visual signals on substrates where vibration transmission is poor (Gordon and Uetz 2011). In a related species (*S. rovneri*), courting males use behavioral feedback from responding females to determine whether vibrational signals are effectively propagating through the substrate and adjust relative signaling investment across modalities accordingly (Sullivan-Beckers and Hebets 2011).

Receivers too may benefit from the ability to behaviorally alter the coupling of sensory receptors to each acoustic communication channel. In species with peripheral mechanoreceptors that are sensitive to both airborne and substrate-borne vibrations, this would allow receivers to independently assess information from each sensory modality. The spider *Araneus sericatus* can do this by simply altering the positions of its legs, thereby damping the mechanical response of its exoskeleton (Finck 1981). Similarly, elephants appear to shift their weight forward when attending to seismic signals, thereby improving coupling between the "acoustic fat" of their feet and the substrate. Elephants also possess a sphincter-like muscle that can constrict around the ear canal, attenuating the ear's response to airborne sound (O'Connell-Rodwell and Wood 2010).

### 6.4.6 Costs of Multimodal Signaling

While the use of bimodal airborne sound and substrate vibration signals may confer several adaptive advantages to signalers and receivers, there are some potential costs as well. First, as mentioned above, bimodal signals have the potential to reach a wider diversity of receivers and thus to expose signalers to increased rates of parasitism and predation. Bimodal acoustic signaling can also be energetically inefficient (Cremer et al. 2005; Partan and Marler 2005). A signal optimally tuned to couple well to either a solid or fluid medium, and propagate through it with minimal loss, will not function as efficiently in the other type of medium. Likewise, any signal tuned to propagate well in both modalities will not be optimally efficient

in either. Another potential cost stemming from the inherently bimodal nature of acoustic signals is that cross-modal interactions can degrade signal quality. Because of the differing wave propagation characteristics of fluid and solid transmission media, interference between the two communication channels during signal propagation or reception may degrade frequency, temporal, and amplitude properties of the signal. A consequence of this is that even if an acoustic modality is not used by receivers as an information source, incidental vibrations in this modality excited by a calling animal may still affect the evolution of signal structure and signaling behavior by degrading signals in the other modality.

## **6.5 Implications for the Study of Acoustic Communication**

There is a single methodological issue that rises above all others in the experimental study of bimodal airborne and substrate-borne signals. To document their existence and to determine how their components interact during communication requires the researcher to effectively isolate the two communication channels. The very property that makes these two modalities so likely to interact during communication, that they are mechanically intertwined and unavoidably excite one another, makes them difficult to properly control in an experimental setting. Effective methods for experimentally teasing apart the two acoustic modalities include altering a signaler's ability to produce signal components in one modality (Stölting et al. 2002), interfering with the reception of stimuli in one modality through manipulation of the receiver's sensory organs or by masking signal components with noise (Hergenröder and Barth 1983; Lewis et al. 2001), and carefully controlled recording and playback (O'Connell-Rodwell et al. 2007; Rado et al. 1998). It is worth noting, however, that in some cases, controlling each modality during experimentation is not necessary or behaviorally relevant, as receivers may never encounter isolated airborne or substrate-borne signal components in nature.

### **6.5.1 Recording**

Unintended cross-modal contamination of acoustic recordings is a common concern. This can be a significant issue when recording substrate vibrations in the presence of intense airborne sound using a laser Doppler vibrometer, which measures relative velocity between the sensor head and the substrate of interest (Arnott and Sabatier 1990, Caldwell pers. obs.). The thin housing surrounding the sensor head and the large surface area of these sensors (especially portable units) can cause them to vibrate in an airborne sound field. Care should be taken to insure that the sensor head is sufficiently distant from any intense airborne sound sources, and control measurements recorded with the laser focused on a non-vibrating

target may be useful to assess sound-induced vibration of the vibrometer itself. The surface of the sensor head can also be covered with acoustic foam, but this will interfere with heat conduction away from the instrument.

Cross-modal contamination is less of an issue with accelerometers and geophones, which tend to be built of dense materials, have relatively small surface areas, and should not, therefore, be as strongly coupled to airborne sound (Fahy and Gardonio 2007). Furthermore, these two types of sensors are often buried in the substrate, precluding the direct action of airborne sound waves on their surfaces. Unnecessary exposure of instrument wiring to excitation by airborne sound should be avoided, however. Cables can also be taped down to damp vibrations propagating along their lengths.

### 6.5.2 *Playback*

Unintended cross-modal excitations of vibrations can also complicate playback of acoustic signals. Mechanical shakers follow the same basic design as loudspeakers, but lack the speaker cone. Even without the impedance matching characteristics of a cone, shakers can produce sufficient airborne sound that they limit the range of useful substrate vibration presentation amplitudes (O'Connell-Rodwell et al. 2006) and the construction of a small sound attenuating enclosure surrounding the shaker may be necessary. Playback of airborne signals can pose similar problems. When a speaker and a test subject are resting on a common substrate, speaker vibrations can propagate through this substrate to the animal (Caldwell pers. obs.). Suspending playback speakers with vibrational damping material can reduce the amount of unintended energy transferred directly between the speaker and substrate, but cannot eliminate substrate vibrations induced by the action of airborne sound. Although less widely applicable, in some cases closed-field playback directly to an animal's peripheral sensors (Pinder and Palmer 1983) is an alternative to free-field playback and could reduce cross-modal noise. Regardless of the playback setup utilized, when feasible, it can also be helpful to determine response thresholds for animals exposed to signal components in each modality, so it is clear that unintended energy excited in the other modality during playback is not responsible for the response of test subjects (Lewis et al. 2001). Furthermore, collecting re-recordings of both airborne and substrate-borne vibrations excited by playback in both modalities is an important precaution, especially where airborne sound is likely to couple well with the substrate of interest, as it can during playback to plant-dwelling animals. If the facilities are available, re-recordings can be combined with active noise cancelation techniques to reduce unintended cross-modal noise (Ho and Narins 2006). For a more in depth discussion of vibration playback methods, see Cocroft et al. (Chap. 13, this volume).

## 6.6 Some Final Thoughts

This chapter has likely generated far more questions in the minds of readers than it has answered. That disparity mirrors the state of biovibrations as a field of scientific exploration. Several decades of research have now firmly established the importance of substrate-borne vibrations as an information source and a mode of communication nearly ubiquitous across animal taxa (Hill 2008). Now, we have the opportunity start to synthesize what we have learned, to identify patterns in the use of substrate-borne vibrations, and to begin to understand how they fit in among the full spectrum of other sensory modalities as parts of complete communication systems. Investigating the interactions between airborne sound and substrate-borne vibrations is a promising avenue for future study. It is not clear how common or important these cross-modal interactions are to communicating animals, but it is clear that these questions need to be answered.

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