Chapter 13
Vibrational Playback Experiments: Challenges and Solutions

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Abstract Playbacks are one of the most useful experimental tools in animal communication research. Playbacks of substrate vibrations present special challenges, but conducting high-fidelity vibrational playbacks is not difficult and depends less on the specific equipment used than on avoiding some common pitfalls. We review the major issues, describing both the problems and a range of solutions. Our focus is on playback through living plants, but most of the issues apply to playback through other substrates as well. The major challenge for playback through any substrate is that the vibrational signal is almost always changed by the playback equipment and the substrate, so that the signal received by the focal animal is different from the one intended by the experimenter. The general solution to this problem is to measure the changes imposed by the playback system and to pre-filter the playback signal to compensate for them. A second challenge is to ensure that the focal animal receives a signal at the appropriate amplitude. Achieving the proper amplitude is a straightforward process. However, amplitude is substrate dependent (e.g., on a plant, amplitude is inversely proportional to stem diameter), and the experimenter should choose a realistic amplitude for the substrate. Other issues include choices of playback device, natural versus artificial substrates, single versus multiple substrate exemplars, and playback in laboratory versus field. Our goal in this chapter is to give experimenters, especially those just starting out, the knowledge and confidence needed to conduct high-quality vibrational playbacks.

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13.1 Introduction

The playback experiment is one of the most widely used methods in the study of animal communication. Playbacks are essential for testing hypotheses about receiver responses to signals, including how signals function, what form of selection receivers impose on signals, and how receivers are influenced by signal changes caused by the transmission channel. A substantial literature on the proper design of playback experiments reflects this importance to the field (Kroodsma 1986, 1989; McGregor et al. 1992; McGregor 2000; Wiley 2003). Playback experiments require both proper design and proper execution, i.e., using a statistical design that supports the level of inference desired (Kroodsma et al. 2001) and executing this design so that the signal has the proper characteristics when it reaches the subject (McGregor 2000). The statistical issues cut across communication modalities, and there is some level of agreement about statistical design of playbacks. In contrast, the technical challenges differ greatly between modalities. For example, the technical issues arising in video playbacks (Fleishman et al. 1998; Cuthill et al. 2000) are distinct from those arising in acoustic playbacks (Gerhardt 1995), with multimodal playbacks experiencing both (Uetz and Roberts 2002). Our goal here is to review the technical aspects of playback in yet another modality: substrate vibration.

Communication through substrate vibrations occurs in many vertebrates and invertebrates (Hill 2008). In invertebrates, the use of substrate vibration dwarfs the use of airborne sound. In insects, it has been estimated that of all species communicating via some form of mechanical stimuli transmitted through a medium, over 90 % use substrate vibrations alone or in combination with airborne sound and 70 % use substrate vibration exclusively (Cocroft and Rodríguez 2005). The percentages are undoubtedly higher for spiders (Barth 1982, 2002) and possibly other invertebrate groups. However, although vibrational communication is the most widespread of the mechanical modalities, it is comparatively understudied. This lack of attention is changing, as evidenced by the growth of the literature in recent years (see Chap. 1, this volume), but there has been little discussion in the literature of the technical problems inherent in conducting playback of substrate-borne vibrational signals and of how to solve these problems. Hill and Shadley (2001) provide an excellent discussion of the most important problem (see Sect. 13.2, below), which is to compensate for the frequency response of the playback equipment and transmission channel. Wood and O'Connell-Rodwell (2010) provide a more wide-ranging discussion of playback experiments, addressing issues such as choosing sensors, playback equipment, and recording devices, and how to determine whether the wave type produced by the playback equipment matches that produced by a signaling animal. Here, we provide an overview of these and other issues that arise when conducting vibrational playbacks. Hill and Shadley (2001) and Wood and O'Connell-Rodwell (2010) consider issues arising in studying ground-borne vibrations. Because our research deals with insects that communicate through living plants, we will focus on this class of substrates, but most of the issues we address here apply to other substrates as well.

13.2 Frequency Profile of the Played-Back Signal

13.2.1 The Problem

The basic methodological challenge in any playback experiment is to deliver the desired stimulus at the location of the receiver. There are several reasons why accomplishing this goal with vibrational signals is not straightforward and why some common procedures cause the playback subject to receive a signal that differs from what was intended by the experimenter. In this section, we first explore how the frequency spectrum of the played-back signal may be changed in undesirable ways and then show how to correct for this problem.

13.2.1.1 Mismatch Between Recording and Playback Devices

Consider a signal recorded simultaneously with a laser vibrometer and an accelerometer (Fig. 13.1). The waveforms and amplitude spectra of the two recordings are different, although they represent the same physical vibration recorded at the same location. However, the output of a laser vibrometer is proportional to the substrate's velocity, while the output of an accelerometer is proportional to the substrate's acceleration. If the signal were also recorded with a ceramic phonograph cartridge, the waveform would again be different, because the cartridge's output is proportional to displacement. For signals that span a range of frequencies, the displacement, velocity, and acceleration waveforms will differ predictably as a function of frequency (Fig. 13.2).

Just as sensors have their own characteristics, so do playback devices. There are several methods of introducing a signal into a substrate. The most common is an electrodynamic shaker, which uses a coil and magnet to vibrate solid structures. Other common means of vibrating a substrate (Cocroft 2010) include piezoelectric actuators; an electromagnet that drives a magnet attached to the substrate; audio speakers that are modified by removing the diaphragm to reduce airborne sound and driving the substrate by means of a pin attached to the coil; and even airborne sound (Rebar et al. 2012).

One issue to consider is whether the output of the playback device is proportional to the signal's acceleration, velocity, or displacement. In general, the output of shakers is proportional to the stimulus acceleration. Accordingly, a signal recorded with an accelerometer and played back using a shaker should be faithfully reproduced, other things being equal (which they almost never are, as we will see below). On the other hand, if a signal recorded with a laser vibrometer is played back using a shaker, the shaker will reproduce the laser recording as if it reflected the stimulus acceleration, and the higher frequencies will be underrepresented in the playback, with their amplitude dropping by half for every doubling of frequency (see Fig. 13.2). The output of audio speakers (modified to play back vibrations) is proportional to velocity.

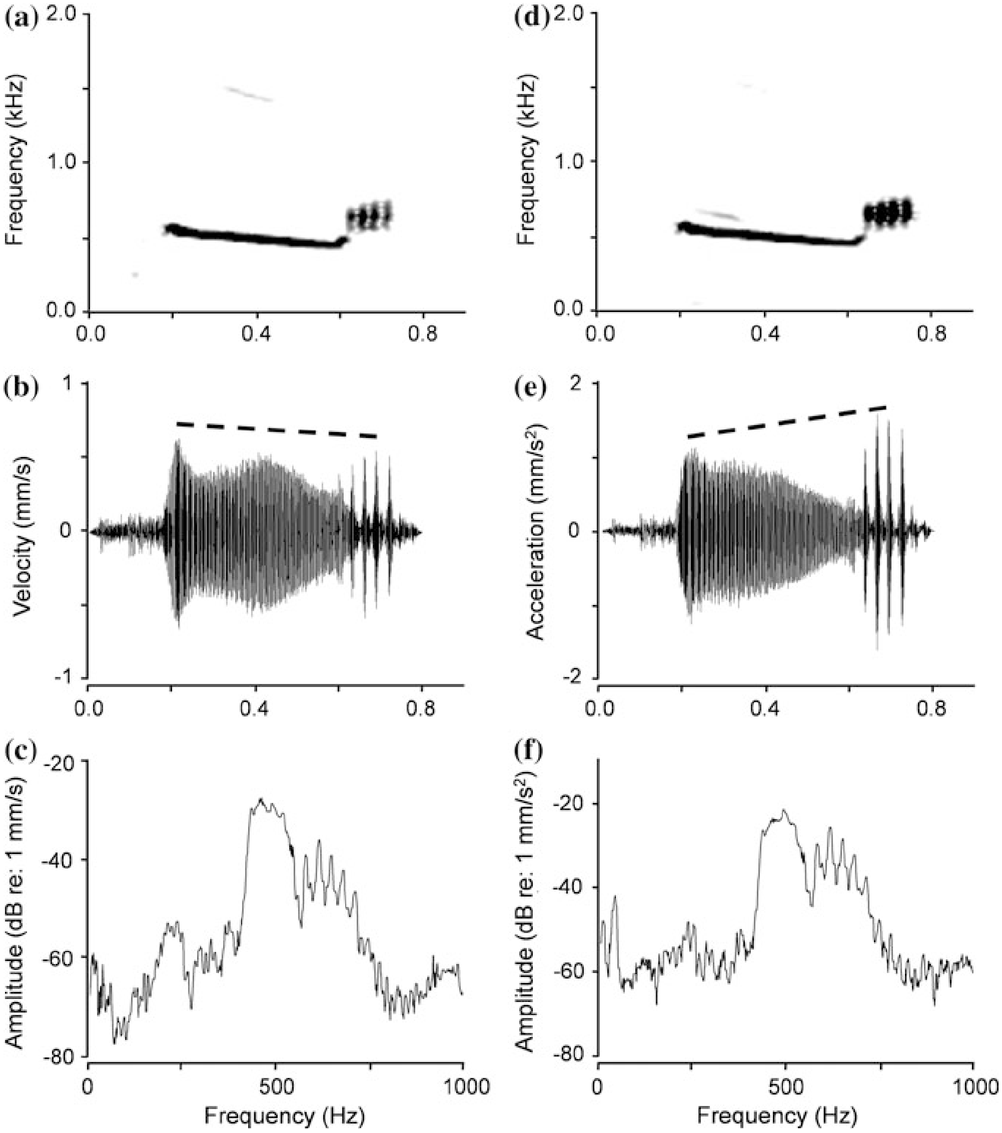

Fig. 13.1 The velocity and acceleration waveforms of the vibrational signal of a male *Tylopelta gibbera* (Membracidae), recorded with a laser vibrometer and an accelerometer at the same location on the host plant stem. Spectrograms, waveforms, and amplitude spectra are shown for the laser signal (**a–c**) and the accelerometer signal (**d–f**). Note that the higher-frequency component of the signal (the pulses at the end) has a greater amplitude in the accelerometer recording

Matching the recording and playback devices (e.g., using an accelerometer/ shaker combination or a laser/modified speaker combination) is, however, neither sufficient nor necessary. The reason such matching is not sufficient is that most playback devices, whether shaker, electromagnet, speaker, or piezoelectric actuator, do not have a flat frequency response. Some frequencies will have higher amplitudes than others, either because of the device's inherent properties (which vary with the mass being driven) or because of the way the device is coupled to the

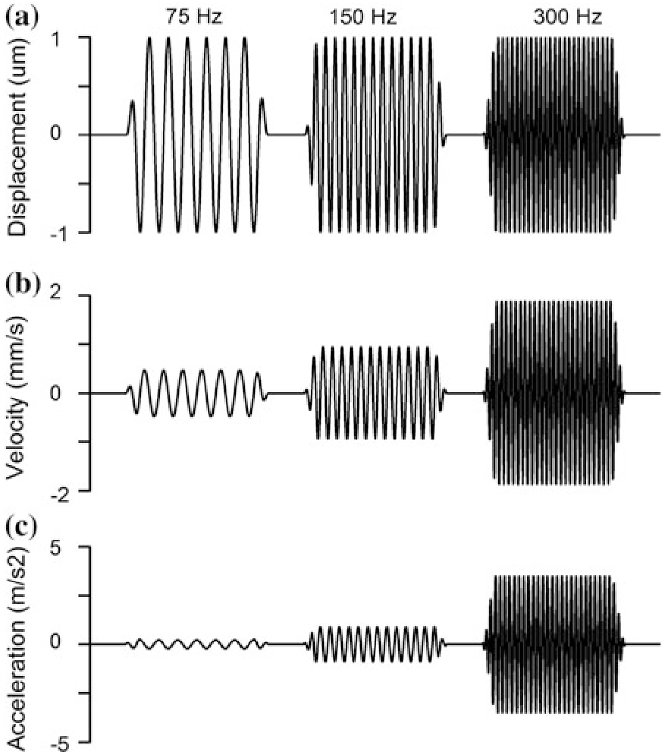

Fig. 13.2 The amplitude relationship between displacement, velocity, and acceleration. **a** A series of three tones an octave apart, each with a peak displacement of 1 µm. **b** The velocity record of the same three tones. The peak velocity doubles for each doubling of frequency. Consider substrate motion within the first quarter of a cycle: For a 75 Hz sine wave, the change from 0 displacement to 1 mm occurs in 3.3 ms, while for a 150 Hz sine wave, the substrate moves through the same distance in half the time, so the velocity is doubled, while the peak displacement remains the same. **c** The acceleration record of the same three tones; the peak acceleration again doubles (with respect to velocity) with each doubling of frequency. A useful generality: For a signal containing a range of frequencies, the velocity amplitude will increase by 6 dB per octave relative to the displacement amplitude, while the acceleration amplitude will increase by 12 dB per octave

substrate. This problem is analogous to substrate filtering, considered in the next section. In Sect. 13.2.2 (below), we explain how this problem can be solved to conduct high-fidelity vibrational playbacks using virtually any combination of recording and playback devices.

13.2.1.2 The Substrate Filters the Played-Back Signal

Plant stems and leaves, like other substrates, act as filters that attenuate some frequencies more than others. As a consequence, even if one could use idealized, ‘perfect’ recording and playback devices, the signal at the playback subject will still differ from that intended. This filtering effect can easily be seen by playing back a noise stimulus with equal amplitude across a band of frequencies and recording it some distance away; the amplitude spectrum will typically be far from flat at the second point (Fig. 13.3). The same filtering, of course, will also occur with an animal signal played back through the same substrate. Filtering varies among plant species (McNett and Cocroft 2008), among plants of the same species (Cocroft et al. 2006), among different parts of a single plant (McNett and Cocroft 2008), and even among locations on the same leaf or stem (Michelsen et al. 1982; Cokl et al. 2007; Magal et al. 2000). Given this level of variability, average differences among substrate types can be revealed only with large sample sizes (e.g., McNett and Cocroft 2008). If substrate filtering is not compensated for (see below), then the focal receiver will experience a signal that departs in unknown ways from the intended signal.

13.2.1.3 Resonance in the Playback Setup or the Substrate

In particular, for playback on a larger plant, it may be necessary to mount the playback device on a tripod or other structure to position it next to the substrate. The result will be a structure with its own resonant frequency or frequencies. If the resonant frequency falls within the range of the playback stimulus, then this frequency will be excited in the structure holding the playback device and will be overrepresented in the played-back signal.

Resonance also occurs in natural substrates, but under what conditions it is important for vibrationally communicating insects remains an open question. Polajnar et al. (2012) documented resonance in a grasslike plant with straight, hollow stems: At certain frequencies, there was a pattern of regular increases and decreases in amplitude along the stem. At a given location on the stem, resonance was seen during playback of a frequency sweep, in the form of sharp increases in amplitude at particular frequencies. Evidence that resonance was the cause of these patterns came from a match between the observed patterns and those predicted in an ideal thin elastic rod. The resonant peaks occurred as a consequence of reflected waves that created standing waves in the plant stem. In contrast, in our work with membracid treehoppers on woody host plants, reflected waves are minimal and the striking resonance phenomena observed by Polajnar et al. (2012) are absent. We do not yet have a general framework for predicting when a system will be dominated by reflected waves and resonance and when it will be dominated by transient one-way wave propagation, so researchers will need to approach playback substrates on a case-by-case basis.

13.2.1.4 The Playback Device is not Adequately Coupled to the Substrate

Playback devices must be attached to the substrate. Shakers function like heavy, robust audio speakers, producing a force proportional to the current supplied to the coil that drives the load. Instead of a membrane that produces airborne sound, there is typically a mounting stud to which a bolt or ‘stinger’ is fitted and then attached to the substrate to be vibrated. For engineering purposes, the stinger is usually a bolt that is coupled to a matching threaded attachment on the substrate or load. For structures such as plant stems, this method of attachment is usually not feasible, and in practice, most investigators position the shaker so that the bolt is in firm contact with the substrate. This method provides less than ideal coupling between shaker and substrate, but the coupling (especially at higher frequencies) can be improved by using an adhesive to attach the bolt to the stem.

Even small shakers are relatively heavy objects (typically a few kg) and can be difficult to position and align to vibrate the substrate at the desired location and along the desired axis. Like any playback device, a shaker requires a fixed base from which it pushes against the substrate. One approach is to place the shaker on a tabletop and position the plant so the desired part contacts the shaker, but this is not feasible for all plants. Another approach, which works even for large branching woody plants, is to use a positioning structure such as a microscope boom stand to securely hold the base of the shaker, allowing the investigator to adjust the shaker position in three dimensions.

The use of audio speakers as playback devices is common in the literature, and usually, the membrane is removed to reduce the production of airborne sound—although in some cases, the insects will respond to playback when placed directly on the speaker membrane (Zunic et al. 2008). To use the speaker more like a shaker, after removing the membrane, a pin or other small rigid device is attached to the moving coil. The speaker is then clamped in position so that the end of the pin contacts the plant substrate. For small plant structures, this approach provides a lighter and more easily positioned device.

Electromagnets have often been used to drive a small magnet glued to the plant stem or leaf (Michelsen et al. 1982). One potential advantage of this method is that it produces a less rigid coupling to the substrate and allows the plant stem to move more freely (though its motion is still constrained by the presence of an attached magnet in the magnetic field of the electromagnet). One disadvantage is that the frequency response of the playback system is highly dependent on the distance between the electromagnet and the magnet, and thus, this distance needs to be maintained. Another disadvantage is that it is more difficult to achieve an alignment that drives the stem or leaf along a single axis, and the magnet may thus produce a more complex whirling motion at the source than does a shaker, modified audio speaker, or piezoelectric actuator.

Piezoelectric actuators are small, light devices that are easy to position and which when properly aligned will produce motion along a single axis. They require more specialized electronics to drive them and in our experience are most useful for signals containing energy above 100 Hz.

One potential disadvantage of all of these methods is that they all require attachment to the substrate, and thus, the coupling of vibrations to the substrate is likely to differ in unknown ways from that produced by a signaling animal. Whether constraining the plant by attaching a playback device alters receiver behavior has been little explored, but two approaches provide a way around the issue that can be used in special circumstances. In one creative study, the investigators glued the insect's back to a stick driven by a speaker coil and allowed the insect to grasp the substrate with its legs. Vibrating the stem via a living insect is the closest any playback experiment has come to replicating signal production by an insect (A. Cokl, personal communication). Another study used broadcast airborne sound (Rebar et al. 2012), which can be perceived by the playback subject either directly (Shaw 1994) or by means of the vibrations produced in the plant by the sound (see Gogala Chap. 3, this volume). This latter approach is especially useful when one needs to expose large numbers of insects on multiple plants to a stimulus, but would not be suitable for more detailed studies of vibration localization or female preferences, because it provides little control over the vibration amplitude and frequency spectrum at the location of the receiver.

13.2.2 The Solution

The changes introduced in a signal by the playback equipment and substrate can be easily diagnosed and in most cases easily solved, by pre-filtering the signal based on measurement of the filter imposed on the signal along the playback path. The solution is conceptually simple and requires only a modest amount of signal processing to carry out. Essentially, one needs to measure the frequency response of the system—i.e., how the signal has been filtered between the computer output and the substrate at the point of the focal receiver—and then compensate for this frequency response (see Hill and Shadley 2001). Figure 13.3 provides an illustration. Once this has been done, then shakers, modified audio speakers, electromagnet/magnet combinations, and piezoelectric actuators can all be used to conduct high-fidelity vibrational playbacks. Furthermore, all will produce bending waves in plant stems, as do signaling insects (Michelsen et al. 1982; Cocroft et al. 2000).

The playback system's frequency response can be compensated for in a number of ways. An approximate, analog method would be to use a graphic equalizer, which uses a series of filters (generally one to three per octave) that allow one to adjust the system's frequency response. This would involve a trial-and-error phase of raising and lowering the amplitude in various bands to approximate a flat frequency response; we are not aware of any published studies that have used this method. Digital signal processing methods are far more flexible. This approach involves playing back a test signal through the system and recording it with a sensor at the site where the playback subject will be placed. Comparing the amplitude spectrum of the test signal between its original and played-back form allows one to characterize the system's frequency response. Essentially, for each frequency bin in the amplitude spectrum, one calculates the ratio of the amplitude of the original test signal to that of the played-back signal. This ratio can be obtained by dividing one amplitude spectrum by the other or by calculating the transfer function between the two signals. The transfer function of the playback

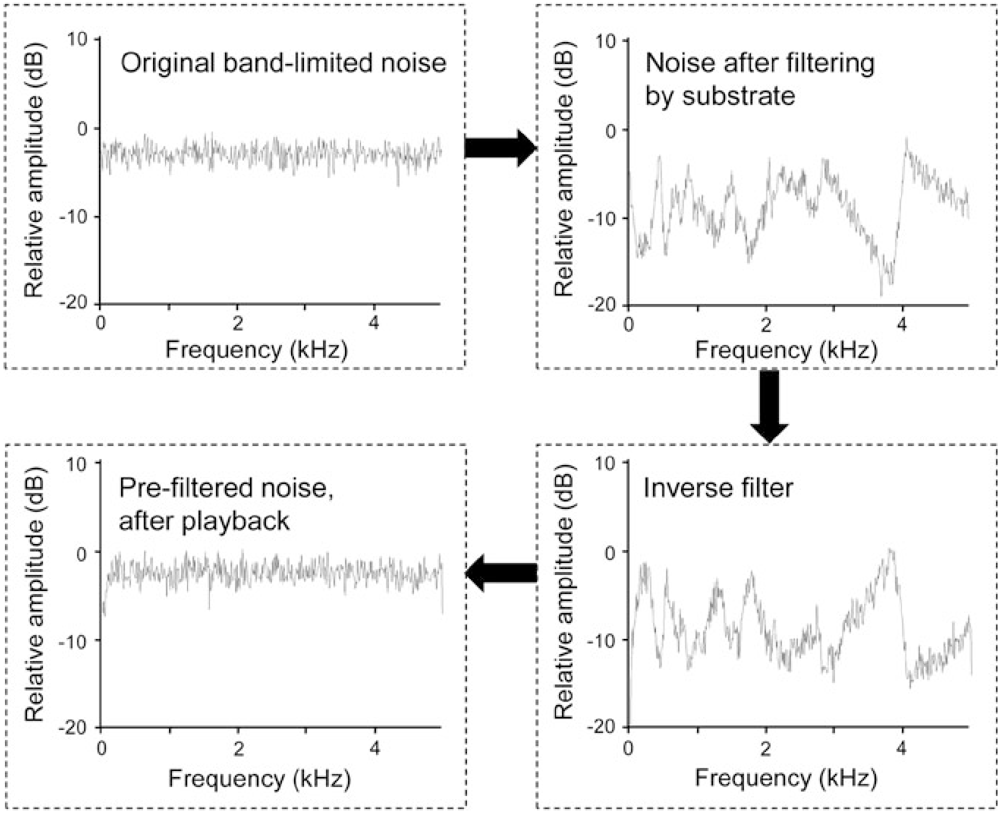

Fig. 13.3 Compensating for the frequency response of the playback system. A band of noise with equal energy across a range of frequencies is played through a vibration transducer and recorded at some distance along the stem, where it no longer has equal energy in all frequencies. The inverted frequency response of the system is used to design a digital filter (*third panel*), and that filter is applied to the original noise signal. When this compensated signal is played through the system, the signal at the location of the playback subject now has equal energy across the relevant frequency range (*final panel*)

system is the ratio of the FFT of the played-back signal to the FFT of the original signal and can be calculated by taking the cross-spectral density between the two signals, divided by the auto-spectral density of the original signal.

Once the frequency response of the playback system is characterized, it can be compensated for. One approach is to multiply the FFT of the playback signal by the transfer function (original signal/recorded signal) and use an inverse FFT to recreate the playback signal with an adjusted frequency spectrum. An alternative is to use the system's frequency response to design a digital filter; this approach is more flexible in that it allows pre-filtering of playback files of any duration (the previous approach requires the stimulus file to have the same number of sample points as the files used to calculate the transfer function). When the compensated signal is played through the system, its amplitude spectrum should now closely match that of the signal when originally recorded (Fig. 13.3), as should the time-domain waveform. The process often requires two or three iterations, because for frequencies that are severely attenuated, the filter estimation improves after the attenuation has been at least partially compensated for. Note that for playbacks conducted in the field (see below), background noise may alter the estimation of the system's frequency response, and its influence should be minimized to the extent possible (Hill and Shadley 2001).

The frequency response of the playback system must be re-calculated for each new playback location, whether this is a different substrate or a different location on the same substrate. One possible exception is for playback transducers that are driving a negligible load, such as a small leaf. Here, it is possible to calculate the system's frequency response once and to use the resulting compensation filter for all future playbacks using that particular playback transducer. However, once there is an appreciable load on the playback transducer—such as a plant stem—the frequency response will be influenced by the nature of the load.

Depending on the purpose of the experiment, playbacks that do not compensate for substrate filtering may give misleading results. For example, suppose a receiver's actual frequency response curve is flat in the 100–4,000 Hz range, but that the receiver responds more (using some assay of response) at higher amplitudes. If the substrate used for the playback experiment imposed a filter like that in Fig. 13.3, then an experimenter playing back a range of frequencies at an equal amplitude *at the source* would mistakenly conclude that the receiver was much more responsive to some frequencies than to others. This conclusion would be an artifact of the substrate filtering, simply because some frequencies had a much higher amplitude than others at the receiver's location.

Note that if the system filter is calculated using an accelerometer or other sensor that contacts the substrate, removing that sensor will change the filter. If it is necessary to remove the sensor prior to the experiment (e.g., some insects we have worked with will climb onto and court an accelerometer), the influence of this change should be estimated, such as by calculating the filter with and without a second sensor attached.

The above discussion assumes that if one is using recordings of natural animal signals, they were recorded with the same kind of sensor as the one used for calculating the system's frequency response. If different kinds of sensors are used for recording the original signals and for calibrating the playback, then the compensation will be incorrect; for example, if the signal was recorded with a laser vibrometer and the amplitude calibration is done with an accelerometer, the compensation filter or transfer function will be off by 6 dB per octave. In this situation, it is still possible to compensate correctly by adjusting the filter using the transfer function between the two sensors or by using numerical integration/differentiation to convert the waveform from acceleration to velocity or vice versa.

If there is resonance in the playback setup or substrate, the frequency response at the resonant frequencies sometimes cannot be compensated for through signal processing. For example, resonance where the motion corresponds to the motion of the shaker head can be compensated, but other modes where the shaker head is pitching and rocking cannot. How one deals with the problem thus depends on the source of the resonance and the questions being asked. If the resonance arises in the equipment or supporting structures used for conducting the playback, then it may be possible to alter the setup, either by isolating parts of it from the plant with vibration-damping material or by adding mass to lower the resonant frequency out of the frequency range of interest (e.g., at a node of a vibrational mode). If the resonance is in the substrate itself, how one deals with it depends on whether the substrate is typical of those used by the insect in nature and on whether the subject will be stationary. If resonance is present in an artificial substrate, or in a host plant much smaller than those used by the insects in the field, then using a different substrate would be appropriate. If the resonance observed is typical of that occurring in natural substrates used by the insects, then if the subject is stationary, it may be possible to find a location where resonance is not an issue for the frequency range of interest. If the subject is moving, then the resonance is something it would encounter in nature, and the best approach may be to use the 'post hoc' method described below (see Sect. 13.9).

Finally, an exception to the above discussion: There is one situation in which it is more effective to simply calibrate the stimulus amplitude, without first obtaining the system filter. When the stimulus contains only a single frequency, playing the signal through the substrate and adjusting the amplitude at the desired location allows precise adjustment of the amplitude of that frequency; indeed, for single frequencies, this method can be more precise than an FFT-based method. When the playback experiment involves a modest number of single-frequency stimuli (and especially if the amplitude calibration is automated), this approach is quick and straightforward and yields excellent precision. However, for any stimulus containing a band of frequencies (such as a frequency sweep or a broadband click), pre-filtering based on the system filter is required.

A note on software: The authors use MATLAB (MathWorks Inc., Natick, MA, USA) for signal processing. MATLAB scripts for frequency compensation and for conversion of waveforms between displacement, velocity, and acceleration are provided in the Appendix.

13.3 Temporal Characteristics of the Played-Back Signal

13.3.1 The Problem

In some circumstances, the temporal features of the playback signal, such as its duration, will be changed between the playback transducer and the focal animal. In particular, resonance in the playback setup or substrate, or distortion from reflected waves can cause signal degradation. Furthermore, if the transmission distance is large between source and receiver, and the signal contains a range of frequencies, then dispersive propagation of bending waves (for which transmission speed is proportional to the square root of frequency) could cause changes in the amplitude envelope of the signal [see Wood and O'Connell-Rodwell (2010) for an example of dispersion-related changes in a signal propagated by Rayleigh waves]. Finally, if there is frequency modulation in the playback signal, and the frequency filtering properties of the playback path are not compensated for, then because some frequencies will have higher amplitudes than others, the overall amplitude envelope of the signal will be changed. For example, the amplitude of a frequency sweep that was constant at the source will now fluctuate in unpredictable ways.

13.3.2 The Solution

If the problem arises from reflected waves in the substrate, their influence can sometimes be reduced by choosing a different substrate or lowering the amplitude of the playback. Signal changes due to dispersive propagation can be avoided by conducting the playback close to the focal animal (on a plant, within a few 10 s of cm). Changes in the amplitude envelope caused by substrate filtering can be eliminated by correcting for the system's frequency response as described above. In our experience, changes in the gross temporal features of playback signals due to resonance or dispersive propagation are a less common issue than changes due to uncorrected frequency filtering, but in some study systems, these changes are much more frequent (Cokl and Virant-Doberlet 2003; Polajnar et al. 2012). The extent of the problem may depend on the nature of the substrate; with small insects on woody host plants, we have encountered little reflected energy, but signals on simple rodlike structures with little damping may create substantial resonance (Polajnar et al. 2012).

13.4 Amplitude Calibration

13.4.1 The Problem

For vibrational signals produced on solid structures, the amplitude of the signal depends on properties of the substrate including its density and mass and on the impedance between the signaler and the substrate. On a plant, an insect signaling on a thin leaf petiole will produce a much higher-amplitude signal near the source than the same insect signaling on a thick woody stem (Fig. 13.4). Measurements of signal amplitude alone, then, without reference to the structure on which they were produced, are not very meaningful. Likewise, playback of vibrational signals on plants should take into account the diameter of the stem or petiole on which the signal was recorded or on which amplitude was measured. Whether insects take account of the inverse relationship between mass and velocity to assess signal power has not been investigated, but it seems prudent for investigators to keep this relationship in mind. That is, suppose the peak velocity of the signals an insect produces on a thin leaf petiole is 5 mm/s and the peak velocity of the signals it produces on a thick woody stem is 0.1 mm/s. With a shaker, it would be possible to play back signals to a receiver on a thick woody stem using a peak velocity of

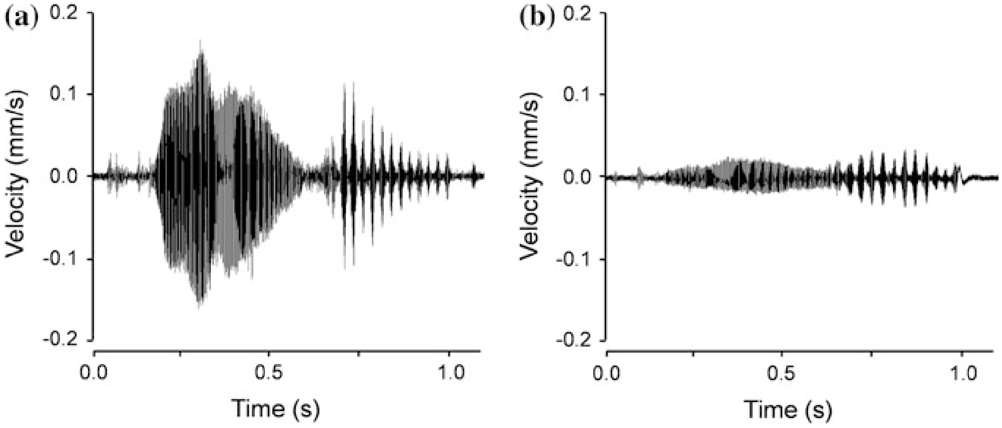

Fig. 13.4 What is the amplitude of an insect's vibrational signal? A male treehopper (*Tylopelta gibbera*) signaled at two locations on a host plant and at each location was recorded with a laser vibrometer focused on a point 1.5 cm from the male. Signal (**a**) was recorded on a green stem with a diameter of 2.2 mm, while signal (**b**) was recorded on a woody stem with a diameter of 7.2 mm. There is a 13-dB difference between the peak velocity of the signals (0.16 vs. 0.035 mm/s)

5 mm/s, but this would create a very unnatural situation in which the receiver's behavior may be difficult to interpret.

The relationship between amplitude and substrate is a particularly important issue for playbacks in which the insect must localize a vibration source or is otherwise moving around the plant; if the trunk at the base of the plant is shaken at an amplitude typical of that on a leaf petiole, the thinner stems toward the apex of the plant may vibrate at an amplitude outside the range experienced by communicating insects.

13.4.2 The Solution

There are several ways to achieve the appropriate signal amplitude for a playback.

(a) The most straightforward way to ensure the proper signal amplitude is to use a calibrated transducer and data acquisition system and adjust the output of the playback device to match the value of the desired peak or RMS amplitude (at the receiver's location) of the played-back signal. This value might be the amplitude of that same signal when originally recorded, or the average amplitude of a sample of signals, or some other value of experimental relevance. The playback substrate should be similar to the substrate on which the signals were recorded (see Sect. 13.4.1).

(b) The proper playback amplitude can be obtained when using a sensor whose output is not calibrated or when using a recording system with some unknown multiplier of the incoming voltage signal, as is typical for systems with a variable gain (e.g., computer sound card, audio recorder). As long as the recording system and gain settings are the same as those used to record the original signals, the amplitude can be faithfully reproduced by matching the played-back signal amplitude to that of the original signal.

(c) The correct amplitude can be obtained even with sensors such as phonograph cartridges or piezoelectric film, whose output level varies with the nature of the connection (e.g., the pressure applied, the angle between the stylus and the substrate). If a sensor used to record some insect signals is left at its original position, and the signals are played from the site of the original signaler, then simply matching the amplitude of the original recording is sufficient.

(d) Finally, with any recording system, it is possible to set up the playback, record a sample of individuals on that substrate, and adjust the output of the playback device to achieve the appropriate amplitude.

13.5 Substrate Effects on Receiver Behavior

13.5.1 The Problem

For playbacks in the field (see below), the substrate choice will be dictated by the location of the study animals. For playbacks in the laboratory, there are more choices: natural substrate or artificial? Host or non-host? Which plant part? This choice can have important consequences. For example, *Enchenopa binotata* treehoppers are host plant specialists. Although males will signal on a non-host plant, they produce fewer and shorter signals than they do on a host (Sattman and Cocroft 2003). Wolf spiders prefer to produce their vibrational signals on leaf litter, and when signaling on less conductive substrates like soil or rock, the spiders accompany their vibrational signals with more visual signals (Gordon and Uetz 2011).

For studies of vibration localization, the choice of substrate is critical. Artificial substrates may behave completely differently than natural substrates, and this may influence whether or how a focal subject responds to a stimulus. For example, an animal on an artificial substrate that appears unable to localize a signal may not have access to the same information as an animal on a natural substrate. In such cases, we suggest comparing localization cues (e.g., time delays between sensors in different legs, amplitude gradients) between natural and artificial substrates.

13.5.2 The Solution

There is no way to know a priori whether individuals of a given species will behave and respond to playbacks similarly on their usual substrate and on an artificial substrate in the laboratory. For example, in treehoppers, males of a host plant specialist signal differently on hosts and non-hosts (Sattman and Cocroft

2003), while males of a species with a larger host plant range have the same signaling behavior on hosts and non-hosts (Cocroft et al. 2006). The use of a substrate closely resembling the one on which communication usually takes place is the safest bet. However, sometimes artificial substrates are extremely useful, and in that case, one simply needs to compare the behavior of the animals on the natural and artificial substrate.

13.6 The Substrate Vibrates Along More Than One Axis

13.6.1 The Problem

The vibrational motion of physical structures occurs in three dimensions. In a plant stem, motion can occur along the long axis of the stem or in a plane perpendicular to that axis. Michelsen (Chap. 11, this volume) points out that no one has yet characterized the extent of motion along the long axis of plant stems, and the importance of longitudinal vibrations along the stem remains an open question. For the remaining two dimensions (Fig. 13.5), there are two issues. First, if the stem is vibrating along only one axis, the focal animal may or may not be aligned with that axis. Rohrseitz and Kilpinen (1997) found that the subgenual organ of honeybees is about 10 dB more sensitive to motion along the long axis of the tibia than to motion perpendicular to that axis. To the extent that the same is true of other species, then this issue needs to be taken into account. For example, suppose a playback device causes the plant stem to move along a single axis. If the most sensitive axis of the study subject's vibration receptors is parallel to the axis of motion, the subject will experience a much higher-amplitude signal than if the most sensitive axis of its sensors is perpendicular to the axis of motion. This alignment issue is important for behavior: Male treehoppers locating a female made more accurate decisions when their dorsoventral axis was aligned with the major axis of stem motion (Gibson and Cocroft, in preparation). Second, the use of two sensors whose axes of sensitivity are perpendicular to each other reveals that although plant stems sometimes vibrate along a single axis, they typically vibrate with a whirling motion (Fig. 13.5), a phenomenon Michelsen et al. (1982) first described by observing plant motion using a strobe light. How the whirling nature of stem motion influences insect vibration perception is still unknown, but two-dimensional motion of the substrate is a ubiquitous feature of the insect's perceptual world.

13.6.2 The Solution

We know of no studies that have controlled the two-dimensional motion of a plant stem at a distance from the playback device. Doing so would require two playback devices placed at right angles to each other, and even this approach

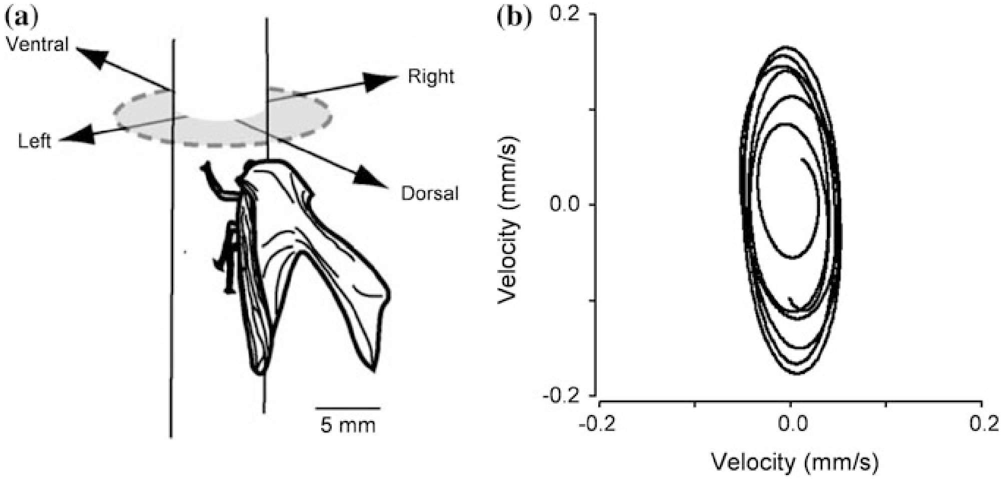

Fig. 13.5 Vibrational signals produced on plant stems are transmitted as bending waves that cause motion perpendicular to the long axis of the stem. This motion can occur along any axis in a plane perpendicular to the stem (**a**) [Reproduced from McNett et al. (2006), with permission]. Typically, the motion occurs along more than one axis during the transmission of insect signals, so that stems vibrate with a whirling motion (**b**). The motion of a point on the stem can be seen by plotting the output of two transducers whose axes of sensitivity are in the plane shown in (**a**) but are oriented at 90° with respect to each other. The trace in (**b**) shows stem velocity during 3.4 ms of a mating signal from a male *Umbonia crassicornis* [illustrated in (**a**)] recorded close to the signaler using two orthogonally positioned laser vibrometers

would allow one to influence the two-dimensional motion of the stem only at specific locations. Once the signal has travelled beyond the point at which the compensation was done, uncontrolled variation in substrate properties will affect the motion. However, measurements taken at varying distances from a signaling treehopper on a plant stem show that, close to the insect, the vibrations occur with a relatively linear motion aligned with the dorsoventral axis of the insect. Although the nature of the motion imparted to the stem will depend on the method of vibration production, it seems likely that for many signaling species, the results will be similar to the treehopper example. If so, then keeping the playback device within 10 cm or so of the focal insect, with the major axis of motion aligned with the insect's dorsoventral axis, should minimize the variation introduced by changes in the two-dimensional motion of the stem. Note, however, that this assumes that the playback device is imparting uniaxial motion to the stem, which will be largely true for a shaker or piezoelectric stack. For a magnet/electromagnet combination, however, depending on the alignment between magnet and electromagnet and the attachment of the magnet to the stem, the magnet may have a 'fluttering' or side-to-side rocking motion rather than simple motion along one axis (RBC, pers. obs.).

13.7 Conducting Vibrational Playback Experiments in the Field

13.7.1 The Problem

Field playbacks present additional challenges over those encountered in the laboratory, including limited choices of playback location, difficulty in maintaining alignment between playback transducer and substrate, the presence of background noise, and variable weather conditions. Only a few researchers have conducted vibrational playback experiments in the field (Hill and Shadley 2001; Morales et al. 2008; O'Connell-Rodwell et al. 2006, 2007; Caldwell et al. 2010). We continue to focus on playbacks of signals through plant substrates.

Only a fraction of potential receivers will be in suitable playback locations. Subjects must be within reach of the playback apparatus and in a location where the influence of environmental noise and of other members of the biological community is minimized.

Using a pre-filtering procedure to assess and compensate for filtering by the substrate and playback apparatus is also more challenging than in a laboratory environment. For example, if wind moves the plant substrate and changes its position relative to the playback transducer, one must re-compensate for frequency filtering. It is thus necessary to stably align transducer and substrate.

In addition to changing the alignment between the playback transducer and plant substrate, wind is also the single greatest source of environmental noise (Cocroft and Rodríguez 2005). Other sources of environmental noise include rain, birdsong, and signaling by other invertebrates on the focal plant. Environmental noise should be minimized because it can alter the estimation of the system's frequency response (Hill and Shadley 2001; O'Connell-Rodwell et al. 2006) and because it can influence receiver behavior. For example, wind inhibits vibrational communication by insects (McNett et al. 2010; Tishechkin 2007), and birdsong inhibits signaling by male wolf spiders (Gordon and Uetz 2012).

Variable weather conditions pose significant challenges for playbacks in the field, given that most electronic gear used in vibrational communication research is fragile and costly. If one is using wax, putty, or similar adhesive to couple a transducer to a substrate, direct sunlight or heat can cause the transducer to shift position.

13.7.2 The Solution

Desirable playback locations are dependent on the playback apparatus, other members of the biological community, environmental and anthropogenic noise sources, and the experimental design. Playback subjects that have fixed locations are advantageous, in that a playback apparatus can be assembled on site and left in place for several treatments (e.g., as with a paired or repeated-measures design).

For playbacks on plants, stationary alignment between transducer and substrate can be achieved by fixing both the transducer and the plant substrate with separate tripods. However, note that metal tripods in particular may introduce resonance into the playback system and that fixing the plant substrate loads it with additional mass and changes it in ways that are likely to affect signal transmission. Therefore, the system filter should be estimated after all of the playback apparatus is in place.

Wind noise in many environments can be largely avoided by conducting playbacks in the early morning. To avoid contact by nearby plants with the focal plant, assessing the focal plant area in advance and clearing or trimming contacting vegetation is recommended. Additionally, the area surrounding the playback subject should be carefully examined, because undetected invertebrates may vibrationally 'chime in' during a playback treatment.

Field playbacks are replete with trade-offs. Part of the benefit of conducting playbacks in the field is to assess not only the effect of the playback stimulus, but also the relative importance of environmental predictors on receiver response. By minimizing the influence of environmental noise, by conducting playbacks during early mornings, when wind is rare and temperatures are coolest, and by modifying the physical environment of the plant substrate, one limits the potential interference. However, with these efforts, field playbacks are possible and add a layer of biological reality that complements laboratory studies. Of course, the communicating animals themselves will only experience these conditions for a limited time during the day, and there are few studies of how vibrationally communicating animals deal with the varied signaling conditions they encounter (McNett et al. 2010; Tishechkin 2007; Lohrey et al. 2009). However, the evidence so far suggests that the animals communicate when the conditions are favorable [as with animals using other modalities, e.g., Brumm and Slabbekoorn (2005)], so conducting the playback under ideal, low-noise conditions is reasonable.

13.8 Should Experimental Designs Use Multiple Exemplars of Substrates?

13.8.1 The Problem

Every natural substrate is unique; two leaves from the same plant, two areas of leaf litter, or two square meters of soil will differ from each other in their vibration-transmitting characteristics. For some experimental questions, it is reasonable to use the same substrate exemplar for all replicates of the experiment, while for others, using a single substrate would limit the inferences that are possible.

13.8.2 The Solution

The issue is whether the focal animal's response is dependent on variation in the nature of the substrate. For a female preference test, for example, as long as the substrate is appropriate and the system's frequency response is taken into account, using one substrate exemplar may be sufficient. In contrast, for any question for which the nature of the substrate is relevant, using more than one substrate exemplar is important. In particular, localization abilities are highly substrate dependent (depending on propagation velocity, reflected waves, angle of motion relative to the subject's body, etc.), so for making general statements about localization ability, it is critical to use more than one substrate. One approach is to use 'substrate' as an additional experimental treatment. For example, if localization is occurring on a plant and there are to be 15 experimental subjects, one might use three plants, with 5 subjects within each plant. 'Plant' could then be treated as a random effect in a statistical model to evaluate the results. While this would not necessarily provide a representative sample of variation in plant substrates, it would allow one to assess the extent to which differences among plants influence localization.

13.9 Mobile Playback Subjects

13.9.1 The Problem

We have argued that the most basic and widespread problem in vibrational playbacks is the unpredictable frequency response of substrates and playback devices. This problem is easily solved, but only for a single location on a plant or other substrate. If the focal animal remains at or very near the location where the system frequency response was calculated, the animal will experience the desired signal or one very close to it. This method works well for playbacks to animals whose position can be predicted and/or controlled by the experimenter. The picture changes if the playback subject will be moving around during the playback. Because the frequency response of solid substrates varies so much from place to place, the animal will experience different signal properties at different locations.

13.9.2 The Solution

There are at least three solutions to the moving-subject problem. One approach is to determine the frequency response at multiple points on the substrate and generate a series of playback stimuli, each adjusted for the frequency response at a different location. When the animal is at a given point, the playback stimulus appropriate for that location can be played back. This approach is time-consuming but feasible (Gibson et al., in preparation) and is appropriate for some experiments with moving subjects. For example, suppose one wanted to characterize female preference functions with respect to some signal feature such as frequency, but females made substantial movements between responses to signals. If the signal properties have only been controlled at one location, then using female responses at other locations where the signal differs in unknown ways from that intended will introduce a large amount of noise (and possibly bias) into the statistical results. In this case, it would be necessary to play back signals that were previously adjusted for the female's potential locations (or to use the 'post hoc' approach, below). It is not possible to say a priori how close is 'close enough'; for example, would the system response need to be calculated at 1-cm intervals, 5-cm intervals, or 10-cm intervals? It is difficult to predict the signal properties at a given distance from the source because of unknown material properties and complicated branch geometry. To estimate the appropriate spatial scale, one should first characterize substrate filtering at different locations. For example, if the amplitude of a tone changes by less than 3 dB within 10-cm, then adjusting for the system filtering every 10-cm may be sufficient.

A second approach to the mobile-subject problem is to compensate the signals for the system's frequency response very close to the location of the playback device and to assume that the distance-dependent changes in the signal are similar to those that would occur with a real signaling animal at the same location on the substrate. This assumption may not be warranted if the playback substrate is not representative of natural substrates and ideally would be evaluated before conducting the playbacks. This approach may not work well for some experiments, such as tests that relate signal properties to receiver responses, because those signal properties will vary between locations. But animals in nature always have to deal with substrate filtering, so this approach is fine for questions such as those dealing with the timing of movement or signaling relative to the playback stimulus (Cocroft 2005; Legendre et al. 2012).

A third approach to dealing with the mobile-subject problem is to determine 'post hoc' what signal properties the animal experienced at each location (Gibson and Cocroft, in preparation). This first requires tracking the locations at which the animal responded to the signal, then after the experiment is finished, playing back the signals again and recording them at each of the relevant locations. This method allows the signal to be influenced in unpredictable ways at different locations on the substrate, but the measurements taken at each of those locations provide high precision in relating signal properties to behavioral responses. This post hoc approach requires the use of a vibration transducing method that does not influence the substrate's properties, such as laser vibrometry for small structures or accelerometers for large structures or the soil. Signal characteristics (e.g., amplitude) at each location can then be used as predictors in a multiple regression, with the behavior of the animal (e.g., move forward or reverse direction) as the dependent variable.

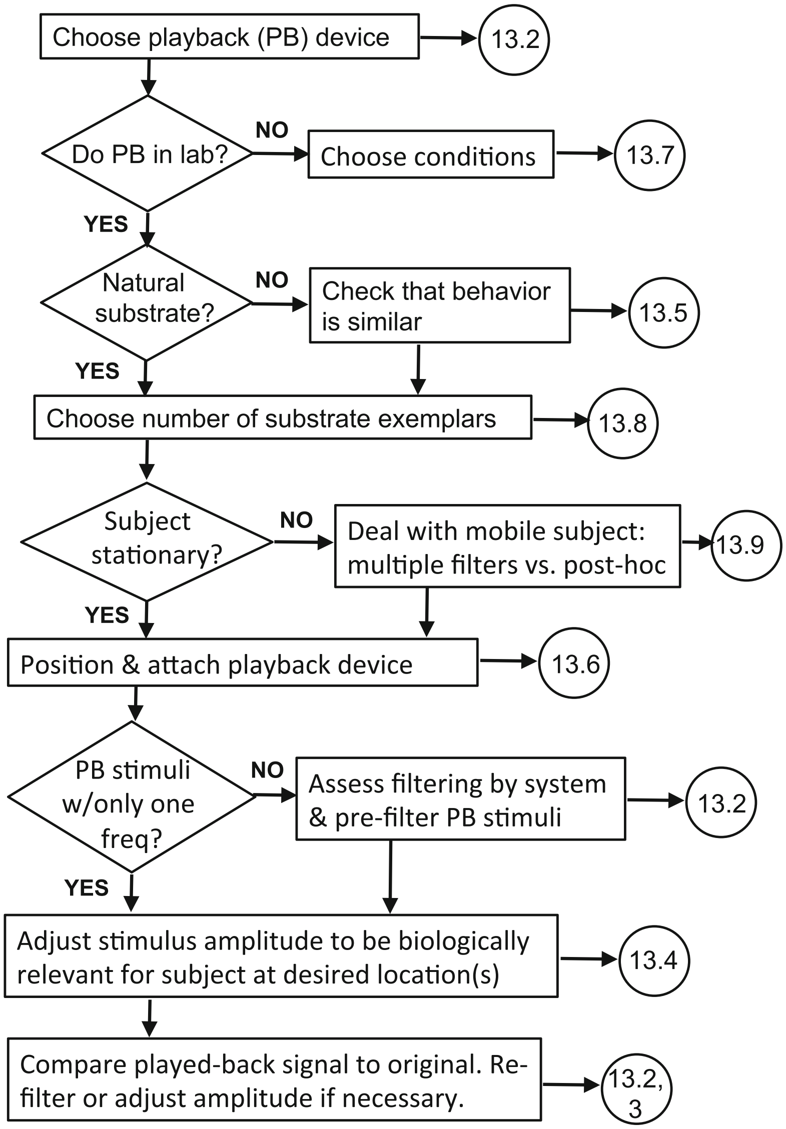

Fig. 13.6 A decision tree for conducting vibrational playbacks. *Numbers in the circles* indicate the section(s) of the text relevant to the decision

13.10 A Decision Tree for Conducting Vibrational Playbacks

Here, we provide a flowchart (Fig. 13.6) to assist in the design and execution of vibrational playbacks and to address the issues discussed in this chapter. Although our discussion has largely focused on playbacks on living plants, most of the issues are relevant to vibrational playbacks through other substrates such as soil or leaf litter.

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A.1 Appendix

The following MATLAB programs use the Signal Processing Toolbox and the Control System Toolbox and have been confirmed to work in MATLAB 6.5 (R13) through to MATLAB 8.1 (R2013a).

A.1.1 Digital Equalization Filter

This program obtains the system equalization filter from stored measurements. A typical system would include the digital-to-analog converter, amplifier and vibration exciter, vibration medium, measurement transducer, anti-aliasing filter, and analog-to-digital converter. Prior to running this code, a continuous random signal (stored in WAVE file ‘Playback1.wav’) is played through the system, and the response is measured and saved (WAVE file ‘Recording1.wav’).

The power spectral density functions are estimated and used to obtain the magnitude of the input-to-output transfer function. The useful data range is taken between the specified lower and upper frequencies in hertz (variables ‘f_lo’ and ‘f_hi’), and the digital filter coefficients are estimated and saved (MATLAB data file ‘FilterCoefs.mat’). For evaluation purposes, the equalization filter is applied to the original playback signal and stored (WAVE file ‘Playback2.wav’). Arbitrary signals of different duration can be filtered this way using the identified filter coefficients, as long as the sample rates are the same.

MATLAB script for acquiring and implementing digital equalization filter:

```
close all, clear all


[out,fs,NBITS]=wavread(‘Playback1.wav’); %WAVE file with
original playback
[in,fs,NBITS]=wavread(‘Recording1.wav’); %WAVE file with
recorded signal dt=1/fs;
t_out = [0:dt:(length(out)-1)*dt];
t_in = [0:dt:(length(in)-1)*dt];


fftLength=4096;
[PSDout,Freq]=pwelch(out,ones(fftLength,1),
[],fftLength,fs);
```

```
[PSDin,Freq]=pwelch(in,ones(fftLength,1),
[],fftLength,fs);
Hcmp=sqrt(PSDout./PSDin); %Amplitude compensation filter


f_lo=40; f_hi=10000; %lower and upper cutoff frequencies in
Hz.
lo=round(f_lo/(fs/fftLength))+1;
hi=round(f_hi/(fs/fftLength))+1;
Hcmp(1:lo)=0; Hcmp(hi:length(Hcmp))=0;


wn=Freq/max(Freq);
B=fir2(fftLength,wn,Hcmp); %this calculates the digital
filter coefficients
A=1;
save FilterCoefs.mat B A


outcmp=filter(B,A,out); %this applies the digital filter to
the signal
outcmp=outcmp*.9/max(abs(outcmp));
wavwrite(outcmp,fs,16,'Playback2.wav');
```

A.1.2 Differentiation and Integration of Playback Signal

This MATLAB script numerically differentiates and integrates the time signal stored in a WAVE file (‘ArbPlayback.wav’). Differentiation of the signal can be approximated using the finite difference method (with ‘diff.m’), while integration of the signal can be approximated using trapezoidal integration (with ‘cumtrapz.m’). These methods work well if the time step is sufficiently small and if there is no noise in the signal.

When the signal has additional noise, the higher-frequency noise is increased by the differentiation process, while the lower-frequency noise is increased by integration. This noise can be reduced by using a first-order band-pass filter to perform the differentiation or integration. The band-pass center frequency is set to a high frequency for differentiation (variable ‘f_hi’), so the frequencies below the center frequency approximate a differentiation filter, while frequencies above are attenuated. For integration, the center frequency is set to a low frequency (variable ‘f_lo’), so frequencies below the center frequency are attenuated, while frequencies above approximate an integration filter. The appropriate center frequency also depends on the frequency content of the signal.

MATLAB script for differentiation and integration of playback signal:

```
wavfile=‘ArbPlayback.wav’; %WAVE file name with playback
signal

[out,fs,NBITS]=wavread(wavfile);
dt=1/fs;
nt=length(out);
t_out =[0:dt:(nt-1)*dt];

%numerical differentiation by finite difference:
outdiff=diff(out)/dt;
outdiff(nt)=outdiff(nt-1);

%numerical integration by trapezoidal rule:
outint=cumtrapz(t_out,out);

% Differentiation filter: Band pass filter with high corner
frequency
f_hi=10000; %upper cutoff frequency in Hz.
SYSc=tf((2*pi*f_hi)^2*[1 0],conv([1 f_hi*2*pi],[1
f_hi*2*pi])); SYSd=c2d(SYSc,1/fs,’foh’);
[Bcmp,Acmp]=tfdata(SYSd);
outfiltdiff=filter(Bcmp{1},Acmp{1},out);

% Integration filter: Band pass filter with low corner
frequency
f_lo=10; %lower cutoff frequency in Hz.
SYSc=tf([1 0],conv([1 f_lo*2*pi],[1 f_lo*2*pi]));
SYSd=c2d(SYSc,1/fs,’foh’);
[Bcmp,Acmp]=tfdata(SYSd);
outfiltint=filter(Bcmp{1},Acmp{1},out);
```

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