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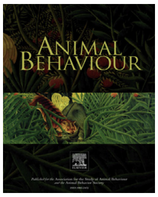

Review

# Biotremology: Do physical constraints limit the propagation of vibrational information?

Beth Mortimer*

*School of Biological Sciences, University of Bristol, Bristol, U.K.*

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Vibrations are a ubiquitous source of information in the environment, and are utilized by a wide range of animals. In this review, I concentrate on the propagation of vibrations across and through substrates, which are materials and surfaces. During the propagation process, physical constraints act on vibrational signals and cues, including loss of energy, filtering or distortion of information. An understanding of these physical mechanisms is important for answering biological questions about communication and information gathering, particularly the reach of signals/cues and how information can be separated from background noise. In this review, I explore the interdisciplinary links central to the field of biotremology to probe the extent to which physical laws limit information propagation. In what follows, I start with a primer in wave theory, before focusing on how the physical factors of wave type and substrate properties affect vibration propagation. I then turn to the interacting biological factors that influence signal/cue propagation during animal-substrate coupling, discussing the numerous behavioural and morphological adaptations employed to mitigate physical constraints. Following this, I then move from limits to possibilities, discussing how animals harness physical laws to provide useful information. Using examples from a wide range of animal systems and biological contexts, I highlight the array of evolutionary strategies to promote the propagation of information given inevitable physical constraints.

The research field of vibrational communication, recently coined biotremology (Hill & Wessel, 2016), studies the transfer of information through and across surfaces and materials, known as substrates. Incorporating plant stems, water surfaces and spider webs, substrates are distinct from the bodies of air or water. Substrate-borne vibrations are used by a wide variety of organisms, so far recorded to be used in over 200 000 species, spanning elephants to water striders, humans to plants (Cocroft & Rodríguez, 2005; Gagliano, Mancuso, & Robert, 2012; Hill, 2008).

Vibrational information can just as commonly be produced incidentally (giving a cue), or purposefully as part of a communication strategy (giving a signal; Lehmann, Goldman, Dworkin, Bryson, & Wagner, 2014). Biotremologists are interested in both and in this review I use examples of cues and signals when discussing the interplay between the physical environment and the propagation of information.

Vibrational information is ubiquitous in the environment and can come from a variety of sources, whether abiotic or biotic, and its use covers a wide range of biological contexts, from communication during courtship, to locating prey items, to detecting far-off rainfall (Hill, 2009; O'Connell-Rodwell, Hart, & Arnason, 2001). To achieve effective information transfer, signals/cues must be above a detection threshold and the receiver must separate the signal/cue from background noise (Mazzoni, Eriksson, Anfora, Lucchi, & Virant-Doberlet, 2014; Virant-Doberlet et al., 2014). Like information transfer in other modalities, vibrational signals and cues inform on the location, identity and often on the state of the sender (Guilford & Dawkins, 1991; Pollack, 2000). Multimodal signalling is often employed to increase the efficacy of information transfer in variable environments (Hebets & Papaj, 2005). However, animals can also use vibrations to actively probe their environment, for example locating blockages in an underground tunnel (Kimchi, Reshef, & Terkel, 2005) or assessing the quality of a wood food source (Inta, Lai, Fu, & Evans, 2007).

Despite its prevalence and scope, however, vibrational communication has not received as much research attention as other modes, one hurdle being the action of complex physical constraints on propagating signals/cues. In this review, I focus on the propagation phase of vibrational information transfer, highlighting the important interdisciplinary links between biology,

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* Correspondence: B. Mortimer, School of Biological Sciences, University of Bristol, Tyndall Avenue, Bristol BS8 1TQ, U.K.
*E-mail address:* beth.mortimer@bristol.ac.uk.

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physics and materials science. This is an intersection at the heart of the field; for it is physical laws that limit the reach of vibrational information, and filter and distort vibrational content. I build on other authors' work focusing on the known behavioural contexts and mechanisms of vibration generation and detection (Cocroft & Rodríguez, 2005; Hill, 2008; Lakes-Harlan & Strauß, 2014; Virant-Doberlet & Čokl, 2004), as well as the physical aspects of information transfer (Elias & Mason, 2014; Markl, 1983; Michelsen, 2014). In what follows, I discuss the physical constraints acting on propagating signals/cues, how physical and biological factors influence and mitigate the extent of these constraints, and how animals can make use of physical laws for biological information.

## PRIMER IN WAVE THEORY AND ANALYSIS

In this section, I introduce the different physical constraints acting on propagating information: energy loss, filtering and distortion. Each of these constraints modifies biological information as it propagates from source to receiver, thus affecting information transfer. All three physical constraints arise from physical laws acting on the wave parameters of temporal pattern, magnitude and speed of waves. In what follows, I provide a primer of the basic theory and analytical transformations needed to quantify, analyse and interpret these parameters. Later in the review, I discuss the physical and biological factors influencing these wave characteristics.

### *Temporal Patterns of Vibrations*

To a physicist, vibration is periodic motion (oscillation) of a particle around an equilibrium position (Main, 1993). Applying this to biology, the definition of substrates can be simplified as a series of particles (molecules) joined by springs (intermolecular forces) that transfer vibrational energy over time and distance.

If frequency remains constant over time, a vibration is a pure tone, where motion over time resembles a sine wave. The position on a single sinusoidal oscillation relative to the resting position is known as the phase (Main, 1993). Substrate vibrations in nature are often not strictly pure tones, but have complex timing patterns that may not resemble simple oscillatory motion. These complex wave patterns contain many frequencies simultaneously, which are known collectively as either narrowband (Fig. 1a) or broadband vibrations (Fig. 1b), depending on the relative scope of frequencies present (although there is no clear definition to separate the two). Using wave theory, we can describe these patterns in terms of the linear summation of its component single-frequency sine waves (Main, 1993). A mathematical function known as a Fourier transform uses this theory to extract the frequency components from a magnitude-time plot, outputting the magnitude of each frequency, known as a power spectrum (see Fig. 1). In practice, this is often done with a fast Fourier transform (FFT), the output of which depends on the sampling rate and total duration of the input data (Duhamel & Vetterli, 1990).

The filtering of frequency is the first physical constraint acting on information propagation. Substrates often act as such frequency filters, meaning that the amount of vibrational energy of each frequency may go up or down during propagation. For example, on the surface of water, frequencies above 20 Hz lose energy over propagation distance, compared to lower frequencies which retain their energy (Lang, 1980). This means that the range of frequencies present during vibration propagation is important, as it affects the potential for frequency filtering to occur.

Furthermore, changes in temporal patterns of magnitude (e.g. signal duration) are also important for conveying biological meaning for a range of systems (Hill, 2008). Sonograms (or spectrograms) combine information on frequency, time and magnitude and are formed by running a series of FFT analyses in discrete time segments (or bins), giving a frequency versus time plot, where the magnitude is plotted as grey values or colour (see Fig. 1). Time and frequency resolution of the sonogram is dependent on the signal sampling rate and the size of the time bins. Both are usually inversely proportional to each other, so that one can only increase temporal resolution by decreasing frequency resolution and vice versa.

Exploring frequency and temporal patterns of magnitude are both useful in biotremology. Each often provides complementary rather than redundant information for organisms. For example, in wandering spiders, frequency is used to discriminate between biotic and abiotic vibration sources (Barth, Bleckmann, Bohnenberger, & Seyfarth, 1988), while syllable duration allows discrimination between species (Schmitt, Schuster, & Barth, 1994).

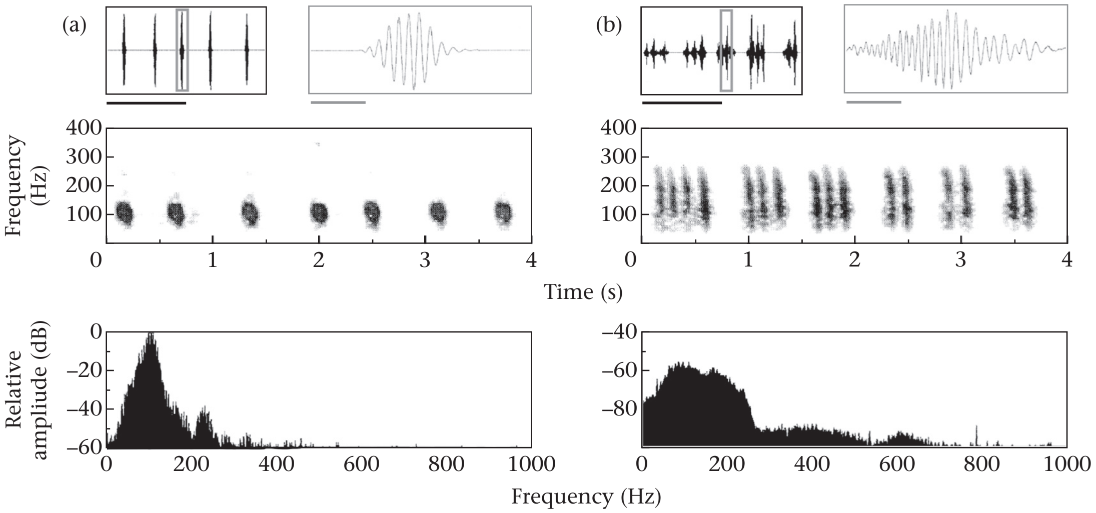

**Figure 1. Presentation of vibrational recordings**. Time-velocity oscillograms (top), sonograms (middle) and power spectra (bottom) of (a) narrowband and (b) broadband pulses of male calling songs of the southern green stink bug, *Nezara viridula*. Black bar indicates 2 s for the oscillogram with the black outline, whereas the grey bar indicates 50 ms for the oscillogram with the grey outline, which is a subsection of the former oscillogram. Adapted from Figure 2 in Čokl, Virant-Doberlet, and Stritih (2000), reproduced with permission from the publisher John Wiley and Sons.