ANNUAL REVIEWS

Annual Review of Entomology

Functional Diversity of Vibrational Signaling Systems in Insects

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Annu. Rev. Entomol. 2023. 68:191–210

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-120220-095459

Keywords

biotremology, substrate-borne communication, signaling context, vibrosensory evolution, multimodal signaling, pest management

Abstract

Communication by substrate-borne mechanical waves is widespread in insects. The specifics of vibrational communication are related to heterogeneous natural substrates that strongly influence signal transmission. Insects generate vibrational signals primarily by tremulation, drumming, stridulation, and tymbalation, most commonly during sexual behavior but also in agonistic, social, and mutualistic as well as defense interactions and as part of foraging strategies. Vibration signals are often part of multimodal communication. Sensilla and organs detecting substrate vibration show great diversity and primarily occur in insect legs to optimize sensitivity and directionality. In the natural environment, signals from heterospecifics, as well as social and enemy interactions within vibrational communication networks, influence signaling and behavioral strategies. The exploitation of substrate-borne vibrational signaling offers a promising application for behavioral manipulation in pest control.

1. INTRODUCTION

Communication by mechanical waves traveling through a medium surrounding a signaler is common among insects (18, 50). Vibrations of the body generate mechanical waves in the surrounding media (in most cases, air and substrate), and traditionally, studies of mechanical communication have all been incorporated within the study of bioacoustics. Recently, the distinction of the signal pathway through the substrate (i.e., the vibrational communication channel) from airborne sound communication has been recognized, leading to the emergence of biotremology as a new scientific discipline studying animal behaviors associated with substrate-borne vibrations (62).

At the vibrating source (e.g., the signaling insect), the differentiation of mechanical signals on sound or substrate vibration may not be evident, but the transmission medium (gas, liquid, or solid) crucially affects wave propagation and the resulting signal properties on the receiver's side, including its mode of detection (62, 138). An acoustic signal (sound) is transmitted in homogeneous fluid media (gas, liquid) via longitudinal compressional pressure waves characterized by particle oscillations in the direction of wave propagation and detected by hearing organs that function as pressure or pressure difference receivers (50, 58, 62, 138). In contrast, vibrational signals are transmitted via diverse types of mechanical waves propagating along the boundary (i.e., surface) between fluid and solid media and are received by various types of mechanoreceptors that detect the particle displacement perpendicular to the direction of wave propagation (50, 58, 62, 138).

Initially, bioacoustic studies in insects were dominated by investigations of airborne sound communication in orthopterans, cicadas, and fruit flies; communication via substrate-borne mechanical waves has received much less attention (50), and knowledge about it has remained fragmented. However, by the beginning of the twenty-first century, it became clear that vibrational signaling is the most common and widespread form of mechanical communication in insects (18, 157).

Increased awareness about the importance of vibrational communication and its long evolutionary history (16) resulted in increased numbers of studies and diversified research topics. However, our understanding of this communication modality and the selection pressures guiding its evolution still remains incomplete and fragmented. Despite the enormous diversity of the approximately 200,000 insect species thought to use vibrational signaling (18), only a few taxa have been studied in depth (154). In addition, the lack of a phylogenetic approach to vibrational signaling and of comparative investigations of trade-offs and adaptions arising from various selection pressures make generalizations difficult. Overall, hemipterans are probably the best-studied group behaviorally (154; see also **Supplemental Table 1**); however, there is a general lack of knowledge on their sensory and neurophysiological mechanisms due to their small size. By contrast, these mechanisms have been well investigated in orthopterans (140); however, due to their well-developed airborne sound communication, the importance of vibrational signaling in this insect group is often overlooked (143).

To increase awareness of the importance of vibrational communication, its diversity, and the emerging potential for practical applications among general readers interested in the entomological research, we summarize the characteristics and specifics of this communication channel and provide an overview of existing information, as well as highlighting new research topics and ongoing challenges. In the article, we primarily focus on references published after the latest comprehensive reviews (18, 157); we provide a more comprehensive list in the **Supplemental Material**.

2. DEFINING CHARACTERISTICS OF THE VIBRATIONAL COMMUNICATION CHANNEL

The specifics of the vibrational communication channel are largely related to the constraints imposed by signals propagating through the heterogeneous natural substrates inhabited by signalers and receivers, given that transmission properties crucially affect the characteristics of vibrational signals and, consequently, the behavioral strategies associated with vibrational communication.

Given the close association between insects and terrestrial plants, herbaceous and woody plants are the most important substrates for insect vibrational communication (18). Transmission of vibrational signals has recently been a topic of comprehensive reviews (37, 106, 112), and we provide only the essential information. The physics of mechanical waves in solids is complex, and current simplified models (13, 104, 120) do not reflect plant geometry and nonhomogeneous internal structure, but bending waves seem to be the only type of mechanical waves important for insect vibrational interactions on plants (13, 91, 100). They are mainly characterized by low propagation velocity, strong attenuation of frequencies above 5 kHz, and lower attenuation of frequencies below 1 kHz, and propagation velocity and damping vary with the mechanical properties of different plant parts (5, 106, 155). In concert with low-frequency geophysical vibrations, plants thus channel the long-range vibrational communication space to a narrow frequency range of roughly 50 to 5,000 Hz (146), with progressive attenuation in the upper half of this range (100).

Waves that travel through the plant are reflected at free or fixed ends (100), and reflections cause resonance resulting in a frequency-specific pattern of standing waves characterized by amplitude oscillations (120). The formation of pressure waves may also be possible within larger wooden stems and trunks (91), but with complex transmission because fibers act as wave guides (112). The role of pressure waves in communication is still unclear.

Vibrational signals traveling through the plant may also cross areas with substantially different propagation, filtering, and damping properties. The active space of vibrational signals (i.e., the effective range, where the signal amplitude is above the detection threshold of intended receivers) can reach several meters and extends to neighboring plants (40, 145). The active space strongly depends on the damping imposed by the transmission properties of the substrate (37, 106), and signals may be distorted by crossing structures with different physical properties. To ensure efficient transmission and reliable detection, vibrational signals with narrowband and harmonic frequency structures must be tuned to the particular substrate (i.e., host plant and/or preferred plant parts) to avoid excessive damping (25). Frequency-dependent attenuation of signals on different plant species has been suggested as an important factor driving signal evolution (98).

Narrow-band signals tuned to specific plants would be undetectable at resonance nodes due to standing waves (120); this situation can be avoided by producing signals containing both harmonic and broadband components or frequency modulation, thus assuring that signal amplitude is high enough at any point on the plant. Such signals are found in many Psylloidea and Heteroptera (47, 83), although frequency-dependent propagation (13) may lead to distortion because bending waves are dispersive, i.e., lower-frequency vibrations propagate faster than higher-frequency ones, and the signal envelope may change progressively with distance from the source.

Low propagation velocity and varying attenuation of vibrational signals in plants provide cues for direct orientation of the receiver toward a signaler via time delay and amplitude differences (52, 158). Vibrating insects induce plant movements in three dimensions, and locating the signaler most likely involves processing a combination of temporal, spatial, and spectral patterns of stimulation of mechanoreceptors in all six legs. These patterns detected by the receivers are affected by both the mechanical properties of the substrate and distance from the source (46). In a natural situation, time delay between the arrivals of low-frequency vibrational signals to spatially separated receptors appears to be the most reliable directional cue (121), although amplitude gradients that can be sampled serially may also be important, especially in small insects whose leg spacing does not impose sufficiently long delays (46, 117). The quality of directional cues varies across the plant, and searching insects may compensate for unclear directional information, e.g., by correcting a directional decision after a wrong turn (46, 117).

Ground-dwelling insects face different environments. On loose sand surfaces, Rayleigh waves are the most important type of mechanical waves for vibrational interactions, especially if disruption occurs near the surface, where only a minor portion of the energy is transformed to compressional waves, which are also attenuated more rapidly (10). Surface waves can convey biologically relevant information at least some tens of centimeters away from the source (10, 74). Similar processes occur in soil, where transmission properties are influenced not only by granularity, but also by water content (91). Finally, the environment of ground-dwelling insects may include leaf litter and other scattered objects, thus potentially introducing even higher variability (38).

Although the insect's body is not part of the transmission channel sensu stricto, it represents the ultimate part of the signal transmission pathway. The body's mechanical response to vibrations may be complex and is highly dependent on the morphology and behavior of an organism (137). Postural changes, such as lifting and lowering the body or flexing and extending the legs, were shown to strongly influence the effective stimulus reaching vibratory receptors and consequently alter their sensitivity (137, 142). The extent to which such effects may be used by insects to behaviorally control for vibration detection remains to be studied. Mechanical properties of the insect body and legs possibly influenced the evolution of vibration receptor organs and facilitated their differentiation across insects (137; see also Section 7).

3. PRODUCTION OF VIBRATIONAL SIGNALS

Our literature review shows that vibrational signaling has been described in 148 families from 18 of the 26 orders of winged insects (Pterygota) (**Figure 1*a***; **Supplemental Table 1**). By contrast, communication by airborne sound (far- and near-field) is limited to six insect orders (18).

3.1. Signaling Mechanisms

Insects produce vibrational signals mainly by tremulation, percussion (drumming), stridulation, and tymbalation (**Figure 1*a***). Tremulation involves vibration of the whole body or any individual body part, and drumming or percussion involves striking of body parts against the substrate. Stridulation refers to friction of specialized body parts against each other or against the substrate, while tymbalation is associated with buckling of abdominal plates. Tremulation and drumming occur in most insect orders, with tremulation occurring in 68% and drumming in 39% of the signaling families (**Figure 1*b***). Such widespread use of these mechanisms reflects the ease of producing signals with them, without evolving specialized structures. Typically, tremulation produces low-frequency signals depending entirely on the emitter's muscle activity, while drumming induces broadband noisy signals whose spectra depend primarily on the substrate. These signaling behaviors are likely ancestral in many lineages but can also be considered particularly prone to evolutionary plasticity (see also 56, 131, 139). In some taxa, tremulation signaling may have evolved by ritualization of aggressive movements (as has been hypothesized for bees; 129).

Stridulation is phylogenetically more limited than tremulation (**Figure 1*a***) but employs a wider diversity of body segments and structures (**Supplemental Table 1**). A particularly high diversity of stridulatory organs is known from Heteroptera and Coleoptera, although sometimes without information on their function (47, 163) (**Supplemental Table 1**), with multiple evolution and convergence seen even in the same families. Stridulatory vibrations are broadband with at least some airborne components and are most often associated with insect defense or disturbance behaviors (86). Defense stridulation aimed at predators represents one possible precondition to its intraspecific use, as appears to be the case in some Orthoptera (42). A similar primary function of stridulation in alarming conspecifics has long been suggested to occur in ants, although this was not confirmed in a recent phylogenetic analysis (48).

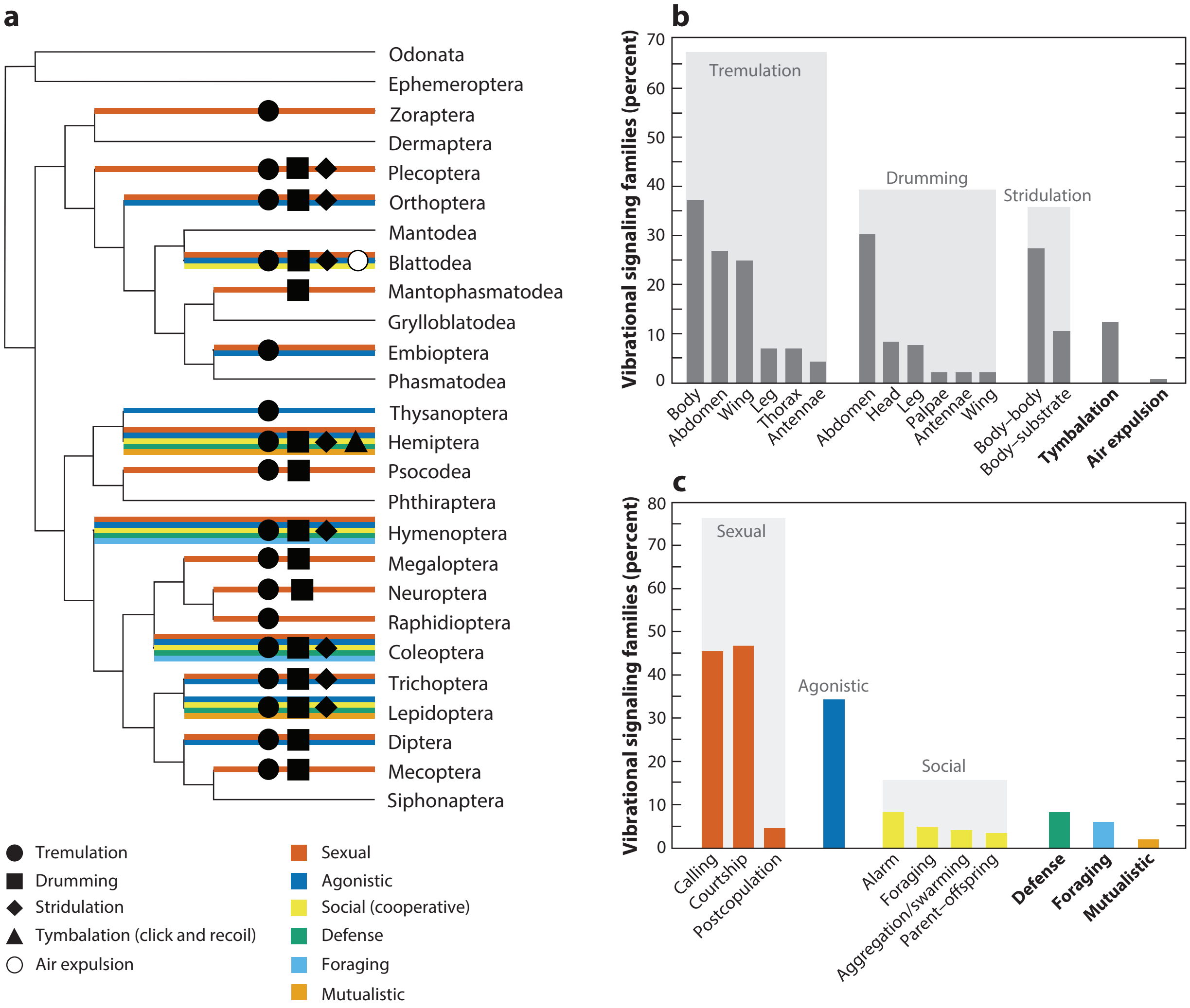

Figure 1

Vibrational signaling mechanisms and contexts (*a*) in a phylogenetic framework (phylogenetic relationships based on those in References 162 and 165) and (*b*,*c*) quantified by the family-level occurrence [(*b*) mechanisms, *n* = 145; (*c*) contexts, *n* = 146]. The analysis is based on the information in **Supplemental Table 1**. In addition to the four predominating mechanisms, air expulsion in cockroaches (traditionally considered acoustic) elicits intense vibrations in the substrate (147). Of the overall social functions quantified, only the most common are shown individually. Defense only relates to examples where the deterring function of substrate-borne signals has been demonstrated or suggested based on arthropod predators. Contact vibrational signaling and the hypothesized modes or contexts are not considered in this analysis.

Tymbalation associated with vibration production is found only in Hemiptera (29, 164). The tymbal organ is located in the first two abdominal segments and consists of usually striated dorsolateral cuticular plates, enlarged apodemes, and specialized muscles that buckle the plates by contraction (29, 164). Vibrational signals produced by tymbals are highly diverse, ranging from a series of single broadband pulses to complex broadband signals that may include tonal or frequency-modulated sections. Recently, a functionally similar snapping organ situated between the metathorax and abdomen and acting via elastic recoil has been described as a distinct signal production mechanism in planthoppers (Hemiptera: Fulgomorpha) (28). The evolutionary origins and potential homologies of tymbal and tymbal-like mechanisms across all Hemiptera, excluding Sternorrhyncha, are still under debate (29, 164).

Insects typically use more than one vibrational signaling mechanism and apply these mechanisms either in different contexts or simultaneously and/or in succession during the same context (**Supplemental Table 1**), thereby increasing signal information content and specificity (103, 143). Due to the diverse spectral characteristics of signals induced in the substrate by different mechanisms, multicomponent vibrational signaling also facilitates detection and improves signal transmission over heterogeneous substrates (37). The adaptive value of multicomponent signaling is generally suggested by the evolution of increasing complexity in the signaling mechanisms seen in some phylogenetically well-resolved and behaviorally described groups, such as Plecoptera and Neuropteroidea (56, 131).

3.2. Energetics of Signal Production

The energetic costs of vibrational signaling have received little attention. In the beetle *Psammodes striatus* (Tenebrionidae) (84), bushcricket *Docidocercus gigliotosi* (Tettigoniidae), (127) and hemipteran *Aphrodes makarovi* (Cicadellidae) (77), signal production is always associated with markedly increased energy consumption, although these species use different mechanisms to produce vibrational signals (drumming, tremulation, and tymbalation, respectively). In the leafhopper, indirect physiological costs associated with emission of advertisement signals also had a negative effect on male survival (77).

4. SIGNALING CONTEXTS

4.1. Sexual Signaling

Sexual signals, mostly used in calling and courtship, are the most common type of vibrational signal and are described for 76% of the families that utilize vibrational communication (**Figure 1*a*,*c***). These signals and signal repertoires are species specific and usually also sex specific (but see 57). Most information is usually contained in the signal's temporal pattern, although in some species, the frequency content conveys information, as well (19). In closely related species, signals can be highly divergent (33) or show variations on the same design pattern (19). Signals produced by males often show higher levels of structural complexity (33, 83, 125).

Calling or advertisement signals advertise presence and readiness to mate over longer distances, and in most species, the male initiates a mating sequence. Typically, a stereotyped coordinated duet is established between partners, with the male searching for a stationary female (52, 76, 158). Vibrational duets represent a dynamic interaction of mutual influence and stimulation between the sexes, also associated with sexual selection (76, 125). Among Hemiptera, precise timing of signal exchange appears to be crucial for recognition and accurate localization (33, 75, 76).

While the role of vibrational signals as reproductive barriers has been studied extensively for many taxa (e.g., 19, 27, 33, 57, 83, 93), much less is known about their function and information content as fitness indicators in precopulatory mate choice (3, 31, 143). In close-range courtship or postcopulatory mate guarding, vibrational signals are often produced in concert with signals of other modalities, such as visual, tactile, and acoustic signals (see Section 5).

4.2. Agonistic Signaling

Agonistic vibratory signaling as part of long-range male rivalry, territoriality, or short-range aggression has been described in 10 insect orders and 34% of the families in which vibrational signaling is present (**Figure 1**). Vibrational aggression in direct encounters is especially common, mostly in males fighting for access to females, although it is also expressed by females and larvae competing for the same resources (1, 166) (**Supplemental Table 1**). In Orthoptera, the most thoroughly investigated order in this respect, signals convey aggression, size, and/or postcontest status via body tremulation, sometimes combined with stridulation (34, 124). Their territorial vibrational signals are used for spacing individuals either in combination with sound (61) or operating only via the substrate (72). Vibrational rivalry has been described for several groups of Hemiptera, where male–male interactions are based on call alternation (82), emission of rivalry signals (24), or emission of masking signals overlapping female reply, which can disrupt a duet (96) and/or confound a rival searching for a female (78). The focus on natural assemblies of multiple individuals revealed the first cases of female vibrational rivalry (23), as well.

4.3. Social (Cooperative) Signaling

In social and other group-living insects, vibrational signaling serves various functions important to regulating social structure and coordinating activities. Most widespread are alarm signals, enabling fast transmission of information about danger within the group or colony (**Figure 1*c***). Such signals may be used directly as defense against an intruder (107) but most often elicit other behavioral responses, like synchronizing defense activities and recruitment of defenders (53, 54), stopping recruitment to a feeding site (109), and eliciting parental defense (14). Vibrational signals also coordinate foraging (64, 167) and hatching (39) or influence aggregation or group movement (15, 44). They play an important role in brood care, influencing larval development (101, 150) or facilitating feeding or bonding with the parent (4, 115). Vibrational signals of social Hymenoptera can also be modulatory, increasing the rate of group activity for multiple purposes depending on signal amplitude (123) or influencing tuning of activity levels among different group members (65).

4.4. Defense, Foraging, and Mutualistic Signaling

Acoustovibratory defense (distress, disturbance, or protest) signaling is widespread among insects and has been recently reported from 69 families in 12 insect orders (86; also including defense recruitment signaling to conspecifics, as described above). Such mechanosensory defense often occurs in concert with visual signals and clearly is highly adaptive, although its actual effects have rarely been tested (86). Little is known about the importance of individual signal components, and it is not possible to infer the number of taxa that employ vibrational signals to deter attackers. At present, vibratory defense aimed at natural enemies has been demonstrated, or strongly suggested, for several species of Hemiptera, Hymenoptera, Coleoptera, and Lepidoptera (**Figure 1*a***). Most of these cases relate to maternal defense (e.g., 108), defense of larvae or pupae against predators and parasitoids (e.g., 85, 107), and pupal defense against perturbation by conspecific larvae (70) and vibrational mimicry (35) (**Supplemental Table 1**). These cases definitively underscore the actual use of vibrations as deterring signals.

Vibratory signaling can also be a part of foraging tactics, largely known from Hymenoptera, such as detection of larval hosts in the wood by vibrational sounding, or detection of vibrational signal echoes, by parasitoid wasps (156). Other examples include vibration of spider webs during hunting by thread-waisted wasps (6) and vibration of stamens by thoracic muscle contraction during pollen collection in thousands of bee species (buzz pollination) (30).

Vibrational signals also play a significant role in mutualistic interactions between ants and treehoppers or lepidopteran larvae, which signal to increase the level of ant attendance or protection (105, 153).

5. VIBRATIONS AS AN ELEMENT IN MULTIMODAL SIGNALING SYSTEMS

Research on multimodal communication in insects has become more common in recent years. However, despite the great importance of vibrational signals for insect communication, their high information potential and flexibility (92, 114), and their effectiveness at night and in dark habitats, their complementary role to other signaling modalities has been largely overlooked (143). The integration of vibrations into complex multimodal displays has been extensively studied in spiders (Lycosidae and Salticidae), where substrate-borne components are often an essential part of the signal, improving the reliability and the amount of transmitted information and, thus, the response of the receiver (73). Because vibrational signals are inherently associated with body movements, which are visually perceptible in diurnal species, and often simultaneously generate acoustic signals in the air (11), insects that rely solely on vibrational signals for communication (such as Auchenorrhyncha) may not be common.

5.1. Vibroacoustic Signaling

The courtship behavior of Orthoptera is one of the best-studied examples of vibroacoustic communication, in which males produce sound and vibrational signals simultaneously by stridulation (67) or combine them with independent vibration-production modes, such as tremulation (31, 143). The simultaneous sound and vibration components may act synergistically to facilitate detection and localization of signalers (132) or may be intended for different receivers and function simultaneously in sexual and agonistic interactions (34, 60). In neotropical crickets and bushcrickets, a partial shift from acoustic to vibrational signaling has evolved as a strategy to avoid aerial predators that exploit airborne sound (127), which also has led to a unique multimodal exchange of male acoustic calls with female vibrational responses (122, 152).

5.2. Vibrovisual Signaling

Production of mechanical signals often requires distinct, high-amplitude movements of body parts. Addition of contrasting visual components to moving appendages, such as wings (8, 55), legs, or antennae (113), is not uncommon. Such signals also induce intense vibration in the substrate (e.g., 69), but the specific functions and interaction of visual and substrate-borne signals in displays has rarely been investigated (but see 55). The extent to which the vibratory and visual components of these signals are used for communication remains to be investigated.

5.3. Vibrochemical Signaling

In insects, chemical signals have multiple functions, including long-range attraction (12); however, when insects are on the same plant, mate choice and localization are often also controlled by vibrational signals (26). In stink bugs (Pentatomidae), vibrations have been shown to modulate, in turn, the production of aggregation pheromones in males (102). A similar positive feedback loop between alarm pheromones and vibrational signals is also known from termites (Isoptera) (32).

5.4. Vibrations in Complex Multimodal Signaling

Besides the few examples of bimodal communication presented above, insects can also convey information to potential mates by combining several signal modalities. One of the most-studied examples is fruit flies (Drosophilidae), in which the importance of vibrational signals in complex courtship, which includes visual, acoustic, and contact chemical signals, has been demonstrated only recently (41, 97). Moreover, in many insect species, vibrations are an important part of contact precopulatory, copulatory, and postcopulatory communication, which functions via multiple sensory pathways (e.g., 27, 126).

6. INSECT VIBRATIONAL COMMUNICATION NETWORKS

In recent years, our understanding of vibrational communication modality changed significantly with the realization that, in nature, vibrational communication usually takes place in the presence of other conspecific and heterospecific individuals that can detect the emitted signals (160, 161). Interactions arising from such network environments reveal selection pressures on vibrational communication systems that are not apparent when vibrational communication is considered to take place exclusively in a signaler–receiver dyad.

6.1. Social Interactions

Intraspecific eavesdropping appears to be common in leafhoppers (Hemiptera, Cicadellidae). In this group, satellite behavior, in which an intruder silently locates the female duetting with another male, is a common element of male–male interactions (78, 82, 96). In such situations, the most important factor in obtaining the female appears to be the ability to locate the female before the rival. Because signaling effort may also be negatively correlated with longevity (77), males may invest more in effective location of the female than in competitive signaling when faced with a rival (78), especially when longevity may also predict higher male lifetime mating success (149).

6.2. Predator–Prey and Parasitoid–Host Interactions

Substrate vibrations play a key role in mediating many predator–prey and parasitoid–prey interactions (for a review, see 160). While the majority of the information obtained is associated with incidental vibrations caused by prey movements, host or predator species- and sex-specific vibrational signals used in communication can also be exploited by specialized parasitoids (81) and generalist predators (159). Because eavesdropping and exploitation of vibrational signaling by enemies is difficult to observe, such interactions are probably more common than current evidence suggests (160).

7. VIBRATION DETECTION

7.1. Types and Locations of Vibrational Sensilla

Sensitivity of insects to substrate vibrations is mediated by a variety of mechanoreceptors located mainly in and on the legs, including campaniform sensilla, hair sensilla, and the scolopidial sensilla (for reviews, see 80, 138). Campaniform and hair sensilla are located externally and detect cuticular strain and contact mechanical stimuli, respectively, but can also respond to high-amplitude, low-frequency substrate vibrations (137). Scolopidial sensilla are internal ciliated stretch receptors found all over the body and primarily function as proprioreceptors, although some are specialized to sensitively detect external stimuli such as sound and vibration (43).

Two compound scolopidial (chordotonal) organs located in all legs, the subgenual organ (SGO) in the tibia and the femoral chordotonal organ (FeCO), represent the most important vibration sensors (80, 138). The tibiotarsal and the tarsopreatersal chordotonal organs in distal leg joints also can detect higher-intensity vibration, and their role in vibrational behavior has been shown in specific environments like the surface of water (49).

The location of vibration sensors in the legs, which are in direct contact with the substrate, reflects not only adaptation for the most efficient signal detection, but also perception of directionality by six spatially separated inputs (52, 158). In addition, vibrational stimuli are transmitted effectively over the insect body (20, 142), and chordotonal organs in the thorax or abdomen have been suggested to underlie substrate vibration detection, as well (79, 133). Finally, the Johnston's organ, a chordotonal organ in the antennae, may be used for vibration detection when the antennal tips are in contact with the substrate (66).

7.2. Femoral Chordotonal Organ

The FeCO occurs in all insects and primarily monitors the movements and position of the femur–tibia joint (43). Additionally, it sensitively responds to substrate vibrations in orthopteroids, neuropterans, hemipterans, and dipterans (80, 138). The proprioreceptive and vibratory functions are largely separated between anatomically distinct groups of sensilla (scoloparia) with different attachments, and thus activation mechanics, that project into different functional regions of the ventral nerve cord (87, 111).

The number of (presumed) vibratory FeCO sensilla varies substantially among insect orders, from a few to several hundred (110, 111). The organ is usually tuned to vibrations below a few hundred Hz but can also show sensitive responses up to 2,000 Hz (87, 130). In *Drosophila*, individual sensilla express differential frequency tuning, and two interneuron classes that receive the FeCO input were described as being crucial in vibration detection and mediating a female's freezing response to male courtship vibrations (2, 97). Insect startle and freezing responses to low-frequency vibration can be largely attributed to FeCO excitation (140, 151) and may indicate the evolutionary origin of communication responses to vibration via sensory exploitation (50, 152).

7.3. Subgenual Organ

The SGO occurs in the proximal tibiae of most Pterygota and is the most sensitive and specialized insect vibration detector, with broadband sensitivity (typically between approximately 500 and 1,500 Hz) and thresholds reaching the subnanometer displacement range (138, 140). In Orthopteroidea and most Hymenoptera, it contains a few dozen scolopidial sensilla spanning the tibia; in an extreme case among parasitoid wasps, it even contains 300–400 sensilla (156). Such SGOs are stimulated by hemolymph motion and are most sensitive to vertical tibial vibration (68, 135). Only one to three subgenual sensilla are found in Mecoptera, Megaloptera, Hemiptera, and Neuroptera, with a different orientation from that in other insect groups, and the organ is missing in Coleoptera and Diptera (80, 138), so its homology across insect taxa has been questioned (80). However, the highly increased number of sensilla does not greatly change the organ's sensitivity or its ability to discriminate frequencies, as compared to organs in species with only a few sensilla (21, 22).

A unique sensory elaboration is found in the legs of Orthopteroidea, which have one to three vibration-sensitive scolopidial organs developed next to the SGO (called the SGO complex) (134). This complex has been a subject of intense research, since part of it plays a role in hearing in part of Ensifera (138). Its constituent organs appear in different arrangements in different lineages, reflecting diverse patterns of mechanosensory evolution (138). The adaptive significance of these additional organs in vibration detection has not been clarified; for example, they only moderately extend frequency sensitivity below and above that of the SGO (22, 128, 141). Yet different organs appear to be stimulated via different mechanical pathways within the leg and over the cuticle (128, 141) and, consequently, may differ in their posture-related sensitivity to signals (137). This sensory physiology aspect has important implications for (active) perception of vibrational stimuli and should be experimentally tested in the future.

7.4. Factors in Vibrosensory Evolution

No general correlation has been found between SGO or FeCO variation and the requirements of vibrational behaviors or signaling environments of different taxa. The insects with the lowest numbers of sensilla in both organs (e.g., hemipterans and lacewings), or even lacking the SGO (e.g., flies), rely strongly on vibrational communication (**Figure 1*a***). In contrast, taxa with an apparent lack of such communication, such as mantids and stick insects, can possess an elaborate SGO or SGO complex (80, 134) (**Figure 1*a***). However, the highly enlarged SGOs in the front legs of parasitoid wasps correlate with their use of vibrational sounding in host location (9). Among nonhearing Ensifera, the presence of the auditory precursor organ in the SGO complex relates to the use of signaling modes based on high-frequency substrate vibration (139). In a troglobitic cave cricket which inhabits rock substrates that highly constrain vibration transmission, the SGO complex shows a significant structural regression (136). All of this indicates a complex interplay of selection imposed by communication, interactions with other organisms, and transmission environments that may be driving insect vibrosensory evolution. Our understanding of these processes is minimal and remains an obvious target for future research.

8. EMERGING TOPICS IN RESEARCH ON INSECT VIBRATIONAL COMMUNICATION

8.1. Vibroscape and Ecotremology

Insect vibrational communication takes place in the natural environment, where vibrations of other signaling species and from geophysical sources like wind, rain, running water, and even human activities can have crucial impacts on the availability of vibrational communication space (99, 144–146, 160). The importance of a natural vibroscape (i.e., a collection of biological, geophysical, and anthropogenic vibrations in a given environment; 145) in the evolution of vibrational communication has been long overlooked; to date, studies of the vibroscape have focused only on a single temperate hay meadow (144–146). In this habitat, plant-dwelling insects communicated in an environment rich in species-specific vibrational signals with overlapping frequency characteristics and where vibrationally signaling species primarily shared communication space by dividing it on a temporal scale over seconds to minutes. Geophysical vibrations induced by wind provided nearly constant background vibrational noise, with most energy contained in the low-frequency range below 50 Hz.

Recognition of the vibroscape as a reliable source of information in the environment led to the establishment of ecotremology as a discipline, using substrate vibrations to study ecological processes and ecosystem dynamics (144). While ecoacoustics is already an established approach in habitat assessment and conservation biology (148), it neglects species that do not communicate by airborne sound and therefore excludes the majority of insects, which are essential for ecosystem functioning. Ecotremology provides an approach for noninvasive monitoring of insect communities, but several technical challenges remain to be resolved before ecotremological monitoring can be implemented (144).

8.2. Applied Biotremology

Almost half a century since the first experiments with pheromone-based mating disruption, the analogous use of substrate vibrations in pest management is still in its infancy (51, 116).

Nevertheless, it is becoming more generally accepted that insects produce detectable vibrations with nearly every activity and that substrate-borne vibrational signals are important in premating in many agriculturally important insect pests. Following the first field implementation of vibrational mating disruption (95), interest in this potential pest management approach has been increasing (138).

The use of nonspecific vibrational cues (i.e., incidental vibrations induced as a byproduct of other activities) for detection and rough identification of concealed insects such as stored-product pests and wood-boring insects is already well known (89). It can provide a technological basis for the development of methods for exploiting communication in the narrower sense, which promises greater specificity toward target species. This could improve forecasting of pest outbreaks and reduce the need for the current practice of time- and effort-intensive identification by specialists. However, real-time automated detection and identification at the species level requires reliable reference libraries, as well as reliable long-term recording in the field (90, 145, 146). Developing such methods and databases will in many cases require starting from basic research on sexual behavior of target species.

Behavioral manipulation of insect pests is most commonly achieved with artificially synthesized volatile pheromones that are applied using dispensers (63). Application of substrate vibrations avoids several shortcomings of the use of chemical active substances in the field to control susceptible pests, such as the influence of weather and dispenser design on release; the influence of wind and landscape on dispersion; unpredictable concentrations on the micro scale; decay due to environmental factors; and, perhaps most notably, the complexity and cost of chemical synthesis. In comparison, modification of vibrational playback is trivial. However, major technical challenges in applied biotremology include developing methods and equipment capable of transmitting vibrational signals through large areas such as agricultural crops (95, 116, 138).

The most promising developments in behavioral manipulation involve facilitating transmission of vibrational playback. For example, mating disruption of grapevine pests in Europe exploits the vineyard trellis system for signal transmission and has progressed to long-term field trials using commercially developed transducers programmed to transmit broadband vibrations that appear to be effective against the leafhoppers *Scaphoideus titanus* and *Empoasca vitis* (94, 95, 118). Attraction for identification and trapping via playback of species-specific sexual signals is under active development for the psyllid *Diaphorina citri* (88) and the stink bug *Halyomorpha halys* (119, 168), in both cases relying on shorter-range attraction to vibrations after the animals are attracted to the vicinity of the transducer by other signals or cues.

However, potential nontarget effects also need to be considered, especially with vibrational mating disruption, which can be less species specific than other methods (95). The interplay between vibrations and chemical effectors such as pheromones or plant-produced kairomones may be ecologically significant but is virtually unknown outside of small-scale laboratory studies (e.g., 7, 45, 71).

SUMMARY POINTS

1. Signaling by substrate-borne mechanical waves is the most common form of mechanosensory communication in insects.
2. We anticipate that the number of known taxa using vibrational signals and the number of known contexts in which these signals are used will increase, given the ubiquity of insect vibrational sensilla and sensory organs capable of detecting substrate vibration.

3. Future studies should focus on the role of vibrational signals in multimodal communication and as fitness indicators of signaler quality.
4. Understanding insect vibrational communication requires a multilevel approach that links natural vibrational community structure and the physical properties of the environment to behavior and considers data from a phylogenetic perspective.
5. Given the long evolutionary history and the diversity of the vibrational modality, future studies will likely uncover mechanisms that provide crucial insights into processes central to understanding communication in general.
6. Emerging topics such as the use of insect vibrational signals to monitor ecosystem processes and control insect pests should open new opportunities for entomological research.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors are financially supported by the Slovenian Research Agency (Research Core Funding P1-0255 and research projects J1-8142 and J1-3016).

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