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Vibrational Communication in Insects

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A Comunicação Entre Insetos Através de Vibrações

RESUMO - A comunicação através de vibrações originárias do substrato tem sido reconhecida há muito tempo, mas tem recebido muito menos atenção que a comunicação através do som propagado pelo ar. Recentemente, entretanto, tem se tornado cada vez mais claro o papel crucial que sinais vibratórios desempenham na comunicação em muitos grupos de insetos, o que motivou essa revisão suscinta. Sinais vibracionais estão relacionados ao comportamento sexual, de alarme e de defesa, e são em geral usados para mediar ações coordenadas em grupo e interações sociais complexas. Para insetos pequenos esses sinais representam um custo energético mínimo, com alcance máximo, e que não são percebidos facilmente por predadores e por parasitóides em potencial. Sinais originários dos substrato são produzidos por diversos métodos e detectados por receptores presentes nas seis pernas. O comportamento de corte do percevejo verde, *Nezara viridula* (L.) (Hemiptera: Pentatomidae) é analisado como um modelo representativo na ilustração de alguns mecanismos importantes na comunicação vibracional em insetos. Sinais vibratórios são específicos das espécies e de sexos, os quais são produzidos durante a corte e que são adequados para serem transmitidos pelas plantas, contendo informações relevantes sobre a espécie e o sexo do organismo emissor, bem como informações de onde localizar o parceiro. O papel de sinais originados do substrato, os quais são únicos para cada espécie, faz com que os estudos em sinais vibracionais sejam uma importante ferramenta para resolver problemas taxonômicos.

PALAVRAS-CHAVE: Comunicação vibracional, vibração do substrato, comportamento, *Nezara viridula*

ABSTRACT - Communication through substrate-borne vibrations has for long been recognized but in comparison with air-borne sound it has received very little attention. However, in recent years it has become increasingly clear that vibrational signals play a crucial role in communication in many insect groups and we provide a short overview. Vibrational signals are related to sexual behavior, alarm and defensive behavior and are often used to mediate coordinated group actions and complex social interactions. For small insects they are probably the least costly and most far-reaching signals for intraspecific communication and also not easily perceived by a potential predator or parasitoid. Substrate-borne signals are produced by diversed methods and detected by sensitive receptors in all six legs. The courtship behavior of the southern green stink bug *Nezara viridula* (L.) (Hemiptera: Pentatomidae) is taken as a representative model in illustrating some principal mechanisms of vibrational communication in insects. Species and sex specific vibrational signals produced during the courtship are well suited for propagation through plants and to transmit the relevant information about the species and sex of the sender as well as provide the directional cue for locating the mate. The role of substrate-borne signals as a part of the specific mate recognition systems which are unique for each species makes studies of vibrational signals a very useful tool for resolving taxonomic problems.

KEY WORDS: Vibrational communication, substrate vibration, behavior, *Nezara viridula*

Studies of insect communication have revealed a great variety of mechanisms, tactics and systems, which are either chemical, visual or acoustical. Many insects like crickets, katydids, grasshoppers and cicadas produce air-borne sounds which can be heard by humans and consequently have been extensively investigated for many years. On the other hand, we can detect and measure substrate-borne signals only with sensitive equipment and since substrate vibrations generally do not play any important role in our interactions, we can hardly imagine what it is like to live in a 'vibratory world'. Therefore it is not a suprise that although vibrational communication has been recognized for centuries

it was thought to be of minor importance. However, in recent years it has become clear that the use of substrate-borne vibrations in insect communication is more widespread and more important than previously thought.

The objective of this paper is to provide a brief overview of the substrate-borne vibrational communication in insects. However, special emphasis is put on the vibrational communication in the southern green stink bug *Nezara viridula* (L.) (Heteroptera: Pentatomidae). *N. viridula* has been a model species for the whole family and studies of vibrational communication in this species extended our knowledge on substrate-borne communication in small plant dwelling insects. We have tried to keep the amount of cited literature to a minimum and therefore we mostly cite the latest or most comprehensive publications.

Vibrational Communication in Insects - Overview

Table 1 provides a summary of major insect groups in which vibrational communication has been described. Substrate-borne communication is involved in a variety of interactions and serves several functions. Most of the investigated vibrational signals are related to sexual behavior, to finding and attracting a partner. Vibrational communication as a part of the courtship has been found in Orthoptera (Loher & Dambach 1989, Field & Bailey 1997), Plecoptera (Stewart 1997), Sternorrhyncha (Kanmiya & Sonobe 2002), Auchenorrhyncha (Claridge 1985), Heteroptera (Wilcox 1995, Čokl & Virant-Doberlet 2003), Neuropteroidea (Henry 1994, Devetak 1998), Coleoptera (Birch & Keenlyside 1991, Hirschberger 2001), Mecoptera (Rupprecht 1974), Diptera (Hoy *et al.* 1988, Kanmiya 1990) and Trichoptera (Ivanov 1993).

Even insects using air-borne sounds during their courtship, can use vibrational components of these signals as an additional channel in intraspecific communication. In Tettigoniidae, substrate vibrations improve the localization of the stridulating male (Kalmring *et al.* 1997) and it seems that in Gryllotalpidae vibrational component of the male call plays a role in male-male spacing (Hill & Shadley 2001). However, even in the above-mentioned insect groups vibrational signals are not important only in intrasexual communication. Stridulatory signals are often related to defensive behavior, especially in Coleoptera (Schmitt & Traue 1990, Wilson *et al.* 1993, Serrano *et al.* 2003) and Heteroptera (Gogala 1985, Schilman *et al.* 2001).

In group-living treehoppers (Membracidae) vibratory signals are also associated with defense and parental care (Cocroft 1999), locating the new feeding site and possibly also in ant-mutualism (Cocroft 2001). In beetle larvae (Chrysomelidae) vibrational signals have been observed as a part of defensive behavior and group movement (Cocroft 2001, Greenfield 2002). It seems that vibrational signaling during group movement is also present in tingid bug nymphs (Cocroft 2001).

In Isoptera, Lepidoptera and Hymenoptera vibratory signals are not associated with mating behavior. Caterpillars and pupae of ant-associated butterfly species produce substrate-borne signals that attract ants and ensure high attendance level thus increasing their protection against predators (DeVries 1990, Travassos & Pierce 2000). Caterpillars of the family Drepanidae use vibratory signals in territorial displays while defending silk nests from conspecifics (Yack *et al.* 2001).

Many termite species produce substrate-borne vibrations as an alarm signal in response to a disturbance of the nest by a predator (Kirchner 1997). A different vibratory alarm signal is apparently used to convey the information about the presence of pathogenic fungal spores (Rosengaus *et al.* 1999).

Young honeybee queens communicate through vibrational signals called queen piping (Kirchner 1997). In honeybees most other vibratory signals are generally regarded as modulatory communication that elicits a general increase in activity that may help to mediate complex social interactions (Nieh 1998, Lewis *et al.* 2002). They are associated with queen competition (Schneider *et al.* 2001), house hunting (Dohanue *et al.* 2003) and activating or deactivating foraging (Kirchner 1997, Nieh 1998). Vibratory signals are also transmitted during the waggle dance (Nieh & Tautz 2000), however, their role is not clear. In social wasps vibrational signals have been implicated in adult-larval communication (Savoyard *et al.* 1998, Cummings *et al.* 1999) and also associated with worker-queen communication and intensification of activities within the nest (Ishay *et al.* 1974). A very special way of using vibrational signals is vibrational sounding. Some parasitoid wasps locate their hosts by vibrations produced by tapping the substrate with their antennae and detecting the echoes with subgenual organs in the legs (Broad & Quicke 2000, Vilhelmsen *et al.* 2001).

Sawfly larvae living gregariously use vibratory signals to keep the colony together and in locating fresh food sources (Cocroft 2001).

Although ant workers produce acoustic signals that are audible to humans, they are insensitive to air-borne sound, but instead they are highly responsive to the substrate-borne components of these signals (Hölldobler 1999, Roces & Tautz 2001). Vibrational communication in ants occurs in a variety of contexts, often as a part of multimodal signal (as a modulatory signal) and the effects can depend on the social context where the signals are perceived. It plays a role in underground alarm communication, recruitment to food sources and communication between castes in the context of defense against parasites (Kirchner 1997, Hölldobler 1999).

Signal Production. Every movement of the insect body or its parts induces vibrations in the substrate and even such inadvertent signals could be used in intraspecific interactions, as shown for some beetles (Hanrahan & Kirchner 1994). However, most of the signals used for communication are species-specific and their production involves specific movements of the body and/or specialized structures. The most simple and widespread production mechanisms of vibrational signals are percussion on the substrate and tremulation (Table 1). Percussion is often called drumming and involves striking of different body parts directly against the substratum. Tremulation is associated with oscillating, rocking and jerking movements of the body and signals are produced without striking the substrate and transmitted to the substrate

Table 1. Distribution of substrate-borne communication in insects.

Insect taxa	Production mechanism	Reference
ORTHOPTERA		
Anostostomatidae (Stenopelmatidae)	Tremulation	McVean & Field (1996)
Gryllacrididae	Drumming with hind legs	Field & Bailey (1997)
Gryllidae	Tapping with abdomen and maxillary palps, tremulation	Loher & Dambach (1989) Bell (1980)
Gryllotalpidae	Vibratory component of air-borne calling signal	Hill & Shadley (2001)
Rhaphidopohoridae	Tremulation	Virant-Doberlet, pers. observ.
Tettigoniidae	Tapping with hind feet, tremulation vibratory component of air-borne calling signal	Sismondo (1980) De Luca & Morris (1998) Kalmring *et al.* (1997)
ISOPTERA		
Rhinotermitidae	Drumming with head	Kirchner (1997)
Termitidae	Drumming with head	Röhrig *et al.* (1999)
Termopsidae	Drumming with head, vibrating the body	Kirchner (1997) Rosengaus *et al.* (1999)
PLECOPTERA		
Capniidae, Chloroperlidae, Leuctridae, Nemouridae Peltoperlidae, Perlidae, Perlodidae, Pteronarcyidae, Taeniopterygidae	Percussion - drumming with abdomen, rubbing the abdomen against substrate (abdomen-substrate stridulation), tremulation	review Stewart (1997)
PSOCOPTERA		
Trogiidae	Tapping with abdomen	Dumortier (1963)
STERNORRHYNCHA		
Aleyrodidae	Oscillations of the abdomen	Kanmiya & Sonobe (2002)
Aphididae	Rubbing the abdomen and hind legs against substrate	Kubota (1985)
Psyllidae	Possibly tymbal-like	Percy (2002)
AUCHENORRHYNCHA[1]		
Acanaloniidae	Possibly tymbal	Wilson M.R., personal comm.
Aphrophoridae	Tymbal	Ossiannilsson (1949)
Cicadidae	Vibratory component of air-borne calling signal	Stölting *et al*. (2002)
Cicadellidae	Tymbal	Claridge (1985)
Cixiidae, Dictyopharidae, Tropiduchidae	Tymbal	Tishechkin (1997)
Dephacidae	Tymbal, vibrations of the abdomen	Claridge (1985)
Flatidae	Possibly tymbal	Virant-Doberlet, personal. observ.
Issidae	Tymbal	Tishechkin (1998)
Membracidae	Striking the substrate with abdomen, vibrations of the abdomen, wing flicks	Hunt (1994)
Tettigarctidae	Abdominal vibrations	Claridge *et al.* (1999)
HETEROPTERA[2]		
Acanthosomatidae	Possibly tymbal-like mechanism	Gogala (1984)
Alydidae	Stridulation, tymbal, vibrations of the abdomen	Gogala (1990) Numata *et al.* (1989)
Belostomatidae	Vibrations of the body	Wilcox (1995)
Coreidae	Stridulation, tymbal-like mechanism	Gogala (1984, 1990)
Cydnidae	Stridulation, tymbal	Gogala (1984)
Gerridae	Oscillations of the fore or midlegs	Wilcox (1995)
Miridae	Stridulation, vibrations of the abdomen	Gogala (1984) Groot *et al.* (1998)
Pentatomidae		
Pentatominae	Vibrations of the abdomen	Čokl & Virant-Doberlet (2003)
Asopinae	Vibrations of the abdomen, tapping with front legs, tremulation	Gogala M., personal comm., Virant-Doberlet, personal observ.

Table 1. Cont.

Insect taxa	Production mechanism	Reference
Phymatidae	Stridulation, popping locomotory signals, possibly tymbal-like mechanism	Gogala (1984)
Plataspidae	Tymbal-like mechanism	Gogala (1990)
Reduviidae	Stridulation, tymbal-like mechanism	Gogala (1984)
Rhopalidae	Tymbal-like mechanism	Gogala (1990)
Scutelleridae, Lygaeidae	Tymbal-like mechanism, stridulation	Gogala (1984)
Thaumastellidae, Tessarotomidae	Stridulation	Gogala (1984)
Tingidae	Adults - signals associated with jerking movements of the abdomen	Gogala (1984)
	Larvae - vibrations of the abdomen	Cocroft (2001)
Vellidae	Vibrations of the body	Wilcox (1995)
MEGALOPTERA		
Sialidae	Tapping with abdomen and wings, tremulation	Rupprecht (1975)
RAPHIDIOPTERA		
Raphidiidae, Inocelliidae	Tremulation	Devetak (1998)
NEUROPTERA		
Chrysopidae	Tremulation,	review Henry (1994)
	striking the substrate with wings	Devetak (1998)
Conipterygidae	Fluttering the wings	Devetak (1998)
Hemerobiidae	Tremulation	Henry (1994)
Sisyridae	Tremulation	Devetak (1998)
COLEOPTERA[3]		
Anobiidae	Drumming with head	Birch & Keenlyside (1991)
Bruchidae	Stridulation	Kingsolver *et al.* (1993)
Carabidae	Stridulation	Serrano *et al.* (2003)
Cerambycidae	Stridulation	Breidbach (1986)
Chrysomelidae	Stridulation (adults),	Schmitt & Traue (1990)
	tapping (larvae),	Cocroft (2001)
	vibrations of the body (larvae)	Greenfield (2002)
Curculionidae	Stridulation	Wilson *et al.* (1993)
Erotylidae	Stridulation	Ohya (1996)
Geotrupidae	Stridulation	Hirschberger (2001)
Platypodidae	Stridulation	Ohya & Kinuura (2001)
Scolytidae	Stridulation	Hirschberger (2001)
Scarabeidae	Stridulation	Hirschberger (2001)
Silphidae	Stridulation	Hirschberger (2001)
Tenebrionidae	Drumming with abdomen,	Pearson & Allen (1996)
	stridulation	Slobodchikoff & Spangler (1979)
MECOPTERA		
Panorpidae	Drumming with abdomen, tremulation	Rupprecht (1974)
DIPTERA		
Chloropidae	Tremulation (rocking the whole body),	Mook & Bruggeman (1968)
	vibrations of the abdomen	Kanmiya (1990)
Drosophilidae	Vibrations of the abdomen	Hoy *et al.* (1988)
TRICHOPTERA		
Brachycentridae, Glossomatidae, Goeridae, Hadropsychidae, Hydroptilidae, Rhyacophilidae, Odontoceridae, Philotamidae, Phryganeidae, Psychomiidae, Sericostomatidae	Drumming with the abdomen, scrapping with the abdomen, tremulation	Ivanov (1993)
LEPIDOPTERA		
Riodinidae	Caterpillars - stridulation with vibratory papillae	DeVries (1990)

Table 1. Cont.

Insect taxa	Production mechanism	Reference
Lycaenidae	Caterpillars, pupae - unknown mechanism, possibly drumming and/or stridulation	DeVries (1990), Travassos & Pierce (2000)
Drepanidae	Caterpillars - drumming with the abdomen, scraping the mandibles, scraping with abdomen	Yack *et al.* (2001)
HYMENOPTERA		
Apidae	Contractions of thoracic muscles transmitted directly to the substrate,	Kirchner (1997)
	vibrations of the body	Nieh (1998), Schneider *et al.* (2001)
Formicidae	Drumming with mandibles and gasters,	Kirchner (1997)
	scraping with abdomen,	Kirchner (1997)
	stridulation	Kirchner (1997)
Ichneumonidae	Tapping with antennae (vibrational sounding)	Broad & Quicke (2000)
Orrusidae	Tapping with antennae (vibrational sounding)	Broad & Quicke (2000)
Pergidae	Tapping with abdomen	Cocroft (2001)
Tenthredinidae	Scratching with abdomen	Cocroft (2001)
Vespidae	Drumming with antennae,	Savoyard *et al.* (1998)
	drumming with abdomen,	Ishay *et al.* (1974)
	vibrations of the abdomen,	Cummings *et al.* (1999)
	scraping with mandibles (larvae)	Ishay *et al.* (1974)

[1]The detailed mechanism of signal production in Auchenorrhyncha has not been elucidated. Vibrational signals are supposed to be produced by a mechanism homologous to the tymbal system used to produce air-borne sounds in cicadas. However, in many species in which vibrational signals have been recorded, morphological investigations have not revealed any structure similar to tymbal or specialized muscles associated with this mechanism. A similar situation has been found in the primitive cicada from the family Tettigarctidae. In all cases vibrational signals were associated with dorsum-ventral vibrations of the abdomen.

[2]In many Heteroptera the fused first and second abdominal tergite form a tergal plate, which together with the attached muscles has been called tymbal. However, in some groups the tergal plate is probably not acting like a cicada tymbal. Contractions of the muscles probably cause the movements of the tergal plate and signal production is associated with dorsum-ventral movements of the whole abdomen.

[3]In Coleoptera, stridulatory structures are often taken as a systematic character since they show species-specific patterns and can be examined with the aid of scanning electrone microscope. However, sounds are often not recorded and it is not clear whether such putative stridulatory structures are actually used for signal production.

via the legs. Substrate-borne signals are also produced by tymbal or tymbal-like mechanisms and stridulation (Gogala 1984, Claridge 1985, Gogala 1985, Ewing 1989).

Sensory Organs. The best known receptors for substrate vibrations are campaniform sensilla and leg scolopidial organs. Campaniform sensilla are often located near the intersegmental joints on the legs. They are most sensitive for substrate vibrations below 100 Hz, however their sensitivity is low. The most sensitive organ is a complex scolopidial organ named the subgenual organ located in the tibia of all six legs, distal of the femur-tibia joint (Debaisieux 1938, Menzel & Tautz 1994, Devetak 1998, Vilhelmsen *et al.* 2001). The subgenual organ detects displacements of the substrate below 1 nm and acceleration values below 0.1 ms^{-2} in the optimal frequency range between 700 and 1500 Hz (Shaw 1994, Devetak 1998). The structure of subgenual organ differs between insect groups. It can consist from only one sensory cell like in Panorpa (Mecoptera) (Debaisieux 1938) or two as in Auchenorrhyncha (Cercopidae) (Debaisieux 1938) and Heteroptera (Michel *et al.* 1983) to up to 400 in orussid wasps (Vilhelmsen *et al.* 2001). Up to now, subgenual organ has been found in all Pterygote insects, except Coleoptera and Diptera. Substrate-borne vibrations could be detected also by Johnston's organ in antennae (Jeram & Čokl 1996).

Why Use Substrate-Borne Signals? Signals used for communication should convey the context (the meaning of the message) as well as provide the information about the identity and location of the sender. It is essential for successful communication that signals should travel over some distance without losing their specific characteristics. For effective communication with air-borne acoustic signals insects have to be relatively large in respect to the wavelength of the emitted sound (Markl 1983, Bennet-Clark 1998). Smaller insects should produce higher frequency signals; however high frequency sound propagates through environment with greater attenuation and degradation of signal structure (Markl 1983, Bennet-Clark 1998). As a result, many small insects use substrate-borne signals, since vibrations are probably the least costly and most far-reaching signals for communication. This could be also true for insects living on water surface (Markl 1983). Although vibrational signals allow communication range of several meters, vibrational communication is considered a short-range communication channel. However, in comparison with the size of the insects, communication range can be up to 1000 times the length of the body (Stewart 1997, Bennet-Clark 1998). Propagation of vibrational signals is also less diffuse and the signal is confined within the substrate and is therefore on one hand easier to locate, but on the other hand is also less likely to attract the enemies (Bennet-Clark 1998, Barth 2002). For as

long as continuity of the substrate is maintained, the transmission of vibrational signal is not greatly affected by obstacles in its path, which is especially important in the complex environment of the plant.

Constraints of Vibrational Communication. As well as the above mentioned advantages, substrate-borne communication also has some disadvantages. The main one is that vibratory signals are distorted during the transmission through the substrate in time and frequency domain and become increasingly more degraded with increasing distance from the source (Michelsen *et al.* 1982, Markl 1983, Bennet-Clark 1998). An additional complication arises from the fact that on plants the intensity of the signal often does not decrease monotonically with the distance from the emitter (Michelsen *et al*. 1982, Barth 2002). Regardless of these complications, if vibratory signals are used for communication, insects should be able to extract from them the relevant information about the context, species, sex, and position of the sender.

Vibrational communication can be regarded as an interaction between the physical properties of the environment and insect's anatomy and physiology and resulting behavior. How insects overcome the constraints imposed by the physical properties of their natural environment is exemplified with the studies of vibrational communication in the southern green stink bug *N. viridula*.

Vibrational Communication in *N. viridula*

The southern green stink bug *N. viridula* (Fig.1) is a member of the family Pentatomidae which with over 4000 described species is one of the largest families within Heteroptera (Panizzi 1997). *N. viridula* is a cosmopolitan species and highly polyphagous and among several pentatomid pests of legume crops, is ecologically and economically, perhaps one of the most important ones.

As a part of the courtship males and females produce several stereotyped species and sex-specific vibratory signals called songs that are often exchanged in a duet (Čokl *et al.* 2000) (Fig 2). These songs are low frequency signals with the dominant frequency range between 80 Hz and 120 Hz. Signals are produced by vibrations of the body. Production of these signals is accompanied by movement of the abdominal tergal plate and dorso-ventral vibrations of the whole abdomen (Gogala 1984, 1990, Čokl & Virant-Doberlet 2003).

Suitability of the Signals. Are such vibratory signals suitable to function as an effective communication channel? Low frequency signals with dominant frequency around 100 Hz propagate through plants with very little attenuation (Barth 2002) and, therefore, enable longer communication range. Furthermore, as it is shown in Fig. 3 some plants might be better suited for transmission of *Nezara*'s songs to greater distances. At distances above 50 cm from the source there is

Figure 1. Adults of the southern green stink bug *N. viridula*.

up to 20 dB (10 times) difference in the attenuation of the signals in the relevant frequency range between the two groups of plants. Bean, for example, showed an outstanding efficiency of transmission of signals below 200 Hz. At distances of 3 m, it filtered out all signals above 120 Hz and 90 Hz signal was not attenuated to any appreciable extent. Bean is one important host plant of *N. viridula*, however, it is not known whether bugs primarily gather on plants on which vibrations relevant to their behavior propagate particularly well.

There is also an additional consideration. Insects use for their communication vibratory signals that travel over the plant in the form of bending waves (Michelsen *et al.* 1982, Barth 2002). Their propagation velocity is relatively low and decreases with decreasing frequency. If vibrational signals are used for orientation, lower propagation velocity results in increased time difference in the arrival of the signal to various legs and thus provides the possible cue for orientation.

N. viridula can detect substrate vibrations with campaniform sensilla, four scolopidial organs in each leg including subgenual organ and also with Johnston's organ in the antennae (Čokl & Virant-Doberlet 2003). Comparing the frequency spectra of *Nezara*'s vibrational signals with the frequency range and sensitivity of it's vibroreceptors in the legs shows that these receptors are well suited for detection of conspecific signals (Čokl 1983).

Specificity of the Signals. One of the most important roles of species and sex-specific acoustic signals used in insect communication is to enable mate recognition and reproductive isolation. How species-specific are the vibrational signals of *N. viridula*? Are bugs able to discriminate among different signals? Most of so far studied pentatominae species show similar acoustic behavior, vibratory repertoire and syntax, although some songs might be missing from the repertoire (Čokl *et al.* 2000, 2001, McBrien *et al.* 2002, McBrien & Millar 2003). A different repertoire has been found in *Holcostethus strictus* (Fabricius) (Pavlovčič & Čokl 2001). All stink bugs so far studied produce vibratory signals that have low frequency characteristics with dominant frequencies around 100 Hz. Tuning of pentatomid vibrational
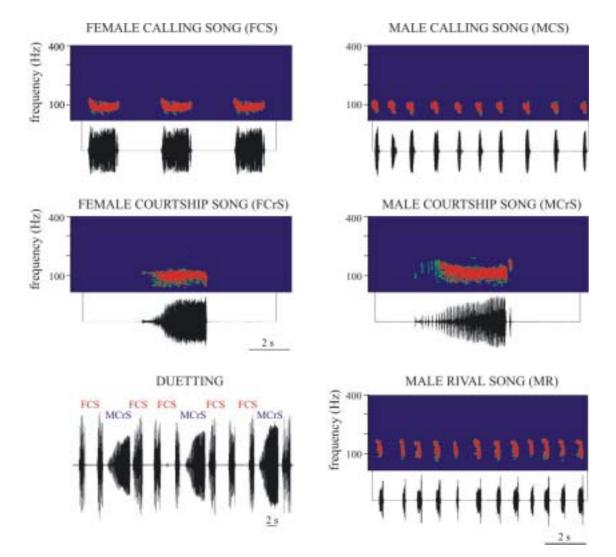

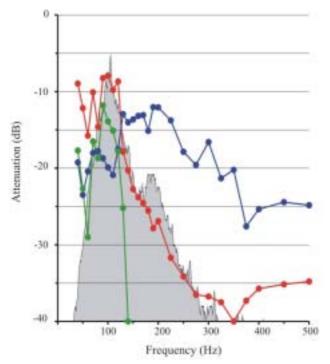Figure 2. Oscillograms (below) and sonagrams (above) of the vibrational songs of *N. viridula*.

Figure 3. Transmission of vibrations through different plants. Plants were vibrated with synthesized pure tone signals and vibrations were measured with a noncontact laser vibrometer at various distances from the source of vibrations. Shown is attenuation as a function of frequency at distances above 50 cm from the site of vibration, superimposed on the frequency spectrum of the female calling song of *N. viridula*. 0 dB attenuation corresponds to the value at the point of vibration. Plants with broadband transmission characteristics (blue): ivy (*Hedera helix* L.), clematis (*Clematis alpina* L.), grapevine (*Vitis vinifera* L.), pea (*Pisum sativum* L.), soybean [*Glycine max* (L.) Merr.], meadowsweet (*Filipendula ulmaria* Mill.). Plants with low-pass transmission characteristics (red): bean (*Phaseoulus vulgaris* L.), potato (*Solanum tuberosum* L.), chicory (*Cichorium intybus* L.), elder (*Sambucus nigra* L.). Green: values measured on bean plant at distance 3 m from the source.

signals to mechanical properties of plants most probably limits frequency characteristics of vibratory songs to play a major role in song and species identification, for as long as the dominant frequency remains in the appropriate frequency range. Species specificity of vibrational signals has been found mainly in temporal characteristics such as duration of the signals and their repetition time.

In the behavioral context of courtship and rivalry males of *N. viridula* are able to distinguish between conspecific male and female signals. They also distinguish heterospecific signals, which differ in temporal parameters from conspecific female signals (Miklas *et al.* 2003a, Hrabar *et al.* in press). However, they did not discriminate between the conspecific female calling song and the heterospecific signal, which has very similar pulse duration and repetition time values (Hrabar *et al.* in press).

Recently it became evident that vibratory songs of existing geographically isolated populations of *N. viridula*

differ in their temporal characteristics, such as duration and repetition time of the signals (Ryan *et al.* 1996; Čokl *et al.* 2000, 2001; Miklas *et al.* 2003a). Fig. 4 shows differences in duration and repetition time for the male and female calling songs. It seems that these differences are genetically determined (Virant-Doberlet *et al.* 2000). Although males recognize female calling signals from another population as a conspecific female call it seems that males still prefer vibratory signals of females from their own population (Miklas *et al.* 2001, 2003a).

Orientation to a Source of Vibration. For a long time it was thought that small insects might be unable to extract information about the position of the sender from vibrational signals, the main reason being that amplitude and time differences of arrival of the signal to spatially separated vibroreceptors in various legs are too small to be evaluated in the central nervous system. Transmission of vibrational signals through plants in the form of bending waves imposes some additional constraints on localization. On plants there is often no predictable relation between the amplitude of the signal and distance from the sender (Michelsen *et al.* 1982, Barth 2002). Furthermore, propagation velocity of the signals can substantially differ even between different parts of the same plant. Behavioral experiments however, showed that males of *N. viridula* can accurately localize a vibration source, i.e., singing female on a plant (Čokl *et al.* 1999). Although the exact mechanism underlying vibrational directionality in small insects is still not known, studies in *N. viridula* provide some insight into possible solutions.

In the complex environment of a plant, at each branching point between the main stem and the side branches, a searching male has to decide which one to take to reach the female. Searching behavior includes characteristic stops at branching points, waiting for the next female calling signal and testing possible paths with the legs.

Larger arthropods like scorpions and spiders use time-of-arrival and amplitude differences in stimulation of various legs as directional cues (Brownel & van Hemmen 2001, Barth 2002). Distances between legs of *N. viridula* do not exceed 1 cm and calculated time delays are on the borderline of the lowest behavioral threshold time delay ever found which is as short as 0.2 ms in scorpions (Brownel & van Hemmen 2001). However, at branching points male stretches the legs between branches and thus increases the distance between legs and the resulting time delay.

On bean plants the measured amplitude differences of vibrational signals at adjacent points around the branching points were large enough that they could release differential neuronal responses at legs positioned at stem and petiolus; however, the amplitude of the signal is not necessarily higher at the branch closer to the source of vibration (Stritih *et al.* 2000).

N. viridula could extract directional information also from phase-shifts in the signals arriving to different legs and from evaluation of differences between components of different frequencies (Michelsen *et al.* 1982, Barth 2002). Directional information could also be available in mechanical response of the body to substrate vibrations as was recently proposed for treehoppers (Cocroft *et al.* 2000) and such mechanism
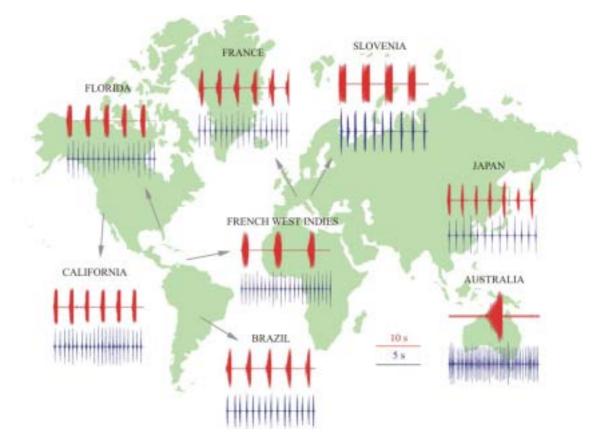
Figure 4. Differences in temporal characteristics of vibrational songs among geographically isolated populations of *N. viridula*. Red: female calling song. Blue: male calling song.

could amplify the effects of very small time differences between inputs from the legs.

Modulation of Pheromone Emission by Vibrational Signals. Mating behavior of *N. viridula* has been divided into two phases: long-range mate attraction and short-range courtship (Borges *et al.* 1987). Sex pheromone produced by males of *N. viridula* is regarded as long-range attractant that brings bugs to the same plant whereas vibrational signals are used on a closer range once bugs are already on the same plant. Recently it was shown that males release larger amount of pheromone when they are stimulated with the female calling song (Miklas *et al.* 2003b). This appears to be a specific reaction since pheromone production did not increase when males were stimulated with male rival song or artificial signals. The female calling song of another population was less efficient in stimulating pheromone emission than the female song from male's own population. Such feedback modulatory mechanism may improve synchronization of sexual activity and provide sensory cues for sexual selection as well as reduce energy costs and the risk of parasitism.

Concluding Remarks and Future Perspectives

Current data indicate that substrate-borne vibrational communication is most widespread in Plecoptera, Hemiptera and Neuroptera but the reason for this might only be that most of the research on insect vibrational communication has been concentrated on these taxonomic groups. More detailed investigations in other groups will probably reveal even wider use and importance of vibratory signals. It is important to bear in mind that the signal modality most obvious (and easily detectable and recordable) to us is not necessarily biologically the most relevant one to the insects. We can not dismiss vibrational signals as a relevant communication channel, because from our current knowledge and perspective they impose too many constraints on communication. Insects have shown us many times that in the field they perform much better than our predictions and theoretical calculations imply. Solution does not necessarily have to be perfect or flawless, just good enough to be effective in 'real life'. Solutions to very complex situations often involve behavioral adaptations and such strategies might not be immediately obvious to the observer.

Vibrational signals are not regarded only as a communication but also as cues (stimuli whose perception by other animals is not beneficial to the emitter). While moving either prey or predator can not prevent inducing vibrations in the substrate. Mechanoreceptors able to detect vibrations of the substrate are so common in insects that vibrational cues are certainly very important even for insects in which vibrational signals are not used for intraspecific communication.

But what use can vibrational signals be to us? Vibrational signals have often been associated with cryptic species as

seen in Auchenorrhyncha (Claridge *et al.* 1997) and Neuroptera (Henry 1994) and they were sometimes the first clue of hidden diversity within the taxon. Their role as a part of the specific mate recognition system, which is unique for each species and results in reproductive isolation, makes the recording of substrate-borne signals a very useful tool for solving taxonomic problems that defy traditional morphology based methods. Ultimately they can tell us more about the species itself than molecular markers since not only they provide the information that differences exist, but also whether we are actually dealing with biological species.

Many insects that use vibrational signals during their courtship are recognized as important pests. It is necessary to stress the possibility that for species in which substrate-borne signals are an essential part of localization, pheromone traps might not be efficient.

Although it is obvious that vibrational signals and cues play a very important role in insect life, vibrations are probably still the least understood channel of communication.

Taking into account the great number and variability of insects, it is not suprising that in many cases even the mechanism of signal production is not known and that for some insect groups a more detailed knowledge about vibroreceptors is lacking. There are only a few studies about processing of vibrational information in the central nervous system, very little is actually known about mechanisms of vibrational directionality in small insects and almost nothing about determining the distance of the source of vibrations. Recently published comprehensive reviews exist for air-borne acoustic communication in insects (Gerhardt & Huber 2002) or vibrational communication in spiders (Barth 2002) but are not available for insect vibrational communication. To close these gaps in our understanding of fundamental mechanisms of vibrational communication some effort should be made to study the vibratory environment of insects using vibrational communication living in different ecological conditions. Some future research should be on the one hand extended to greater number of insect species in different taxonomic groups and on the other hand to more detailed neurophysiological investigations of some model species. Understanding communication system such as insect vibrational communication needs a multi-level approach linking physical properties of the environment to behavior, behavior to processing in the central nervous system and eventually also to evolution. The sheer complexity of such approach and the work needed is of course overwhelming. But this should not prevent us from trying. We sincerely hope that in the future many biologist, entomologists, neurobiologists and evolutionary biologists will find insect vibrational communication as important and interesting as we do.

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