Chapter 3
Sound or Vibration, an Old Question of Insect Communication

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Abstract About one hundred years ago, one of the pioneers of bioacoustics, Johann (Ivan, Joannes) Regen, born in Slovenia and living later in Vienna, investigated acoustic communication in crickets and bushcrickets. Despite many convincing results, he had a difficult dispute with a physiologist Otto Ernst Mangold to prove his ideas about airborne sound communication in insects. Eventually, he succeeded to persuade him with a series of imaginative experiments. However, his findings are by far not valid for all groups of insects. When I started to investigate acoustic communication in Heteroptera with my students and coworkers about half a century later, the question of their communication channel was not clear. After some critical experiments, it became evident that they emit and receive substrate-borne vibrational signals. Similar experiments were performed with "small cicadas" by Ichikawa, Strübing and Traue, who also came to the conclusion that they use substrate vibration as a communication channel. Nowadays, we know that the majority of Hemiptera and also many other insects use the vibrational channel for acoustic communication, some others use true sound or near field airborne vibrations, but not to forget acoustic signalization in aquatic and semiaquatic insects. However, some insects apparently use both channels for acoustic communication or orientation.

3.1 Introduction

From old books and prints, we know that people have been aware of insect sounds for centuries and even millennia. They included singing insects in pictures and mentioned them also in texts and poems. In some cultures, especially in the Far

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East, people have appreciated from the old days until now the songs of crickets and keep them in captivity to hear and enjoy their voices. The old Greeks knew such details, like that only male cicadas emit loud songs and females do not. The Greek poet Xenarchus (fourth century BC) mentioned this in one of his poems with appreciation and a reflection on human life. Xenarchus says in the *Sleep*: *Are then the male cicadas not happy, say you? When they have wives who cannot speak a word?* (Athenaeus 1854). However, they could not know much about the details of sound production or reception and did not care how insects communicated among themselves.

Only with the invention of the microscope and development of natural sciences in the seventeenth and eighteenth century were papers with first descriptions of sound producing organs published (e.g., tymbal: Casserius 1600, stridulatory structures in bugs: Ray 1710). There appeared during the same time also first descriptions of acoustic behavior in some singing insects (e.g., Rösel von Rosenhof 1746–1755; Poda 1761: p. 58, "*Cimex iracundus* sonum edit"). However, the question of how insects communicate, and if they can receive airborne sound or just substrate vibration, scientists began to discuss much later, at the end of the nineteenth century.

3.2 About 100 Years Ago…Ernst Mangold and Johannes Regen

Just about 100 years ago, Ernst Mangold wrote in a renowned German Handbook of Physiology (Mangold 1913) the chapter on hearing and static senses in vertebrates and invertebrates. Pages 885–898 and 905–906 are devoted to insects where the author critically presented and discussed the observations and experiments on this topic that had been published during past decades. He cited publications of V. Graber (1875, 1877, and 1882), who reported simple behavioral reactions of insects to vibrations and sound. However, he mentioned that there were still no exact proofs for biologically relevant reactions to acoustic cues, for instance for orientation of grasshopper females to the singing males.

He mentioned and cited also papers of W. Nagel (1892), L. Oyen (1901), E. Radl (1905), and J. Regen (1909). Mangold's conclusion in his book chapter was that there was no clear evidence for hearing ability of insects despite the opposite but convincing results of Regen's experiments (Figs. 3.3, 3.4 and 3.5). Nevertheless, he admitted (Mangold 1913, p. 887) that:

> Die interessanten Versuche von Regen (s. weiter unten!) an Orthopteren machen denn hier auch einen willkommenen Anfang
>
> The interesting experiments of Regen (see below!) on Orthoptera make for a welcome beginning here.

Mangold expressed his skepticism further on the p. 888, where he wrote:

> Ausserordentlich bemerkenswert erscheinen die Resultate der Beobachtungen von Regen (349) an Männchen von *Thamnotrizon apterus* Fab., da sich daraus ein nicht unwesentlicher Einfluss der tympanalen Sinnesorgane auf die eigene Stridulation der Tiere ergab. Nur lassen sich leider zunächst noch gar zu viele Einwände machen,

> The results of Regen's observations on males of *Thamnotrizon apterus* Fab. appear highly remarkable, showing a significant influence of the tympanic sensory organs on their own stridulation. Unfortunately, though, for the time being too many objections can still be raised.

After this skepticism, Mangold wrote in his chapter (p. 889):

> … die Frage offen bleibt, ob die Tympanalorgane imstande sind, das Stridulationsgeräusch durch Luftleitung als Reiz anzunehmen, oder ob die Übertragung nicht vielmehr nur durch den festen Untergrund, auf dem die Tiere sitzen, vermittelt wird. Letzteres scheint mir nach Regen's Versuchen zunächst das Wahrscheinlichere …

> … the question persists, whether the tympanal organs are capable to receive a stridulation sound as an airborne signal, or rather as vibrations transmitted via the solid substrate on which the animals are sitting. The latter seems to me according to Regen's experiments more probable …

At this point, I would like to introduce both persons, involved in this dispute, Mangold and Regen (Figs. 3.1 and 3.2).

Otto Ernst Mangold (Fig. 3.1) was born on February 5, 1879 in Berlin and died in Hahnenklee-Bockswiese (today a borough of Goslar) on July 10, 1961. He studied medicine and zoology in Jena, Germany. In the year 1905, he received habilitation in zoology and began to teach physiology at the universities in Jena, Greifswald, and finally Freiburg. In the year 1923, he returned to Berlin, where he worked as professor of animal physiology at the Friedrich-Wilhelms-University at the School of Agriculture. In 1933, in the Nazi time, he was eliminated from the University and reactivated only in 1945. In 1921, he was elected as a member of the German Academy Leopoldina. He was known for his strong criticism. More details about his life one can read at the website http://www.sammlungen.hu-berlin.de/dokumente/7679/.

Johann or Ioannes Regen (Fig. 3.2), in his homeland called Janez (Ioannes) or Ivan, was born on December 9, 1868 in a small village, Lajše in Poljanska valley, not far from Škofja Loka in the country that is nowadays Slovenia. At that time, it was a duchy, Krain, in the Austrian-Hungarian monarchy. Regen studied biology at the University of Vienna and defended his doctoral thesis in 1897 [Einige Beobachtungen über die Stridulationsorgane der saltatoren Orthopteren—Some observations on the stridulatory organs of Orthoptera (Saltatoria)]. He devoted his research mainly to questions of sound production, transmission, and perception of acoustic signals in insects and is known as one of the founders of the modern bioacoustics of insects. His main experimental animals were crickets, *Gryllus campestris* (in most of his papers referred to as *Liogryllus campestris*), and bushcrickets, *Pholidoptera aptera* (in Regen's works *Thamnotrizon apterus*).

Fig. 3.1 Prof. Otto Ernst Mangold (5. 2. 1879–10. 7. 1961) (Archive of the Humboldt University, Berlin, with permission)

Fig. 3.2 Prof. Ivan Regen (9. 12. 1868–27. 7. 1947) (Library of the Slovenian Academy of Sciences and Arts)

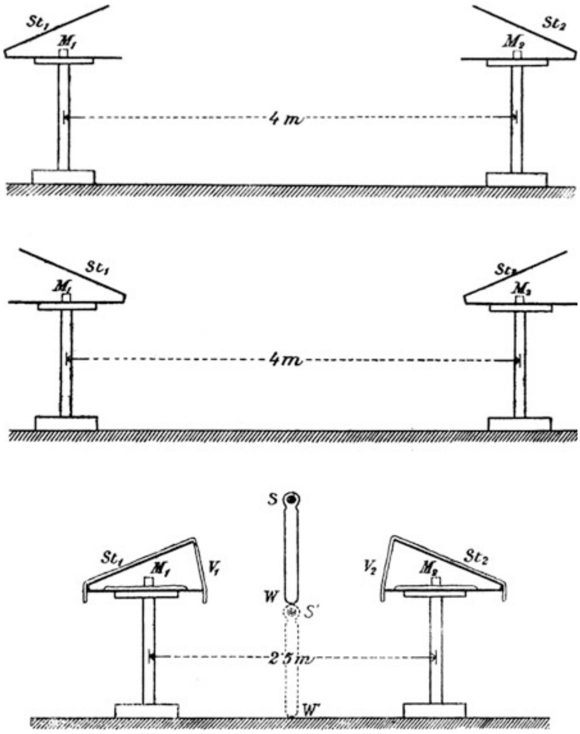

Fig. 3.3 Regen's experiments with *Pholidoptera aptera* bushcrickets. *Above*, males in the cages M_1 and M_2 in the rectangular funnels St_1 and St_2 alternated regularly. If the funnels were rotated for 180° so that the transmission of sound was reduced, the alternation was interrupted, or better, did not occur. In the experiment shown *below*, the funnels were oriented to each other with the open end and insulated by a cotton wool material. When the sevenfold insulation curtain was raised to the upper position S W in complete darkness, the coordinated alternation between males was discontinued (adapted from Regen 1914)

He lived and worked in Vienna and organized his private laboratories. However, this would not have been possible without the financial support of his friend Willy Gutmann and partly also by the Austrian Academy of Sciences. He had vivid contacts with his homeland all the time, became after the establishment of the Academy of Sciences and Arts in Slovenia its corresponding member, and was also invited (1921) to become a professor at the newly founded University of Ljubljana. He was also one of the founders and an honorary member of the Natural History Society of Slovenia. For various reasons, also due to weak possibilities for research there, he decided to remain in Vienna, where he died on July 27, 1947.

He did not publish many papers (about 25), but among them are some that are very important or even crucial for understanding sound communication in insects. In his short paper, published in 1908 about the alternation behavior of *Thamnotrizon apterus*, he claimed that only males with intact tympanal organs were able to respond regularly to the chirps of another male. As mentioned before, Mangold (1913) did not accept his results as a proof for sound communication in insects, nor as a proof that tympanal organs are indeed true hearing organs.

In the following years, Regen published some new papers with a detailed explanation of his experiments on *Thamnotrizon apterus* and *Liogryllus campestris*. In the paper "Untersuchungen über die Stridulation und das Gehör von *Thamnotrizon apterus* Fab."(Regen 1914), he answered exactly all open questions put by

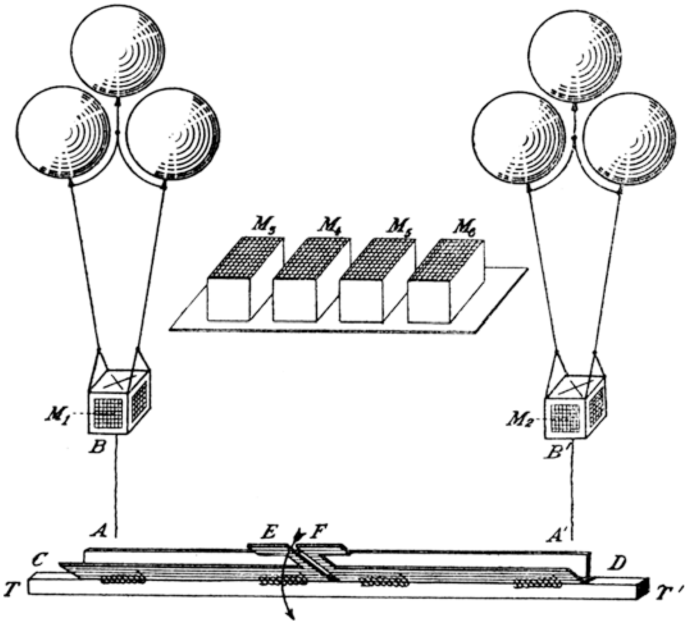

Fig. 3.4 Another interesting experiment of Ivan Regen with *Pholidoptera aptera*. Some males in the cages on the shelf were singing and alternating with the males in the air (Regen 1914)

Mangold. In the series of experiments based on sound alternation in funnels, enabling sound propagation only in one direction, with and without sound insulation material in between, Regen succeeded in proving that these bushcrickets perceive and react to airborne sound (Fig. 3.3). For the final proof, he let the bushcrickets alternate in the air in small paper cages suspended below hydrogen-filled balloons without any contact with the substrate, where the conspecific males were singing (Fig. 3.4).

The biological function of the male song of (*Lio*)*gryllus campestris* he showed in another famous experiment using the telephone for transmission of a cricket male's song to attract a virgin female (Regen 1913, Fig. 3.5). Later, he organized a large-scale experiment on phonotaxis of female crickets toward singing males in a huge insectarium with a 576 m^2 surface area. He called it the "geobiological laboratory" (Fig. 3.6). He used 1600 female crickets in the peripheral part of the experimental field and some males in the central part. Around the singing males, he put traps with electric contacts in such a way that he recorded each capture of females approaching the singing male. He collected the animals, marked them, and released them again in their holes. One part (half) of the females had tympanal organs destroyed. He could show that only animals with intact tympanal organs in the legs were able to locate the singing male and showed efficient positive phonotaxis (Regen 1928).

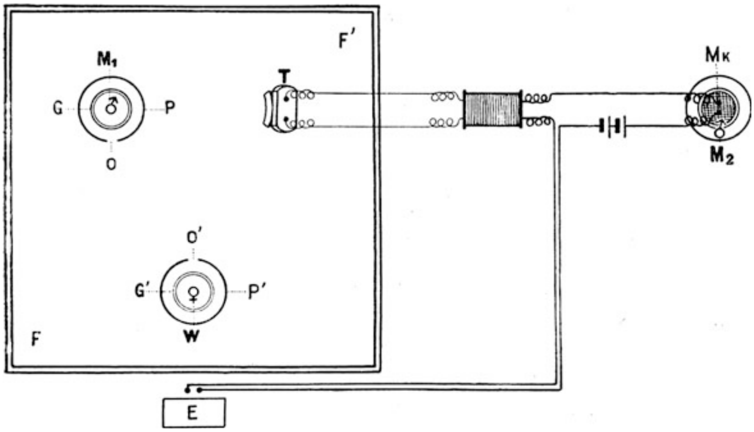

Fig. 3.5 The schematic drawing of the famous Regen experiment with attraction of a *Gryllus campestris* female to the telephone speaker, which was transmitting the calling song of a male, M_2, from a distant room. The experimental female was not attracted to the other silent male sitting in the chamber, M_1 (Regen 1913)

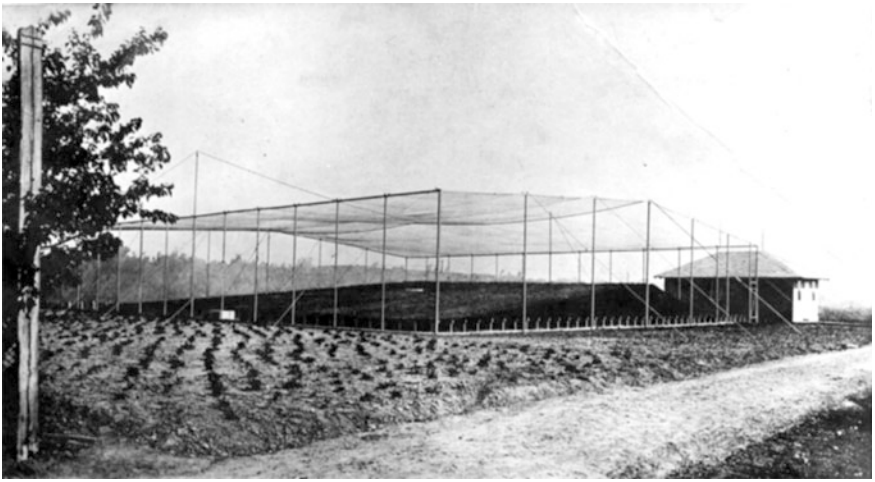

Fig. 3.6 Geobiological station built by I. Regen for the experiments with *Gryllus campestris*. In the experimental surface of 576 m^2, he used 1,600 animals for experiments on the phonotaxis of females to singing males (Library of the Slovenian Academy of Sciences and Arts)

The whole story of the dispute between O. E. Mangold and J. Regen ended with complete victory for the latter. In the year 1924, Mangold wrote a letter to Regen after receiving two recent papers from him (Regen 1922, 1923):

> Ich habe sie mit grossem Interesse gelesen und mich besonders gefreut, dass es Ihnen nunmehr durchaus gelungen ist, sichere Beweise für das Hören von Wirbellosen zu erbringen. Sie haben dadurch meine, noch in der Handbucharbeit in Wintersteins Handbuch zum Ausdruck gebrachte Skepsis vollkommen besiegt… (Archive of the Slovenian Academy of Sciences and Arts Library).
>
> In translation his words were: … I have read them with great interest and I am particularly pleased that you certainly have succeeded to provide firm evidence for hearing in invertebrates. So you succeeded to completely defeat my scepticism, that was still expressed in the chapter of the handbook of Winterstein… (see Mangold 1913).

Mangold later in another letter also supported Regen's application to the Austrian Academy to support financially the construction of the new "geobiological laboratory." Despite this, even in 1924, F. E. Lutz wrote in his publication, *Insect sounds*:

> … I am not aware of a single experiment that has furnished indisputable evidence of communication between insects by sound… (p. 367).
>
> … The suggested purpose of the well-developed insect sounds, a "sex call" is only imagined: it has not been proved and the chief evidence is that usually the females do not make a sound that we can hear (p. 371).

Also R. E. Snodgrass in his booklet, *Insect musicians, their music and their instruments* (1925), was not convinced about the true (airborne) hearing in insects. He wrote: …

> … Experimental evidence of the hearing powers of insects is at present very meager, but it would be surprising if insects do not hear the sounds they themselves produce… (p. 451).

And about the function of tympanal organs in bushcrickets, he also expressed his doubts (p. 417):

> …No one can state positively that any of these organs are ears, the principal reasoning in favor of their auditory nature being "if they are not ears, what are they?" …

Nowadays, there is, of course, no question whether some insects are able to receive airborne vibrations, whether the tympanal organs are true hearing organs, or if insects are able to communicate with sound signals.

3.3 About 50 Years Ago

Fifty years later, some insect physiologists and bioacousticians wondered about the very low level acoustic signals of many Hemiptera, especially Heteroptera, the missing of obvious sound receptors and the possible role in their intraspecific communication (Dumortier 1963; Haskell 1957; 1961; Jordan 1958; Leston 1954, 1957; Leston and Pringle 1963; Moore 1961).

Approximately 50 years ago, also, I got interested in the acoustic communication of Heteroptera, since I already had observed as a young entomologist in middle school the unusual behavior of the bugs from the family Cydnidae, with body vibrations during courtship and mating. At that time and even during my studies at the university in Ljubljana, I practically did not have any possibilities to record and investigate sounds or vibrations of these insects. On a few occasions, I got the opportunity to make some tape recordings in Radio Ljubljana, but since the time was limited in minutes I only succeeded in recording there some disturbance or alarm sounds. In the fifties, I used a stethoscope for listening in most cases in a similar way to that described by Leston (1954) and Jordan (1958). Later, it turned out that this was actually the best method to get an idea about their sound or vibration emissions. Only after 1965, when I received the basic equipment for bioacoustic investigations (tape recorder Revox A77, Oscilloscope Tektronix 502) from the Alexander von Humboldt foundation, was I able to carry out extensive investigations of the acoustic communication of bugs (Heteroptera).

From my field observations, I knew that many Heteroptera, like Cydnidae, perform courting and mating preferably in the early spring, when most of the other insects are still hidden in overwintering places. During this time period, it was not difficult to observe, listen to, or record complicated premating acoustic signals of various species. The important condition for such experiments and observations was, of course, that the males and females had not copulated before, and so, sexual motivation was at a high level.

One of the most important pioneers in investigations of acoustic signals, signal production and perception in the group of land bugs (Heteroptera, Geocorisae) was the German zoologist Prof. K. H. C. Jordan. In his publication (1958), he described the sound producing mechanisms and sounds of some species from the families Cydnidae, Pentatomidae, and Acanthosomatidae. However, the available technical devices for recording and analysis of sounds were not adequate. He was using, in addition to the condenser microphone and indirectly an oszillograph, a stethoscope in a similar way as it was described by Leston (1954). He did not tackle the question of airborne sound transmission or substrate vibrations in this group of insects. However, he discovered that bugs do not use only stridulatory mechanisms for sound production. His conclusion was that some Pentatomidae and Acanthosomatidae emit sounds by the movement (or deformation) of the first two abdominal terga and dorsoventral vibration of the abdomen.

In the sixties, I studied mainly bioacoustics of various bug species of the family Cydnidae (Gogala 1969, 1970). After describing song repertoires of males and females of single species (Gogala 1969) and showing the species specificity of different genera and species of Cydnidae (Gogala 1970, 1978, Gogala and Hočevar 1990), I began also to investigate with my team the question of communication medium. With limited equipment, we succeeded in gaining enough evidence for a conclusion that investigated species of Heteroptera use the substrate as a communication channel (Gogala et al. 1974, Fig. 3.7) and not the air, as supposed by some other authors mentioned above. We used the alternation in rivalry songs as the criterion for successful communication in a similar way as did Regen many years ago. Only the conclusions with our animals were different. Only vibrations transmitted through the substrate were sufficient in cydnid bugs to elicit alternation

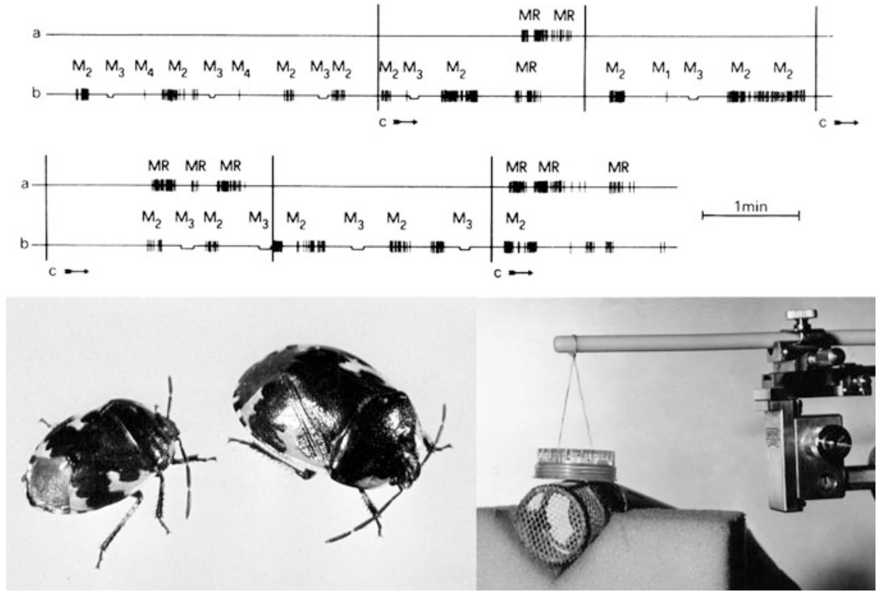

Fig. 3.7 Simple graphic showing the alternation between a couple of the bug *Tritomegas bicolor* during courtship in one cage and another male in the second cage, just 1–2 mm away. When the cages were brought into contact by micropositioner (C, three times), the alternation with the rivalry song started (adapted from Gogala et al. 1974). *Below left* a couple of *Tritomegas bicolor*, *right* experimental setup with two cages, in the upper cage was a single male, and in the lower cage a couple of bugs (male and female)

between males. So, half a century after Regen's papers proved airborne communication in crickets and bushcrickets, we have proven the opposite for another group of insects–bugs communicating by substrate vibration.

Similar questions about the communication channel were asked around half a century ago by some researchers working on acoustic behavior of small Auchenorrhyncha. There, probably the first proof for vibrational communication in intraspecific behavior was published by Ichikawa (1976). Hildegard Strübing, another pioneer in bioacoustic investigations of Auchenorrhyncha (her first publication on this topic was published in 1958; see also Chap. 5, this volume), in a paper discussing the acoustic communication of *Dictyophara europaea* (Fulgoridae) (1977) came to the following conclusion: "…so sprechen doch alle Indizien für eine Verständigung über Substratvibration" (…*yet all the evidence points to an understanding* via *substrate vibration*). Traue worked in the laboratory of Strübing with *Euscelis incisus* (Cicadomorpha: Cicadellidae) and *Euides speciosa* (Fulgoromorpha: Delphacidae) and published two papers (Traue 1978a, b), where he showed evidence for the vibratory communication in premating behavior of these planthoppers and leafhoppers in a similar way as we did with the Heteroptera (Fig. 3.8).

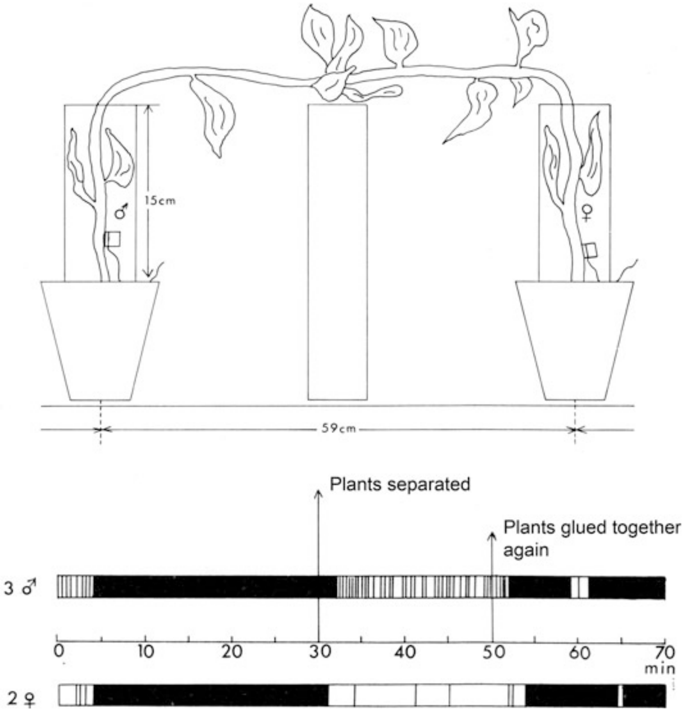

Fig. 3.8 Experiment with substrate-borne communication of *Euscelis incisus*. Three males in one chamber (*left*) started to communicate by vibrational signals with the two females in the *right chamber* as long as the feeding plants were glued together. When the plants were separated, the acoustic (vibrational) activity fell to a very low level (Traue 1978a)

3.4 Recent Investigations and Open Questions

During newer investigations in the last decades, substrate-borne communication of many species of Hemiptera: Heteroptera, Cicadomorpha, and Fulgoromorpha have been studied in detail from ethological and physiological aspects (e.g., Drosopoulos and Claridge 2006; Cocroft and McNett 2006; Čokl and Virant-Doberlet 2003; Gogala 2006; Hill 2008; Michelsen et al. 1982). Many authors using modern techniques also studied in this group of insects signal production mechanisms, transmission of vibrational signals through various substrates, as well as sensory organs and structures. Many results of such investigations (studies) are presented also in this volume. Nevertheless, due to the extreme diversity among insects, and also within the Hemiptera, we have to be open for surprises.

Every sound emission in the air inevitably produces vibrations in the substrate, and vice versa. Therefore, one can expect that many animals are using acoustic signaling either in one, the other, or both media. The question is only if the animals possess suitable sensory structures sensitive for both associated acoustical communication channels and if the vibrations in both media are strong enough to be perceived by the target animal.

There is no doubt that all insects have some kind of mechanoreceptors capable of perceiving substrate vibrations. However, many insects also have true auditory sense organs, which are well known and investigated by many authors from various aspects. But did not we miss in many insect groups, believed to have only vibrational communication, true "ears" that were overlooked? Roeder's discovery of ultrasonic ears in Sphingid moths is a good example of how inconspicuous such sensory organs can be (Roeder et al. 1968). The other good example is the auditory organs of praying mantis (Yager and Hoy 1986, 1987; Yager 1999). The third example for a surprising site of sensory organs was found in parasitoid flies, which search for their prey, singing crickets, by a specialized auditory prothoracic organ. Such ears were first described by Lakes-Harlan and Heller (1992) in the tachinid fly, *Therobia leonidei*, and by Robert et al. in *Ormia ochracea* (Robert et al. 1994, 1996).

The discovery of ultrasonic ears in Sphingid moths by Roeder et al. (1968), but also similarly surprising findings by Miller (1970) on the wings of *Chrysopa*, and by others, who found such ears "on all unlikely places," provoked Pye to write a short poem that was published as a letter in *Nature* (Pye 1968). He pointed out that the ears of insects can be "…on all unlikely places."

In days of old and insects bold
  (Before bats were invented),
  No sonar cries disturbed the skies—
  Moths flew uninstrumented.

The Eocene brought mammals mean
  And bats began to sing;
  Their food they found by ultrasound
  And chased it on the wing.

Now deafness was unsafe because
  The loud high-pitched vibration
  Came in advance and gave a chance
  To beat echolocation.

Some found a place on wings of lace
  To make an ear in haste;
  Some thought it best upon the chest
  And some below the waist.

Then Roeder's key upon the breeze
  Made Sphingids show their paces.
  He found the ear by which they hear
  In palps upon their faces.
Of all unlikely places!

In the systematic group of Hemiptera, which I know best, there are in acoustic communication (in a broad sense, vibrational communication included) some interesting phenomena. In Auchenorrhyncha, or better in the suborder Cicadomorpha, we know a big group of insects with undisputable airborne communication—Cicadidae. And even the closest relatives, Tettigarctidae, apparently use only a substrate-borne vibrational communication (Claridge et al. 1999). On the other hand,

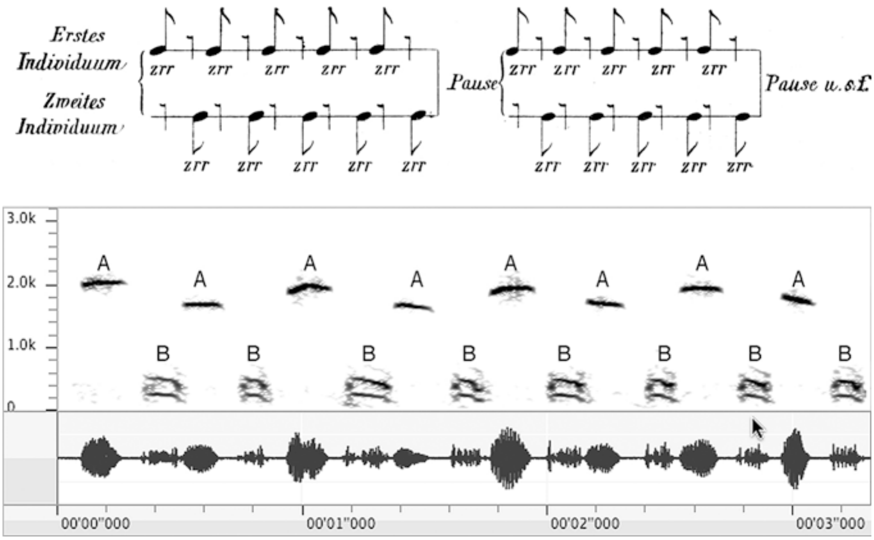

Fig. 3.9 Alternation between two *Pholidoptera aptera* males as shown in Regen's paper (1914) (*above*) and alternation between a whistling person (*A*) and a bug (*Phymata crassipes*) answering with a non-stridulatory vibrational signal (*B*) (Gogala 2008)

there is an interesting case of cicadas of the genus *Pagiphora*, which emit songs with frequencies much too low compared to resonant frequencies of other cicada species of the same size (Gogala et al. 2005; Trilar and Gogala 2012; Bennet-Clark and Young 1994). Is this due to vibrational communication in these species?

In Heteroptera, the other big group of Hemiptera, we know quite a lot about their vibrational communication (see Čokl et al., Chap. 8, this volume, Gogala 2006). Nevertheless, there are some unsolved questions.

One question is why many species of Heteroptera, in addition to low-frequency body vibration by tremulation or the tymbal system, use stridulation or, according to some authors, "strigilation." Stridulatory signals are usually much higher in frequency and are even audible to the unaided human ear. Are these signals directed toward vertebrates? Why then are they used as an important part of the acoustic or vibratory mating behavior? In the order of Heteroptera, the stridulatory mechanisms evolved independently in many families, genera, and species.

Another question is connected with the interesting acoustic behavior of the Ambush bug, *Phymata crassipes*. It has been shown that this predatory insect responds to vibrational and airborne stimuli with low-frequency vibratory signals (Fig. 3.9) (Gogala and Čokl 1983, Gogala et al. 1984, see also Virant-Doberlet et al. Chap. 20, this volume). Apparently, the human voice produces substrate vibrations strong enough to be perceived by bugs. In these species, the stridulatory apparatus has been known for a long time, but we do not know yet how they produce low-frequency signals. Did we also miss auditory organs in *Phymata*?

Stölting et al. (2002) showed that airborne sounds of *Okanagana rimosa* can produce vibrations strong enough to be perceived by other insects through their vibrational sense organs. Is this also the answer to the questions in the case of *Phymata crassipes*?

Similar questions have been put forward also by Caldwell (Chap. 7, this volume). Anyway, if we look back in the history of bioacoustic research, we can see that some authors put forward true vibrational communication and others airborne acoustic communication. But we should be aware that animals are complex organisms with a variety of sensors in their body and can react to various stimuli in the environment in such a way that they do the best for them and their species based on the limits of their reaction norms and adaptations. And this is true also for acoustic or vibrational communication in the broadest sense.

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