Russian Entomol. J. 34(4): 433–451

Modern insect bioacoustics: achievements, problems, prospects

Современная биоакустика насекомых: достижения, проблемы, перспективы

R.D. Zhantiev, O.S. Korsunovskaya
Р.Д. Жантиев, О.С. Корсуновская

Department of Entomology, Faculty of Biology, Lomonosov Moscow State University, Leninskie Gory, 1, Bld. 12. Moscow 119234 Russia.

Кафедра энтомологии биологического факультета Московского государственного университета имени М.В. Ломоносова, Ленинские горы, д.1, корп.12. Москва 119234 Россия.

Rustem Zhantiev: zhantiev@mail.ru ORCID https://orcid.org/0000-0001-8829-8400

Olga Korsunovskaya: korsuno@mail.ru ORCID https://orcid.org/0000-0003-3299-6001

KEY WORDS: insects, acoustic signaling, ecoacoustics, hearing, acoustic signals recognition.

КЛЮЧЕВЫЕ СЛОВА: насекомые, акустическая сигнализация, экоакустика, слух, распознавание акустических сигналов.

The article is dedicated to the 100th anniversary
of the Department of Entomology
at Lomonosov Moscow University

ABSTRACT. This article examines some of the most significant advances in insect bioacoustics in the first quarter of the 21st century, covering vibroacoustic signaling, ecological aspects of acoustic communication (ecoacoustics), and the processing of vibroacoustic information in the mechanosensory system, including mechanisms for recognizing sound signals. Breakthroughs in some areas of bioacoustics have been made possible by the modernization of traditional and the development of new research methods (immunohistochemistry, calcium imaging, microtomography, optogenetics, connectomics, etc.). New information has been obtained on the sound signaling of a vast number of insect species, and representative insect sound libraries, primarily from Orthoptera and Hemiptera, have been compiled. The features of mechanoelectrical transduction in insect auditory receptors are revealed, the structures and mechanisms that enhance sensitivity to sound, nonlinearities in the functioning of receptors and auditory interneurons are identified, and existing hypotheses for the recognition of species-specific sound signals are considered. Within the new field of ecoacoustics, studies have been conducted on acoustic niches, the propagation characteristics of acoustic signals in transmission channel, and the soundscape of biocenoses. The most promising research directions for the coming years have been identified.

РЕЗЮМЕ. Рассмотрены некоторые наиболее существенные достижения биоакустики насекомых в первой четверти XXI века в таких направлениях как виброакустическая сигнализация; экологические аспекты акустической коммуникации (экоакустика), обработка виброакустической информации в механосенсорной системе, в том числе механизмы распознавания звуковых сигналов. Прорыв в некоторых областях биоакустики оказался возможным благодаря модернизации традиционных и разработке новых методов исследования (иммуногистохимических, методов визуализации кальция, микротомографии, оптогенетики, коннектомики и др.). Получены новые сведения о звуковой сигнализации огромного числа видов насекомых, созданы представительные фонотеки голосов насекомых, преимущественно прямокрылых и хоботных. Раскрыты особенности механоэлектрической передачи в слуховых рецепторах насекомых, выявлены структуры и механизмы, повышающие чувствительность к звуку, нелинейности в работе рецепторов и слуховых интернейронов, рассмотрены существующие гипотезы распознавания видоспецифических звуковых сигналов. В рамках нового направления, экоакустики, выполнены исследования акустических ниш, особенностей распространения акустического сигнала в канале связи, звукового фона биоценоза. Сформулированы наиболее перспективные направления исследований в ближайшие годы.

Bioacoustics is the science of animal sound communication. Until recently, it also addressed issues of the emission and perception of vibrational signals. However, the large number of studies devoted to vibrocommunication allowed, in 2016, the identification of a specific field in the study of communication systems using mechanical vibrations: biotremology (the word tremology has a Latin origin from the verb tremere, meaning “to tremble”).

How to cite this article: Zhantiev R.D., Korsunovskaya O.S. 2025. Modern insect bioacoustics: achievements, problems, prospects // Russian Entomol. J. Vol.34. No.4. P.433–451. doi: 10.15298/rusentj.34.4.01

Bioacoustic research has traditionally focused on several areas: vibroacoustic signaling; ecological aspects of acoustic communication (ecoacoustics); vibroacoustic information processing in mechanosensory systems, including signal recognition and signal source localization mechanisms, and applied research. Below, we will review what we believe to be some of the most significant advances in bioacoustics in the first quarter of the 21st century.

First of all, it is worth focusing on new research methods that have made it possible to achieve real breakthroughs in some areas. Furthermore, new devices have emerged that have modernized traditional research methods. These include portable digital recorders with an extended frequency range, enabling the recording of insect ultrasonic signals in natural environments, and laser vibrometers, which enable non-contact study of vibration signals and oscillations of auditory structures. The widespread use of confocal microscopy, new immunohistochemical methods, calcium imaging techniques, microtomography (including optical coherence tomography), optogenetics, and mathematical modeling methods has yielded new data on the structure and functions of auditory organs and auditory receptors, interneurons involved in processing acoustic information, and connectomes [Baker *et al*., 2022]. Examples of the application of these methods can be found, for example, in the works of Baden & Hedwig [2007], Inagaki *et al*. [2014], Ogawa & Miller [2017], Deutsch *et al*. [2019], Vavakou *et al*. [2021].

ACOUSTIC SIGNALING

Following the publication of the classic books by K.-G. Heller, "Bioakustik der Europäischen Laubheuschrecken" [1988] and D.R. Ragge & W.J. Reynolds, "The Songs of the Grasshoppers and Crickets of Western Europe" [1998], devoted to the signaling of Orthoptera in western and central Europe, and the website by T.J. Walker & T.E. Moore, "The Acoustical Insects of North America" (SINA), created in 2000, a large number of taxonomic and bioacoustic studies have appeared, focusing on insect orders other than Orthoptera and Hemiptera. As a rule, they are devoted to revisions of individual taxa, which nowadays almost necessarily include data on the sound signals of acoustical species (see, for example, Naskrecki [2000]; Kaya *et al*. [2014]). A large number of studies are devoted to the acoustic behavior and signaling of representatives of regional faunas, including the tropics (see, for example, Sauer [2002]; Kim [2010]; Şirin *et al*. [2014]; ter Hofstede *et al*. [2020]; Hemp [2021]; Morris *et al*. [2025]), previously unstudied species or taxa of supraspecific rank (for example, the subfamily Phaneropterinae [Heller *et al*., 2015], the genus *Mecopoda* [Heller *et al*., 2021]

Digital recordings of orthopteran songs are currently stored in the largest audio library on the Orthoptera species file website [Chigliano *et al*., 2025], which has supported the SINA website since 2019. Songs of insects from other orders can be found at https://bio.acousti.ca/ — the bioacoustics website.

Among the studies of recent decades, studies related to predator-prey relationships are noteworthy. In particular, it was found that butterflies from 52 genera from several families exhibit acoustic aposematism, mimicry, and sonar jamming. In the latter case, their signals disrupt the echolocation of prey by bats [Barber *et al*., 2022]. A review by Low *et al*. [2021] presents data on defensive sounds, which are common in at least 12 insect orders. They are most often found in representatives of Lepidoptera, Coleoptera and Hemiptera.

We find the results of a study of species with complex vibroacoustic signaling (phyllophorine and pseudophylline katydids [Korsunovskaya *et al*., 2020, Korsunovskaya, Zhantiev, 2022] noteworthy. Each of the studied species not only possesses an extensive acoustic repertoire but is also capable of producing signals using multiple sound apparatuses. Data on acoustic signaling have been supplemented by information on the signals of aquatic bugs (Corixidae) [Sueur *et al*., 2011], dipterans (*Drosophila*: Swain, von Philipsborn [2021]), Scolytidae beetles [Arjomandi *et al*., 2024], and Lepidoptera (see, for example, the review by Greenfield [2014]). In particular, interesting data have been obtained on the defensive signals of butterfly caterpillars from the families Saturniidae, Sphingidae, and Brahmaeidae [Bura *et al*., 2011; Low *et al*., 2024], as well as signals from Licaenidae caterpillars and pupae — both social parasites of ants and free-living species [Riva *et al*., 2017].

By comparing vibroacoustic signaling in different orders, the following conclusions can be drawn or confirmed.

Insects most actively use signals in interspecific communication – these include protest, disturbance, distress sounds etc. These signals, as well as the methods of their emission, are most fully described in the review Low *et al*. [2021]. Only in a few orders does intraspecific communication develop, accompanying mating behavior.

The informative parameters of insect calls used to identify conspecifics are highly diverse and require further study, as does the exploration of acoustic niches, especially in tropical regions.

Ecoacoustics

In 2014, at the first meeting of the International Society of Ecoacoustics, "Ecology and acoustics: emergent properties from community to landscape", studies of sound signaling and the acoustic behavior of animal communities inhabiting the same biotope were combined into a new field called ecological acoustics (ecoacoustics). Its objectives include analyzing the ecological role of sounds of various origins (see, e.g., Riede [1998]; Chesmore [2004]; Ganchev *et al*. [2007]; Potamitis *et al*. [2007]; Riede, Balakrishnan [2025]). The study of animal acoustic signaling as a means of communication, navigation, and a factor in habitat selection is of primary importance in the development of this discipline [Farina, Gage, 2017]. Of particular interest are areas such as the study of acoustic landscapes, adaptations of animal sound apparatus and signals to habitat conditions in different biotopes, testing and substantiating the acoustic niche and acoustic adaptation hypotheses, and studying acoustic communities structure [Sueur, Farina, 2015]. Most ecoacoustic research conducted to date has focused on the role of noise (especially of anthropogenic origin) in ecological processes occurring in ecosystems. Insects have been used as subjects for this type of bioacoustic research far less frequently than vertebrates.

The few studies that have examined insects have focused on the following issues:

1. Acoustic niches. In 1979, the "acoustic niche" hypothesis (by analogy with Hutchinson's ecological niche) was formulated using orthopteran insects (Tettigoniidae) as an example [Zhantiev, 1979, 1981]. Later, similar ideas were presented in works devoted to vertebrates (see, for example, Heller, von Helversen, 1989; Kleyn et al., 2021] and other insects — cicadas [Riede, Kroker, 1995; Sueur, 2002], crickets [Otte, 1992; Schmidt *et al*., 2013], tropical bush-crickets [Greenfield, 1988] and grasshoppers [Bukhvalova, Zhantiev, 1993; Bukhvalova, 2006; Savitsky, 2000, 2011; Tishechkin, Bukhvalova, 2009]. Using the example of Palearctic gomphocerine grasshoppers, it was previously shown that species forming an acoustic community possess signals with non-overlapping or partially overlapping temporal patterns, which enables insects to discriminate between con- and heterospecifics based on the physical characteristics of the perceived sound [Bukhvalova, Zhantiev, 1993; Bukhvalova, 2006]. In the case of their coincidence in the signals of the studied species, additional, distinct elements of the mating signal may appear. In addition, signals of other modalities may be observed, allowing females to confidently recognize conspecific males (see the review by Römer [2013]). In tropical Ensifera orthopterans and cicadas, in addition, a separation of species by vocalization sites and sound emission time [Greenfield, 1988; Sueur, 2002; Diwakar, Balakrishnan, 2007, 2012; Schmidt *et al*., 2013] was revealed, but no correlation was found between stratification by the height of the insect-source of the signal and communication efficiency in tropical bush-crickets [Diwakar, Balakrishnan 2007; Jain, Balakrishnan, 2012]. Other studies (see reviews by Römer [2019]; Schmidt & Balakrishnan [2015]; Balakrishnan [2016]) report that in most cases, there is no separation of biotope space and activity time among members of the acoustic community. It is important to note that the overwhelming majority of studies were carried out on representatives of tropical fauna.

2. Characteristics of acoustic signal propagation in a transmission channel and testing the hypothesis of signal adaptation to the species' habitat. As with the study of acoustic niches, ambiguous results were obtained. The effects of frequency-dependent attenuation and distortion of the temporal pattern of signals during propagation in dense vegetation, studied in several katydid species from southern India, generally did not support the existence of signal adaptation to the acoustic parameters of the landscape [Jain, Balakrishnan, 2012]. Other studies conducted on seven tropical grasshopper species [Couldridge, van Staaden, 2004] also yielded contradictory results: in two species, the signal was transmitted better in the aboriginal biotope, while in the remaining species, it did not exhibit these properties.

3. Studying the soundscapes of biocenoses. This area has been intensively developed over the past decade (see, for example, reviews by Römer [2014]; Riede [2018]; Sugai *et al*. [2019]; Chhaya *et al*. [2021]; Mutanu et al. [2022]; Riede, Balakrishnan [2025]). Most researchers conduct passive acoustic monitoring (PAM) of field soundscapes based on recording the total sounds of a biotope (e.g., Sugai *et al*. [2019]). The stated goal of PAM recording is remote acoustic monitoring of ecosystems. This will potentially make it possible to assess biological diversity, population and community dynamics, the impact of urbanization and other anthropogenic impacts on the natural environment, the state of biocenoses in specially protected natural areas, etc. The "Worldwide Soundscapes" (WWSS) project is currently inventorying PAM datasets to study biodiversity in all regions of the globe (see https://ecosound-web.de/ecosound_web/collection/index/106). To achieve such results and use them by practitioners, it is necessary to be able to automatically discriminate not only "acoustic" [Chesmore, 2004] but also "morphological" (taxonomic) species, which presents significant difficulties. These difficulties are due to the need to use artificial intelligence (as is done in speech recognition), the training of which requires an extensive database of signals from a large number of species, recorded from a sufficient number of specimens, and from different geographic locations. However, the first studies in this area related to manual species identification by frequency filtering and comparison with known insect songs (see, for example, Benediktov [2015]), yielded interesting results. Even without the use of AI, it was possible to identify the species composition of the acoustic community of orthopterans in an agrocenosis in Bulgaria without collecting insects. This approach to collecting information on biocenosis populations is particularly important in protected natural areas. PAM is also useful for identifying the seasonal and circadian activity of acoustic community members. In particular, a study of orthopteran associations in the mountain forests of Colombia [Gomez-Morales, Acevedo-Charry, 2022] revealed which species, with what calls, and at what time of day produce sounds throughout the spring season, and how acoustic activity depends on environmental factors (moon phases, precipitation, etc.). This allows us not only to understand the species composition of the community but also to understand how its members function and interact, and how their activity is influenced by environmental factors.

HEARING

The auditory organs of insects are extremely diverse and can be located anywhere on the body: on the head (Diptera, hawk moths), thorax (Lepidoptera, praying mantises, parasitoid flies, and scarab beetles), abdomen (Orthoptera, Lepidoptera, and tiger beetles), legs (Orthoptera), and wings (lacewings) (see review by Kumar

& Göpfert [2026]). These organs have different origins, have evolved independently and repeatedly in different insects. In butterflies alone, they have evolved at least 11 times [Kawahara *et al*., 2019]. The auditory organs of insects can contain from one (Lepidoptera, Notodontidae) [Surlykke, 1984] to at least 20,000 chordotonal sensilla in Diptera (Culicidae) [Boo, Richards, 1975]. According to the type of structure, the auditory organs of insects are divided into tympanal, which have a thin cuticular membrane, and atympanal (Johnston's, serial organs of grasshopper *Bullacris* and mouth organs of hawk moths). The tympanal organs of moths, orthopterans and cicadas have been relatively well studied to date, but in recent decades new data have appeared on both previously unknown functions of these organs and new hearing organs. In particular, in the South African ancient grasshopper *Bullacris membracioides* (Pneumoridae), 6 pairs of atympanal organs of varying degrees of development were found. They are located on the sides from the 1st to the 6th abdominal segments. The most sensitive of them contained about 2000 receptors [van Staaden, Römer, 1998].

The structure of the long-known [Roeder *et al*., 1970] auditory organ of death's-head hawkmoths was finally established and its mechanism of operation elucidated [Göpfert *et al*., 2002]. It turned out that the auditory receptors are located at the base of the labral pilifer (one of the sclerites of the mouthparts), and the structure that transmits ultrasonic vibrations is a plate formed by scales on the labial palps, which contacts the pilifer. Other hawkmoth species have a tympanal membrane instead of a plate of scales on the labial palps. Abdominal tympanal organs of a different structure compared to those of pyralid moths were discovered in butterflies of the family Drepanidae [Surlykke *et al*., 2003]. They consist of four scolopidia sensitive to ultrasound and an internal tympanal membrane. Auditory receptors are embedded within the tympanal membrane which is formed by two tracheal walls between dorsal and ventral air chambers in the first abdominal segment. The authors suggest that sound stimulates the anterior outer membrane.

The tympanal organs (Vogel's organs) of Nymphalidae butterflies located at the base of the costal vein of the forewing, function as low-frequency receivers [Yack *et al*., 2000; Minet, Surlykke, 2003; Yack, 2004, Lucas *et al*., 2009; Sun *et al*., 2018]. It is assumed that they respond to the sound of the wings of birds hunting these insects.

Properties of auditory receptors

Since the discovery of the tonotopic organization of the auditory organ in bush-crickets [Zhantiev, Korsunovskaya, 1978; Oldfield, 1982; Stölting, Stumpner, 1998], studies of the functions of auditory receptors have been primarily devoted to elucidating the mechanisms underlying the different frequency tuning of individual receptors of these tympanal organs (e.g., Hummel *et al*. [2017]), their mixed vibro-acoustic sensitivity [Kühne, 1982; Kalmring *et al*., 1994; Zhantiev, Korsunovskaya, 2021, 2023], transduction processes in chordotonal sensilla and active amplification in auditory organs (see, for example, the series of works by Göpfert with co-authors, 2001–2025), as well as modulating influences on the functioning of auditory receptors [Andres *et al*., 2016].

Mechanoelectrical transduction (MET) in insect auditory receptors has been studied in fruit flies [Göpfert *et al*., 2006; Albert *et al*., 2007; Effertz *et al*., 2011; Hehlert *et al*., 2025]. Sound evokes deformation of the apical segment of the auditory receptor dendrite (cilia), leading to the opening of the NompC MET ion channel and depolarization of the neuron membrane. This process is preceded by the conformation of elastic elements (the gating spring). The return of the MET channel to its original, closed state occurs due to the elasticity of the gating spring. NompC belongs to the Transient Receptor Potential superfamily of sensory ion channels. Its activation apparently requires physical interaction with the cytoskeletal tubules of the dendrite [Sun *et al*., 2019]. Similar ion channels function in the hair cells of the vertebrate ear, which, according to Göpfert & Hennig [2016], indicates common genetic programs acting during mechanosensory cell development and seem evolutionarily related. Among the proteins that contribute to the functions of MET channels, major visual Opsins (Rh5 and Rh6) were identified, which turned out to be expressed in Johnston's organ. Apparently, they contribute to mechanical amplification and ion channel gating [Senthilan *et al*., 2012; Albert, Göpfert, 2015].

Structures and mechanisms that enhance sound sensitivity. As in vertebrates, active mechanical amplification has been discovered in insects (see review by Mhatre [2015]). It is based on processes occurring in the distal segment (cilia) of the scolopidial neuron dendrite when sound impacts the auditory organ. The cilia, containing nine pairs of peripheral and two central tubules, have an expansion beneath which lie the proteins dyneins. They facilitate sliding between the tubules and thus cause the cilium to bend under the strain of sound. This opens ion transient receptor potential (TRP) channels. The main transduction channel, as noted above, is NompC, located in the apical segment of the cilia. Proximal to the expansion of the cilia are the Nanchung and Inactive channels, which form Nan-Iav heteromers. Active amplification is mediated by motor molecules within the auditory receptor. They generate forces that help external sound vibrations open mechanosensitive ion channels [Nadrowski *et al*., 2008]. Typically, active gain is maximal at minimal stimulus levels at the optimal frequency of the auditory receptor [Nadrowski *et al*., 2008, Mhatre, 2015]. The further the stimulus frequency is from the optimal frequency, the less dependence active gain has on its intensity [Göpfert, Robert, 2003]. It is assumed that Nanchung and Inactive channels amplify subthreshold electrical signals generated by the transduction complex [Göpfert *et al*., 2006; Lehnert *et al*., 2013].

The presence of active amplification in the auditory organ can be assumed by several features, namely: dependence on the sound level and frequency of the stimulus, two-tone suppression, energy production and self-oscillatory processes similar to otoacoustic emission in vertebrates [Mhatre, 2015; Göpfert, Hennig, 2016]. The study of the functioning of the auditory organs of

Diptera (fruit flies, mosquitoes) and Orthoptera (locusts, crickets, bush-crickets), based on the above-mentioned features, allows us to assert that insects, like vertebrates, have active amplification [Mhatre, 2015].

In the tree cricket *Oecanthus henryi* [Guerten *et al*., 2013; Mhatre, Robert, 2013], bush-cricket *Mecopoda elongata* [Möckel *et al*., 2011], locust *Schistocerca gregaria* [Möckel *et al*., 2014], and butterfly *Empyreuma affinis* [Kössl, Coro, 2006], periodically occurring spontaneous vibrations of the tympanal membrane were discovered [Mhatre, Robert, 2013], and in dipterans, spontaneous vibrations of the antenna [Göpfert, Robert, 2001, 2003]. The authors believe that these phenomena are mechanical correlates of otoacoustic emissions in vertebrates, in which the movement of hair cells enhances the mechanical responses of sound-perceiving structures, contributing to an increase in the sensitivity of the auditory organ. In this case, the latter (for example, the mammalian cochlea) functions as a regenerative receiver, which could amplify weak signals [Wit, Bell, 2024].

The processes that mediate spontaneous vibrations of the antennae or tympanal membrane in insects are still not entirely clear, are the subject of debate, and require further investigation [Koessl *et al*., 2008; Mhatre, 2015].

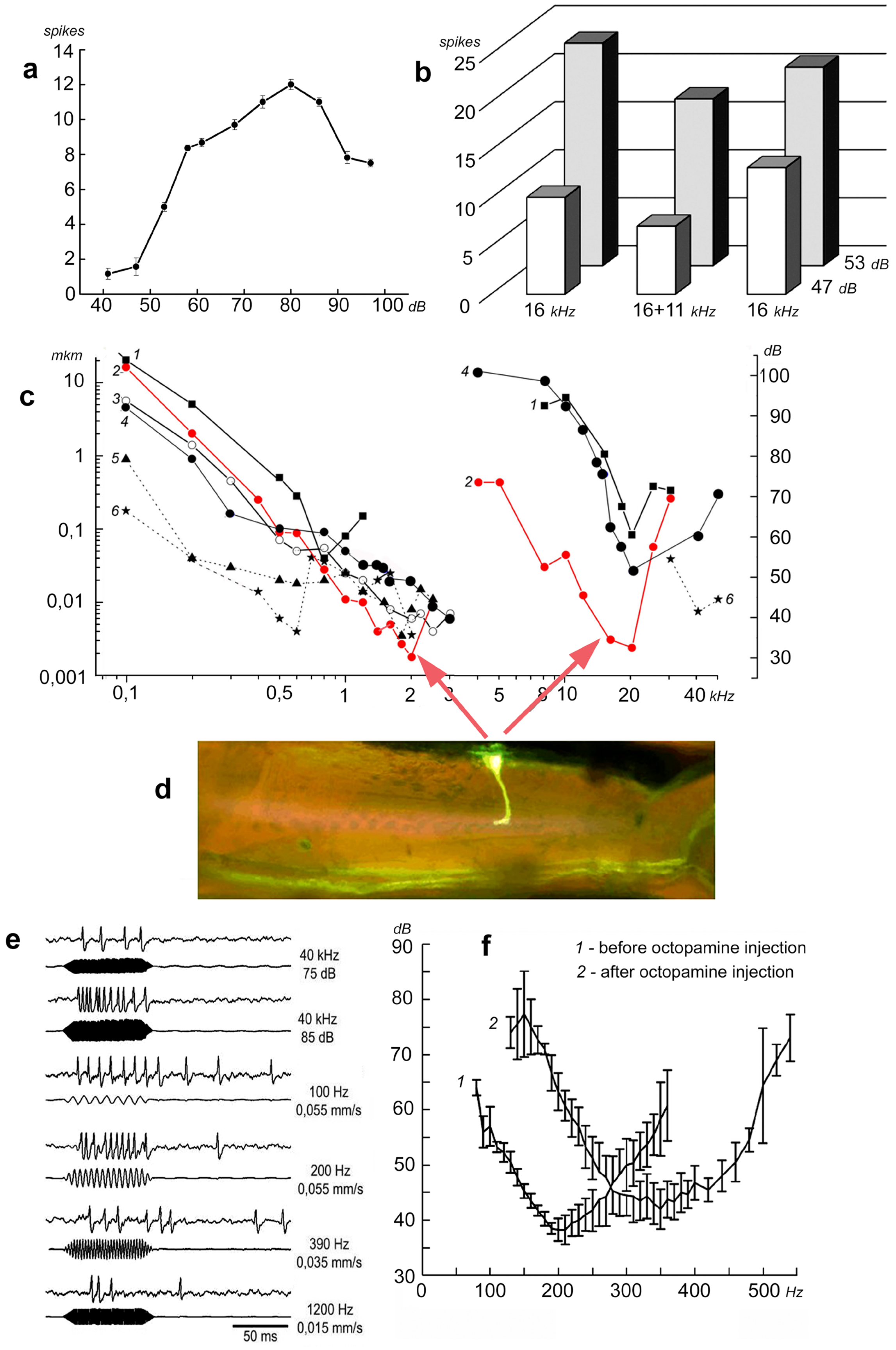
Flight modification as a means of increasing the sensitivity of the auditory organs to biologically significant sounds is observed in mosquitoes. Males recognize a conspecific female and copulate with her, guided by the sound she produces in flight. However, judging by the audiograms obtained, the male's Johnston's organ does not perceive her flight sound, as the range of their hearing does not coincide with the spectrum of wing sounds of both females and males (a mismatch in a mosquito hearing organ). Nevertheless, the male is able to localize a female in a swarm. This occurs when, at dusk, the male changes the frequency of his wingbeats, resulting in distortions produced by mixing the flight tones of the female and male. In *Anopheles gambiae*, the sum spectrum (the result of harmonic convergence) stimulates the Johnstons organ fibrils if the male increases his wingbeat frequency by 1.5 times compared to the female [Somers *et al*., 2022].

Currently, in addition to those mentioned above, several other ways of increasing the sensitivity of the auditory organs are known in various insects. All of them are characteristic of Orthoptera. These include, first and foremost, the already thoroughly studied **(i)** ***acoustic vesicles of bush-crickets*** [Lewis, 1974], which act as an exponential horn amplifying ultrasonic sounds, and **(ii)** ***the transverse trachea in the prothorax of crickets*** [Zhantiev *et al*., 1975; see, e.g., Römer, Schmidt, 2016], which contributes to an increase in the useful signal-to-noise ratio and improves spatial orientation. Furthermore, a specific organ, the **(iii)** ***olivarius***, was recently discovered in the fore tibia of the ancestral species *Hemideina thoracica* (Anostostomatidae). It produces a lipid substance. It is located in a channel isolated from the hemolymph above the intermediate organ and the crista acustica and provides improved (by 20 dB) perception of low-frequency sounds [Lomas *et al*., 2012]. It is believed that the lipid mass prevents the trachea and the crista acustica located on it from shifting dorsally under the influence of vibrations of the tympanal membranes. At the same time, the trachea, limited in its upward movement, stretches the lateral end of the crista acustica, which leads to deformation of the mechanoreceptors and facilitates spike generation.

In many katydids of the subfamily Pseudophyllinae, the tympanal organs are covered by protective cuticular opercula, forming the so-called pinnae. Experiments with 3D-printed models of the ear have shown that these ***pinnae*** act ***as*** **(iv)** ***Helmholtz resonators***, which may also increase the sensitivity of the auditory organs at certain frequencies [Pulver *et al*., 2022].

An expansion of the dynamic range of auditory receptors due to nonlinearity in their responses was recorded in single receptors in both the tympanal nerve and the crista acustica of 11 species of tettigoniine and phaneropterine bush-crickets [Zhantiev, Korsunovskaya, 1997]. These receptors decreased their firing rate after reaching its maximum with further increases in stimulus intensity. Typically, this phenomenon was pronounced at optimal frequencies of the ear. Receptor response curves were S-shaped or campaniform (Fig. 1a). This phenomenon manifested itself differently in different species: either as pauses in the response or a reduction in its duration, or as an off-response. This phenomenon is more pronounced in phaneropterine bush-crickets than in other studied species. Only a portion of the latter's neurons showed a decrease in firing with increasing stimulus intensity. Two-tone stimulation, in which a frequency 1–5 kHz higher or lower than the best frequency was added to a single-frequency stimulus, reversibly suppressed receptor responses (Fig. 1b). However, after a few seconds, the effect of the two-tone stimulus weakened, and the firing rate began to increase again. This phenomenon was observed less frequently when exposed to short-term stimuli. Increasing the stimulus intensity makes the effect of the additional stimulus frequency more persistent. Transection of the tympanal nerve or separation of the foreleg from the body revealed that the source of receptor activity suppression is peripheral. The fact that these phenomena were observed at high stimulus intensities and the level of impulses was restored even under the influence of a two-tone stimulus does not allow us to classify this phenomenon as otoacoustic emission.

According to the authors, this is explained by the reciprocal suppression of adjacent receptors during simultaneous active firing. Receptors of crista acustica are known to differ in frequency tuning, and the addition of another frequency to the stimulus activates the sensillum that is more sensitive to it. It can be hypothesized that their firing rates may be influenced by the potentials of contacting cap cells of adjacent receptors, which have previously been recorded in bush-crickets [Oldfield, Hill, 1986]. Suppression of firing rates of the more sensitive receptor at high stimulus levels is also observed in moths [Perez, Coro, 1985]. However, the mechanism of receptor interaction is unclear, and it is difficult to explain the restoration of firing rates during continued exposure to a two-tone stimulus in bush-crickets.


a
spikes
14
12
10
8
6
4
2
0
40
50
60
70
80
90
100 dB
b
spikes
25
20
15
10
5
0
16 kHz
16+11 kHz
16 kHz
53 dB
47 dB
c
mkm
10
1
0,1
0,01
0,001
0,1
0,5
1
2
3
5
8
10
20
40 kHz
dB
100
90
80
70
60
50
40
30
1
2
3
4
5
6
d
e
40 kHz
75 dB
40 kHz
85 dB
100 Hz
0,055 mm/s
200 Hz
0,055 mm/s
390 Hz
0,035 mm/s
1200 Hz
0,015 mm/s
50 ms
f
dB
90
80
70
60
50
40
30
0
100
200
300
400
500 Hz
1 - before octopamine injection
2 - after octopamine injection

The effect of two-tone suppression of auditory receptor responses has long been known in vertebrates (see, for example, Ruggero *et al*. [1992]). It is explained by the nonlinearity of eardrum vibrations during stimulation with two-tone stimuli.

Bimodality of auditory receptors. In Orthoptera (Tettigoniidae), the auditory receptors of the tympanal organs respond to both sound and vibration stimuli. Staining with a living dye during recording of responses from single receptors in the tympanal organ revealed that both the sensilla of the intermediate organ and the crista acustica were bimodal [Zhantiev, Korsunovskaya, 2021] (Fig. 1c–d). However, when recording the activity of auditory receptors in the tympanal nerve, it was found that several receptors with different responses could be recorded in a single experiment — both to sound alone and to sound and vibration stimuli [Kühne, 1982; Zhantiev, Korsunovskaya, 2023]. It has previously been suggested that bimodal receptors recorded in the tympanic nerve belong to the intermediate organ but morphological identification was not performed (e.g., Kalmring *et al*., [1994]). However, in some cases, the receptors had low response thresholds and responded to ultrasound [Kühne, 1982; Zhantiev, Korsunovskaya, 2023] (Fig. 1e), which, with a high degree of probability, indicates that they belong to the crista acustica. Currently, it remains unclear why all the auditory receptors of the tympanal organ are bimodal, and then some of them lose sensitivity to vibrations

To explain the properties of these receptors, one must assume either a neuromodulatory/neurohormonal influence of some elements whose activity is triggered by the vibration-sensitive system, or the presence of ephaptic interactions, apparently between the receptors of the tympanal organ, on the one hand, and the subgenual and other vibration-sensitive organs (possibly the femoral and/or connected with tarsus), on the other hand. Furthermore, biogenic amines and GABA, markers of efferent control of auditory receptor function, were identified as efferent neurotransmitters or neuromodulators that control auditory receptor activity (see, for example, Andrés *et al*. [2016]; Lapshin & Vorontsov [2023]). To obtain answers to the questions posed, it is necessary to conduct additional studies, both physiological, morphological and immunohistochemical, along the entire vibro-acoustic afferent tract: from the peripheral sections to the first switches to the corresponding interneurons.

As in vertebrates, insects exhibit **efferent control of auditory receptor function**. This has been convincingly demonstrated in studies of mosquitoes [Andres *et al*., 2016; Xu *et al*., 2022; Loh *et al*., 2023; Vorontsov, Lapshin, 2023, 2024]. Immunohistochemical, electron microscopic, and electrophysiological studies have revealed the presence of rows of thickenings on the dendrites and axons of auditory sensory neurons in the mosquito Johnston's organ and the presence of octopamine, GABA, and serotonin as efferent neurotransmitters or neuromodulators. They influence the frequency tuning of receptors, shifting it toward high frequencies (Fig. 1e) and mechanical amplification. In particular, octopamine affects flagellum stiffness, thereby altering the mechanical tuning frequency of antennae [Andres *et al*., 2016; Georgiades *et al*., 2022] and causing erection of flagellar fibrils [Georgiades *et al*., 2022]. It was also found that the action of octopamine, in particular, is influenced by circadian rhythms [Georgiades *et al*., 2022].

Fig. 1. Properties of orthopteran (**a**–**d**) and dipteran (**e**) auditory receptors: **a** — intensity-response function of the 12th sensillum of the crista acustica of the bush-cricket *Tettigonia cantans.* Stimulus frequency is 16 kHz, duration is 50 ms. Vertical bars are standard errors (5–10 stimulus presentations). Registration of activity in the tympanal organ (from Zhantiev & Korsunovskaya [1997]); **b** — histograms of responses of the same sensillum to one- and two-tone stimuli — series of 10 pulses with duration of 20 ms, repeating rate is 36.4 s^{-1}, SPL of 47 and 53 dB. Vertical bars — average number of pulses in response to a series. Standard errors: 0.7–1 (47 dB), 0.6–0.9 (53 dB). One-tone signals were presented before and after two-tone signals. Differences in responses to one- and two-tone stimuli are reliable (P> 0.95 at 47 dB; P> 0.99 at 53 dB) (from Zhantiev & Korsunovskaya [1997]); **c** — frequency-threshold curves of responses to vibration (left) and sound (right) stimuli of receptors of the distal third of the crista acustica of *T. cantans.* X-axis — frequency, left Y-axis — displacement, right Y-axis — sound pressure level (SPL). The same numbers indicate responses to sound and vibration of the same receptor. Morphologically identified receptors: No. 15 (*2*), No. 18 (*5*), No. 20 (*3*); **d** — crista acustica of the bush-cricket *T. cantans*, with the 15th auditory receptor stained with Lucifer Yellow (from Zhantiev & Korsunovskaya [2022]); **e** — auditory receptor of *T. cantans* responses to ultrasound and vibrations. Intracellular recording with a glass microelectrode in the tympanal nerve at the entrance into the prothoracic ganglion. RMS values are given for vibrations (from Zhantiev & Korsunovskaya [2023]); **f** — averaged frequency-threshold curves (mean and standard deviation) of the auditory receptors of male Johnstone organ of mosquito *Culex pipiens pipiens* before (1) and after (2) octopamine thoracic injection. X-axis — sound frequency, Y-axis — VRMS, the root mean square velocity of air particles (from Vorontsov & Lapshin [2023]).

Рис. 1. Свойства слуховых рецепторов прямокрылых **(а–d)** и двукрылых (е): **a** — зависимость числа импульсов в ответе 12-й сенсиллы слухового гребня кузнечика *Tettigonia cantans* от интенсивности звука. Частота стимула 16 кГц, длительность 50 мс. Вертикальные линии — ошибки средней (5–10 предъявлений стимула). Регистрация активности в тимпанальном органе (по Zhantiev & Korsunovskaya [1997]); **b** — гистограммы ответов той же сенсиллы на моночастотные и двухтоновые стимулы — серии из 10 посылок длительностью 20 мс, повторяющихся с частотой 36,4 $с^{-1}$, интенсивностью 47 и 53 дБ. По вертикали — среднее число импульсов в ответе на серию. Ошибки средних: 0,7–1 (47 дБ), 0,6–0,9 (53 дБ). Моночастотные сигналы предъявляли до и после двухтоновых. Различия ответов на двухтоновые и моночастотные посылки достоверны (P>0,95 при 47 дБ; P>0,99 при 53 дБ) (по Zhantiev & Korsunovskaya [1997]); **c** — частотно-пороговые характеристики реакций на вибрационные (слева) и звуковые (справа) стимулы рецепторов дистальной трети слухового гребня и *T. cantans*. По горизонтали — частота, по вертикали: слева — смещение, справа — уровень звукового давления. Одинаковыми цифрами обозначены реакции на звук и вибрации одного и того же рецептора. Морфологически идентифицированные рецепторы: № 15 (*2*), № 18(*5*), № 20 (*3*); d — слуховой гребень T. *cantans*, с окрашенным красителем Люцифером желтым 15-м рецептором (по Zhantiev & Korsunovskaya [2022]); **d** — ответы рецептора *T. cantans* на ультразвук и вибрации. Внутриклеточная регистрация стеклянным микроэлектродом в тимпанальном нерве у входа в проторакальный ганглий. Для вибраций приведены среднеквадратичные значения скорости (по Zhantiev & Korsunovskaya [2023]); **e** — усредненные частотно-пороговые кривые слуховых рецепторов джонстонова органа комара *Culex pipiens pipiens* до (1) и после (2) торакальной инъекции октопамина. Приведены средние значения и ошибки средних. По горизонтали — частота звука, по вертикали — уровень колебательной скорости (по Vorontsov & Lapshin [2023]).

Auditory interneurons

Neurons with inputs in postcephalic ganglia. Currently available data indicate that in insects with developed acoustic communication, information from the auditory receptors is relayed to several dozen interneurons. Even in butterflies (*Heliothis virescens*), which have only two auditory receptors, just one of them (A1) in the thoracic region is connected to at least 7 interneurons [Boyan, Fullard, 1986]. In the most well-studied groups of tympanate insects in this regard — katydids and grasshoppers — several dozen cells that respond to sound and have input branches in the acoustic neuropil or beyond it in the thoracic or even abdominal ganglia have been morphologically identified only in the prothoracic ganglion (e.g., Stumpner & Ronacher [1991]; Korsunovskaya & Zhantiev [1992]; Stumpner & Molina [2006]). According to their morphology, they, like other studied insects with tympanal organs (see, for example, cicadas [Huber *et al*., 1990], flies [Stumpner, Lakes-Harlan, 1996]), they are divided into local (Fig. 2a–c, i) and projection (intersegmental) — ascending (Fig. 2e), descending (Fig. 2f, h), and T-shaped (Fig. 2d, g).

A comparison of the morphology of neurons in insects possessing tympanal organs has shown that some cells may be homologous or develop from homologous elements. For example, local omega cells in crickets and katydids (Fig. 2a) are similar to neurons in grasshoppers [Römer, Marquart, 1984] (Fig. 2d), which, however, are located in the 3rd thoracic ganglion and may have ascending and/or descending axons (cells BSN1, TN2, SN2). The presence of axons extending beyond the prothoracic ganglion has also been noted in some cells of late-instar nymphs or young adult crickets [Atkins, Pollack, 1986]. The most likely neural substrate in the central nervous system for the formation of auditory interneurons appears to be neurons in the centers processing vibrational signals and, possibly, signals from other mechanoreceptors, including proprioceptors. In favor of the latter assumption, in our opinion, is evidenced by the bimodality of some auditory interneurons (see, for example, Zhantiev [1981]; Rössler *et al*. [2006]) and the diversity of tympanal organs in insects, which, according to one point of view, at least some of them arose on the basis of proprioceptors [van Staaden, Römer, 1998].

Brain auditory interneurons. The supraesophageal ganglion of insects undoubtedly plays an important role in the analysis of acoustic information, since it is there that the terminal branches of the auditory interneurons of the ventral nerve cord, descending and local neurons that respond to sound, are located. The interneurons of the brain of Orthoptera (Ensifera) and Diptera (Drosophilidae) have been most thoroughly studied. A brief overview is provided below.

In **orthopterans** the anterolateral region of the brain contains the ascending terminal branches of auditory interneurons (see, for example, AN1-3 in bush-crickets: Stumpner & Molina [2006]). Furthermore, several local neurons have been identified in the cricket brain, some of which respond selectively to signals with a species-specific pulse rate [Schildberger, 1984; Kostarakos, Hedwig, 2012, 2014]. These cells are located either within one hemisphere of the ganglion (Fig. 2i) or cross its midline, connecting symmetrical sections.

A special group of interneurons that respond to sound are descending cells. The responses of at least 32 such neurons in split cervical connective of crickets (*Gryllus bimaculatus*) were discovered as early as 1977 [Zhantiev, Korsunovskaya, 1977]. Transections of the circumesophageal connectives and the 3rd and 2nd commissures of the brain in crickets showed that switching from ascending to descending interneurons responding to sound occurs in both the subesophageal and supraesophageal ganglia. Most of the axons of these cells pass in the connective contralateral to the stimulated tympanal organ. They respond to both low-frequency (lowest thresholds at 5 and 7–8 kHz) and high-frequency (optimum at 16 kHz) sounds. Some of these neurons exhibit strong habituation to repeated stimuli, which can be overcome by, for example, touching the antennae or flashing a light to the eyes. Thus, like the descending interneurons of the locust [Rowell, Reichert, 1986], these cells are multimodal. Morphologically, it was possible to identify two ipsilateral (Fig. 2h) and one of the contralateral neurons in the cricket [Boyan, Williams, 1981; Rogers *et al*., 2022]. The identified neurons copied the rhythm of the calling signal with a conspecific carrier frequency or responded only to high-frequency stimuli. The functions of descending neurons of this type are not fully understood, but they apparently participate in motor control or may influence other organ systems. This, in turn, may provide feedback and control the auditory system [Zhantiev, Korsunovskaya, 1977; Boyan, Williams, 1981; Rogers *et al*., 2022].

In **dipterans** (*Drosophila melanogaster*), approximately 70 types of interneurons receiving information from the receptors of Johnston's organ have been identified [Matsuo *et al*., 2016; Baker *et al*., 2022]. Some of these are local, while most were projection neurons, linking the primary auditory center with other parts of the brain. Based on these latest findings, a connectome characterized by the absence of a hierarchical structure was developed [Baker *et al*., 2022]. One of the neural network includes two pairs of A1 group commissural interneurons of antennal mechanosensory and motor center (AMMC)

Рис. 2. Слуховые интернейроны прямокрылых (**a**–**i**) и двукрылых (**j**): **a**–**c** — локальные интернейроны проторакального ганглия кузнечиков: **a** — омега-нейрон *Isophya modesta rossica* (по Korsunovskaya & Zhantiev [1992]); **b** — тонический нейрон SN3 *Metrioptera roeselii*; **c** — дорсальный непарный медиальный (DUM) нейрон *Ancistrura nigrovittata* (по Cillov & Stumpner [2022]), **d**–**h** — проекционные нейроны: **d** — Т-образный нейрон TN2 в метаторакальном ганглии саранчи *Locusta migratoria* (по Römer & Marquart [1984]); **e** — восходящий нейрон AN1 *A. nigrovittata* (по Stumpner & Molina [2006]); **f** — низкочастотный нейрон DN2 (оптимальная частота 5 кГц) в проторакальном ганглии *Tettigonia cantans* (по-видимому, контактирует с рецепторами промежуточного органа, Корсуновская, неопубл.); **g** — Т-образный нейрон TN1 с on-off-реакциями *Phaneroptera falcata* (по Korsunovskaya & Zhantiev [1992]), **h** — нисходящий из надглоточного ганглия реагирующий на звук нейрон B-DARN1 *Gryllus bimaculatus* (по Rogers *et al*. [2022]); **i** — нейрон B-LI4 надглоточного ганглия *G. bimaculatus*, **j** — нейрон pC2 надглоточного ганглия (детектор свойств пульсов) *Drosophila melanogaster* (по Deutsch *et al*. [2019]).

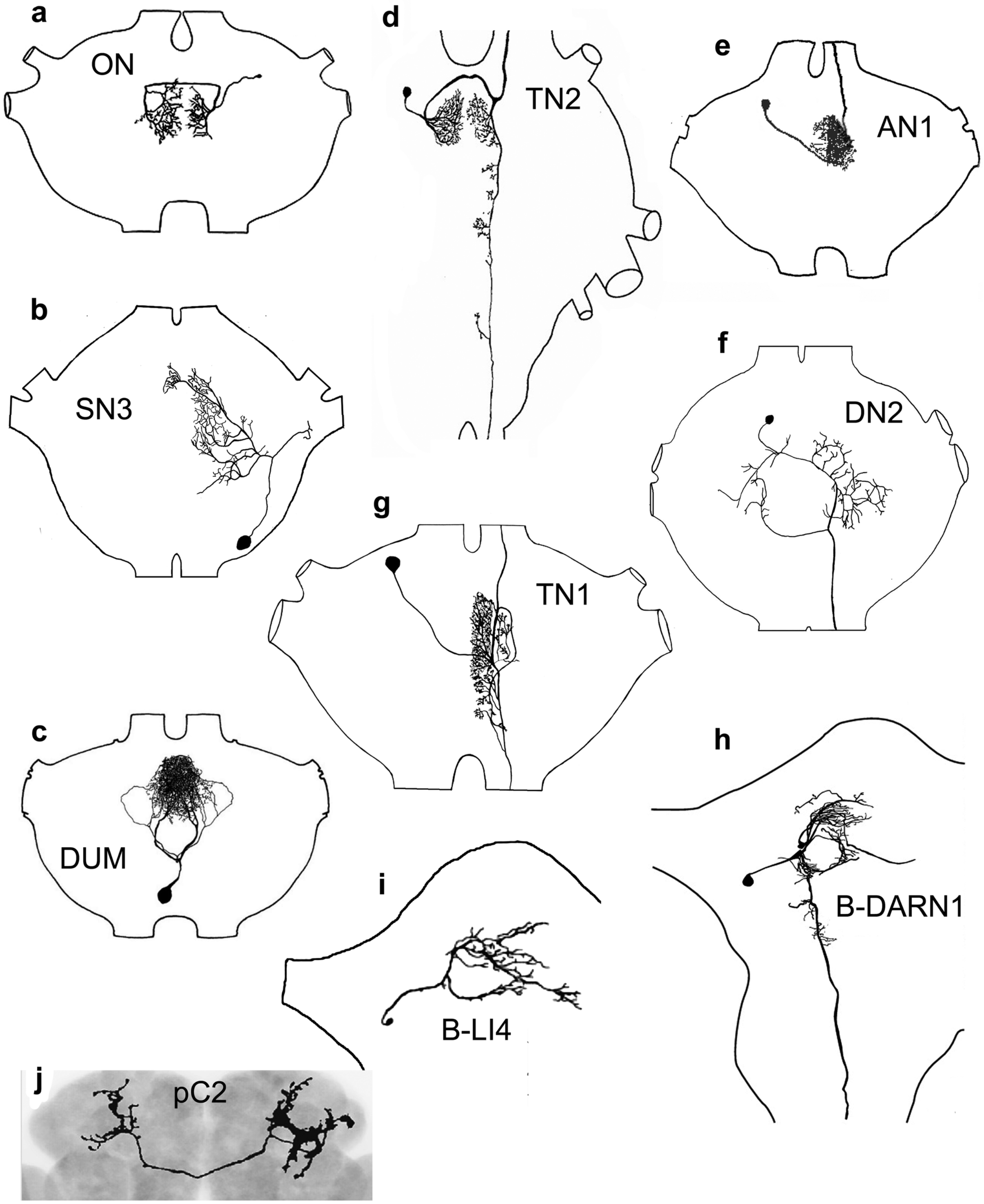


Fig. 2. Orthopteran (**a**–**i**) and dipteran (**j**) auditory interneurons: **a**–**c** — local interneurons of prothoracic ganglion of bush-crickets: **a** — omega-neuron of *Isophya modesta rossica* (from Korsunovskaya, Zhantiev, 1992); **b** — tonic neuron SN3 in prothoracic ganglion of *Metrioptera roeselii* (Korsunovskaya, unpubl.); **c** — dorsal unpaired median neuron (DUM) of *Ancistrura nigrovittata* (from Cillov & Stumpner [2022]), **d**–**h** — projection interneurons: **d** — T-shaped neuron TN2 of metathoracic ganglion of *Locusta migratoria* (from Römer & Marquart [1984]), **e** — ascending AN1 neuron of *Ancistrura nigrovittata* (from Stumpner & Molina [2006]), **f** — low frequency neuron DN2 (best frequency 5 kHz) of prothoracic ganglion *Tettigonia cantans* (Korsunovskaya, unpubl.) apparently contacts with intermediate organ receptors), **g** — T-shaped TN1 neuron with on-off-reactions of *Phaneroptera falcata* (from Korsunovskaya & Zhantiev [1992]), **h** — brain descending auditory-responsive neuron (B-DARN1) of the cricket *Gryllus bimaculatus* (from Rogers *et al.* [2022]), **i** — brain neuron B-LI4 of *G. bimaculatus*, **j** — brain pC2 neuron (pulse feature detector) of *Drosophila melanogaster* (from Deutsch *et al.* [2019]).

and one GF interneuron in each half of the supraesophageal ganglion. They connect the auditory areas: AMMC and the wedge (WED). These cells form a system of giant interneurons (GF) via ephaptic connections. AMMC neurons of the B1 group (about 10 cells in a hemisphere of the brain) send axons to the WED area. These cells are functionally divided into two types: B1a and B1b [Lai *et al*., 2012]; B1a are narrowly tuned to sound perception, about 100 Hz, AMMC-B1b perceives sounds in a wider range. AMMC-B2 neurons (two cells in each half of the brain) connect the right and left B areas of AMMC. All of these neurons are nonspiking. [Tootoonian *et al*., 2012].

Interaction of sensory systems. The interaction of sensory systems is of great importance in the perception of stimuli and the implementation of behavioral acts. This interaction has been identified at both the receptor and CNS levels. In crickets, the thoracic auditory interneuron AN2 is excited not only by sound but also by blowing on the cerci. Combined stimulation by sound and airflow elicits a response of greater amplitude, which facilitates the emergence of the escape response, which is triggered by AN2 activity [Someya, Ogawa, 2018] (Fig. 3a). In Lepidoptera, bat sounds evoke an escape response [Fullard, 1984; Waters, 2003]. However, if a male is previously or synchronously presented with a female sex pheromone, his response thresholds to ultrasound (and, consequently, the initiation of the escape response) increase [Skals *et al*., 2005], resulting in mating behaviour becoming a priority.

Inhibitory influences and response fuctions of neurons. Auditory interneurons in insects process and transmit acoustic information about the frequency, amplitude, and temporal patterns of stimuli to other parts of the central nervous system (see, for example, the review by Hedwig & Stumpner [2016]). The frequency parameters of interneurons are shaped by contact with corresponding afferents and under the influence of inhibitory elements. Inhibition can be both ipsilateral and contralateral. Furthermore, mirror cells, such as omega1 cells in crickets, can be reciprocally connected, exerting an inhibitory influence on each other. Inhibition also plays a major role in shaping the response pattern (phasic, on-off, off) and the intensity-response functions of interneurons. As a result, nonlinear functions of the dependence of the response impulse on the stimulus intensity and/or its duration are observed. Factors that ensure the formation of the dynamic characteristics of interneurons depend on the frequency of the stimulus, its intensity and duration (Fig. 3b). In neurons belonging to the same morphological type and having a similar type of arborization in the ganglion where contact with afferents occurs, responses to the stimulus can also differ significantly. In mole crickets of the genus *Scapteriscus*: ON1 is a low-frequency neuron, ON2 is a high-frequency one [Mason *et al*., 1998]. However, in mole crickets belonging to other genera of the family, such differences in the frequency tuning of this pair of neurons were not observed [Cillov, Stumpner, 2022].

These facts indicate that inhibitory influences play an extremely significant, if not decisive, role in shaping the functional characteristics of insect central auditory neurons, with the weight and ratio of excitatory and inhibitory connections apparently being species-specific. A. Stumpner [2002] expressed a similar view.

In addition to those listed, the source of inhibitory effects, at least in orthopterans, are dorsal unpaired median neurons (DUM) [Stumpner *et al*., 2019, 2020]. In the bush-cricket *Ancistrura nigrovittata*, a cluster of 35–50 local DUM neurons (Fig. 2c) responding to sound was detected in the prothoracic ganglion using immunohistochemistry [Stumpner *et al*., 2020]. These cells have different frequency tuning. Among them, there are low- and high-frequency cells and neurons responding to stimuli in a specific frequency range [Stumpner *et al*., 2019]. Most DUM neurons were GABA-immunoreactive. Exposure to picrotoxin caused an expansion of the frequency range of responses in some cells, i.e., they also experienced an inhibitory effect [Stumpner *et al*., 2020]. In addition to GABA, histamine may presumably be an inhibitory neurotransmitter in orthopterans, since Omega cells, which suppress the responses of both each other and the ascending interneuron AN1, do not exhibit positive GABA immunoreactivity [Cillov, Stumpner, 2022].

Furthermore, central neurons can experience presynaptic inhibition, the source of which is the motor centers of sound emission. In particular, Omega1 activity in crickets inhibited during male singing, even when the male is unable to produce an audible sound due to the removal of one of the elytra (corollary effect, Poulet & Hedwig [2002, 2006]).

RECOGNITION OF ACOUSTIC SIGNALS

Acoustic behavior and informative parameters of acoustic signals

Insects successfully recognize both heterospecific acoustic signals, including those of predators, and conspecific sounds. When recognizing acoustic signals, insects primarily use their temporal parameters. However, when recognizing a predator, such as a bat, it is sufficient to

Рис. 3. Свойства слуховых интернейронов насекомых: **a** — изменение средней частоты импульсов с течением времени в экспериментах с повторяющимися стимулами: воздушный поток (1), звуковые (2) и кросс-модальные стимулы (3) (число нейронов = 8; затененные области — зоны ошибок средней) (по Someya & Ogawa [2018], с изменениями); **b** — зависимость импульсации тонического интернейрона кузнечика *Isophya stepposa* от интенсивности стимула длительностью 3 и 50 мс (19 кГц). По горизонтали — интенсивность звука, по вертикали — число импульсов в ответе (средние значения и ошибки среднего при 5–8 предъявлениях стимула) (Корсуновская, неопубл.); **c** — гистограммы межимпульсных интервалов спонтанноактивного нейрона из 1-го грудного ганглия кузнечика *Metrioptera roeselii* до (черные колонки) и во время предъявления (белые колонки) конспецифического сигнала. По горизонтали — время, мс, по вертикали — число межимпульсных интервалов. Бин — 2 мс, время анализа 5 с. Различия значений интервалов в гистограммах статистически достоверны (p=0,019) (по Zhantiev *et al*. [2004]).

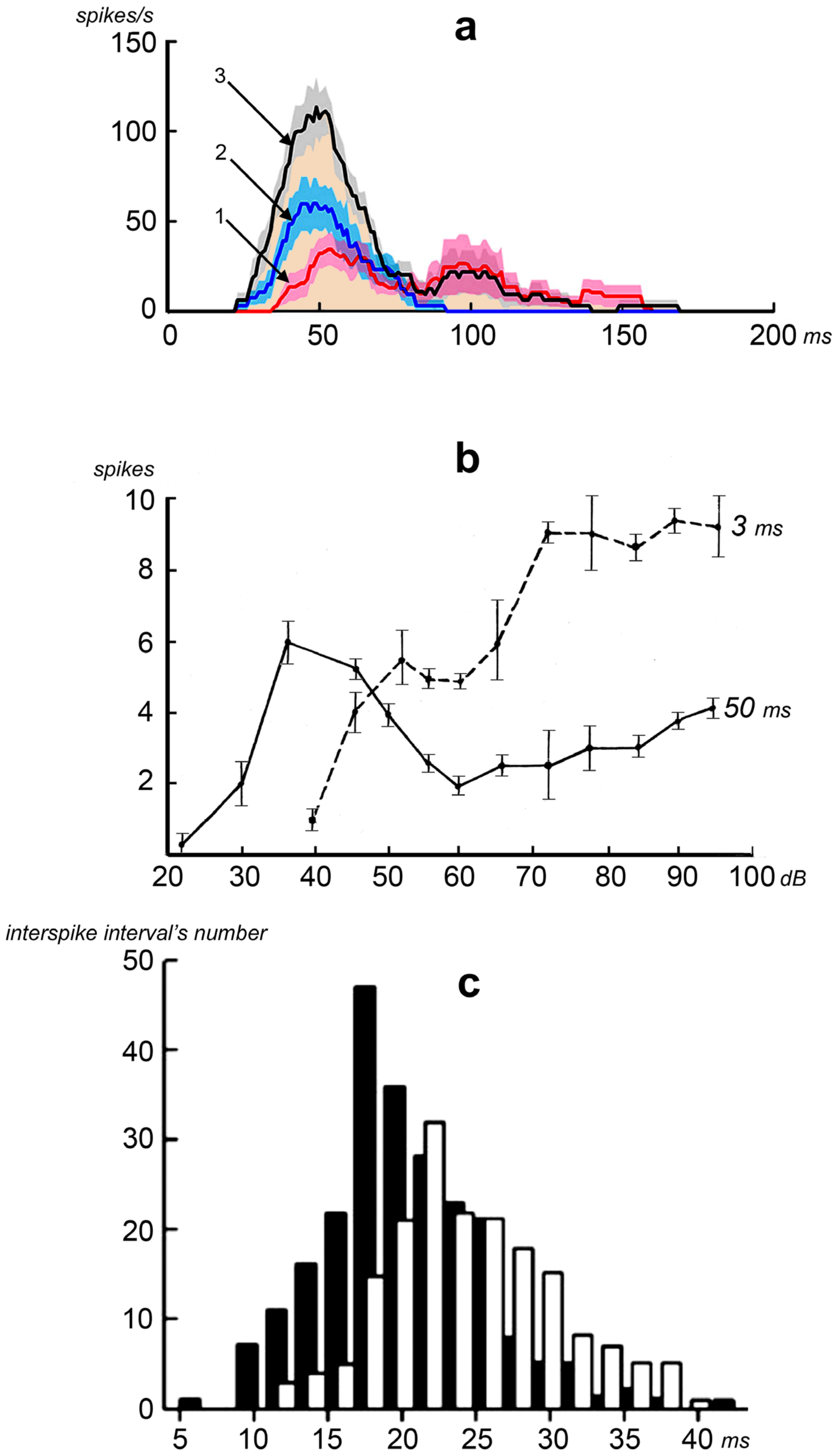


Fig. 3. Features of insect interneurons: **a** — variation in mean firing rate in response to airflow (1), sound (2) and cross-modal (3) stimuli in repetitive stimulation experiments (n = 8 neurons; shaded areas are standard errors) (modofoied from Someya & Ogawa [2018]); **b** — dependence of responses of the tonic interneuron of the bush-cricket *Isophya steppos*a on the intensity of stimuli with durations of 3 and 50 ms (19 kHz). Horizontal axis — sound intensity, vertical — the number of spikes in the response (mean and standard error, number of stimulus presentations 5–8) (Korsunovskaya, unpubl.); **c** — histograms of interspike intervals of a spontaneously active neuron from the first thoracic ganglion of *Metrioptera roeselii* before (black bars) and during presentation (white bars) of a conspecific signal. Horizontal axis — time, vertical — number of interspike intervals. Bin — 2 ms, analysis time — 5 s. The differences in interval values in the histograms are statistically significant (p=0.019) (from Zhantiev *et al.* [2004]).

hear a signal in a specific frequency range. Lepidoptera escaping bat attacks are known to change their flight trajectory or stop flying when they perceive ultrasonic signals. This behavioral response requires two or even a single auditory receptor [Surlykke, 1984]. However, some species have developed an additional adaptation: in response to predator echolocation signals, moths begin to produce acoustic signals in the same frequency range as the bat, thereby interfering with the transmission channel and hindering the animal's orientation when searching for prey [Barber *et al*., 2022].

Orthopterans primarily use temporal parameters when recognizing conspecifics; however, in some bush-cricket species, carrier frequency is also a relevant parameter [Deiley, Schul, 2006]. A study of the phonotaxis of three *Neoconocephalus* species revealed that *N. robustus* females are attracted to sound signals with a pulse repetition rate of the closely related species *N. bivocatus* if the dominant carrier frequencies of the presented models coincide with the dominant carrier frequency of the conspecific signal. When the model signal matches the frequency of heterospecific sounds, the phonotaxis of *N. robustus* and *N. nebrascensis* is suppressed. It is also known that flying crickets change the sign of phonotaxis at different frequencies of the signal that caused it [Moiseff *et al*., 1978]. Positive phonotaxis in a signal model with a conspecific carrier frequency filling changes to negative when stimulated by sounds with a frequency of 16 kHz. Apparently, in flight conditions, insects associate high-frequency sounds with a predator attack.

The temporal parameters of sound signals in intraspecific communication in most studied species appear to play a leading role. Results from studies of phonotaxis and/or sound responses have shown that pulse repetition rates (for terminology, see Baker & Chesmore [2020]) can be informative for recognizing conspecifics in dipterans (*Drosophila*), while syllabic patterns (crickets, katydids) or series (grasshoppers) can be informative for recognizing conspecifics in Orthoptera. Furthermore, orthopterans can use syllabic duration and signal duty cycle [Zhantiev, Korsunovskaya, 1986; Vedenina, Zhantiev, 1990; Tauber, Pener, 2000].

In addition to recognizing conspecifics, females must select the most suitable male for breeding. The few studies that contain data on these informative parameters focus primarily on Orthoptera. Thus, it has been shown that female of Grylloidea, under choice conditions, prefer a male with a louder signal [Forrest, Green, 1991 (*Scapteriscus*)], a longer signal and a lower carrier frequency (within the limits of intraspecific variability) (*Gryllus campestris*) [Nocke, 1972], in bush-crickets with longer syllables [Tauber *et al*., 2001]. Some of these parameters correlate with the size of the male's body and/or spermatophore (a source of additional protein nutrition for the female) (see, for example, Gwynne & Bailey [1988]). In grasshoppers, morphological and immunological traits of the male can also be assessed by females when perceiving their sound signals, since they correlate with certain parameters of the temporal pattern of the song. A short signal for the female indicates the "low quality" of the male [Stange, Ronacher, 2012].

Many factors influence the recognition of biologically significant signals, and in particular, calling songs. The first group of such factors includes those associated with the recognizing individual. It is known that the ability of females to respond to a sound or move toward its source depends on the insect's daily activity, the condition of its gonads, and its age. Fertilized females do not respond to male signals (which, however, does not mean they do not recognize these signals), and the selectivity of responses in older females is significantly reduced [Zhantiev, Korsunovskaya, 1986]. The nature of recognition is also influenced by the females' prior experience. For example, in dipterans (*Drosophila*), it has been shown that presenting females with a conspecific signal for 6 days reduces female acceptance of heterospecific songs in subsequent experiments [Li *et al*., 2018].

Furthermore, it turned out that the response of females to conspecific males depends on the attractiveness of the signals they had previously heard. If such signals were highly attractive, female crickets demonstrated weaker responses to signals with average parameters of the songs in choir of conspecific males. Females that had prior experience with sounds less attractive than the average signal responded more actively to the test average signal [Bailey, Zuk, 2009]. In addition to the factors listed above, the recognition of an acoustic signal is influenced by the communication conditions in a community of acoustically active species inhabiting the same biotope. It is known that in the presence of several synchronously singing species, the selectivity of female crickets' responses increases [Popov, Shuvalov, 1977]. However, even in the presence of isolated acoustic niches, with the synchronous activity of different species, conspecific recognition can be difficult or impossible due to the low noise immunity of the signal. A physiological adaptation developed by the Australian katydid *Sciarasaga quadrata* allows it to successfully tune out interference (the high-frequency song of the sympatric *Metaballus litus* [Römer, Bailey, 1998]. When perceiving the song of *M. litus*, S. *quadrata* closes the prothoracic spiracles leading to the prothoracic acoustic vesicles, which amplify the perceived ultrasound. This results in almost complete loss of sensitivity to the *M. litus* song and dramatically improves the perception of the lower-frequency conspecific signal.

Another factor influencing the recognition of the conspecific signal is the properties of the signal itself: in particular, its intensity and duty cycle.

It is currently unknown exactly how female insects, whose activity as poikilotherms is largely temperature-dependent, recognize a conspecific signal. Its parameters also vary, as singing males in a biotope experience heterogeneous temperature conditions. According to Creutzig *et al*. [2009], these differences may not be significant, as some auditory interneurons (AN12) maintain a constant firing rate at different temperatures. This creates the preconditions for the constancy of signal perception under different temperature conditions. Furthermore, it is possible that signals from a male singing under the same conditions as those experienced by the perceiving female may be selecte, if recognition is performed using a comparison block with an internal template or a signal after a delay line (see below).

Neural mechanisms of sound signal recognition

Insects with developed acoustic communication recognize conspecific signals by demonstrating positive phonotaxis and/or sound responses. The greatest number of studies have focused on Orthoptera and Diptera.

Currently, several hypotheses exist for the recognition of conspecific acoustic signals. The main ones are the filter and resonance hypotheses. The former is supported by data on the presence of neurons in the cricket brain that act as filters for temporal signal parameters [Schildberger, 1984; Kostarakos, Hedwig, 2012; Zhang, Hedwig, 2023], as well as so-called click detectors in katydids [Korsunovskaya, Zhantiev, 1992], which respond only to short sounds. In addition to these neurons, pC2 cells, which detect the discrete calling signal of males, have been discovered in *Drosophila* [Deutsch *et al*., 2019]. Their optogenetic stimulation induced singing in males and reduced the speed of movement in females. *Drosophila* are also thought to possess band pass filters, such as B1 interneurons. The selectivity of their responses is based on the interaction of passive filtering of high-frequency sounds (due to the properties of neuronal membrane Na^+ and K^+ channels) and active filtering — due to voltage-gated conductances — that suppress responses at low frequencies [Azevedo, Wilson, 2017].

While pC2 are undoubtedly command neurons, the affiliation of the a forementioned orthopteran neurons with command elements has not yet been proven, and the mechanisms that lead to the formation of their selectivity are unclear.

One proposed hypothesis is based on the combined effect of low- and high-pass filters on cricket neurons [Bush, Schul, 2006; Zhantiev, Korsunovskaya, 2014; Mann *et al*., 2025]. However, this concept does not explain the ability of female crickets to recognize and demonstrate positive phonotaxis when presented with signals with a multiple of the conspecific rhythm [Bush, Schul, 2006; Zhantiev, Korsunovskaya, 2014; Mann *et al*., 2025]. The second hypothesis regarding the formation of selectivity of central neuron responses is based on the possibility of comparing the response to a perceived signal with the response to it after passing a delay line (e.g., Kostarakos, Hedwig [2014]; Schöneich *et al*. [2015]; Clemens *et al*. [2021]). The latter, according to the authors, in crickets includes interneurons of the supraesophageal ganglion BLI-4 (Fig. 2i).

These concepts, based on autocorrelation processes, are close to the resonance hypothesis, as they assume the presence of a comparison block, the operation of which results in selectivity at the next level of signal recognition.

According to the resonance hypothesis, which was formulated in general form in the works of Stout & Huber [1972] and Schwartzkopff [1974], and model representations were developed later [Zhantiev, 1981], the existence of an internal matrix (template) is assumed, with which the pattern of the perceived signal is compared either during cross-correlation analysis or by adjusting the rhythm of the perceived signal to it.

The essence of this model is as follows. The signal, arriving at the input of the auditory system, enters the feature detector block, where some interference is suppressed, the features of the useful signal are contrasted, and the type of intraspecific signal is determined. This block includes frequency, time and amplitude filters (receptors and lower-order central auditory neurons). The signal then enters the highest association center (brain), where acoustic information is further processed and compared with signals from other sensory systems, the comparison unit, and the motor centers. If the behavioral situation is favorable, a permissive command signal is sent from the brain to the comparison unit. The most important stage of recognition occurs in the comparison unit, where information about perceived sounds is compared with a conspecific signal. If they match, and the conspecific signal is therefore recognized, a command is issued that triggers a response. It's easy to see that for such a mechanism to function successfully, spike activity of the central song pattern generator must precisely match the pattern (for example, rhythm or duration) of the conspecific signal. Interneurons of the auditory center can serve as template. It was assumed that females that do not produce sounds also possess structures similar to those of the male sound producing center, and that there are no significant differences in the functioning of the singing pattern generators of males and females. In cases where females produce song with a pattern different from that of the male (for example, in some bradyporine and phaneropterine bush-crickets), it can be assumed that there is a template based on other cellular basis.

Attempts to prove a common genetic basis for singing and recognition initially yielded negative results (see experiments with body heating in the *Chorthippus* grasshoppers [Bauer, von Helversen, 1987]. However, later genetic studies of crickets of the genus *Laupala* demonstrated the presence of genetic coupling between male signal and female song preference loci [Xu, Shaw, 2019], ensuring the coevolution of the centers of emission and preference of the acoustic signal. In experiments on orthopterans (crickets and katydids), we identified spontaneously active neurons in both males and females that did not respond to sound, but discharged in the rhythm of a conspecific calling signal, or in bursts corresponding in duration to it (if the signal was non-rhythmic and/or non-periodic) [Zhantiev, 1981; Zhantiev *et al*., 2004; Korsunovskaya, unpubl.]. The effect of conspecific calling song models on such rhythmically active neurons of bush-crickets in most cases caused a change in the activity level, phase rearrangements (adjustment of spikes to the rhythm of the stimulus) and a change in the spike repetition period. These effects were particularly clearly observed during the first minute of the stimulus, after which many neurons habituated and returned to their initial activity rhythm. Neurons that responded differently to con- and heterospecific signals were of particular interest. When stimulated by conspecific signals, gradual synchronization of spikes with the macrosyllables of the bush-cricket's conspecific song (CS) was observed. Heterospecific song either did not induce such synchronization, or it was significantly weaker. This suggests that these neurons are capable of detecting conspecific signals. Some interneurons, however, did not adapt to the CS rhythm but, on the contrary, altered their firing rate so that its frequency deviated from the repetition rate of the syllables in CS. This response may be aimed at reducing the level of interference preventing the detection of processes that are similar in rhythm to the CS. Such interference may, for example, include the rhythms of respiration or alimentary canal peristalsis.

Analysis of the firing patterns of spontaneously active neurons stimulated by biologically significant sounds suggests the possibility of another mechanism for recognizing conspecific signals. This mechanism involves adjusting the firing patterns of one or more neurons of different insect systems (with subsequent summation in a feature detector) to the rhythm of the conspecific signal. If this hypothesis is correct, the neural circuits responsible for recognizing conspecific signals, like the connectome of the auditory network in dipterans [Baker *et al*., 2022], may not have a hierarchical structure.

The data accumulated to date, in our opinion, allow us to draw the following conclusion. To recognize a biologically significant signal in simple acoustic communication systems — for example, in communication between predator and prey — simply detecting the signal based on one or a few characters (in particular, frequency band) is sufficient. The selectivity of such a recognition system is quite low. A similar mechanism can also be used to distinguish intraspecific signals (for example, in phaneropterine katydids). However, recognizing species-specific songs in a multispecies community requires the coordinated operation of neural networks that ensure phase adjustment to the perceived signal against a background of both external interference (abiotic noise and signals from other species) and internal interference — the numerous rhythmic processes occurring in the insect's body (respiration, locomotion, etc.). Thus, it appears that in different insects or in insects in different (for example, behavioral) situations, signal recognition can occur according to the four scenarios described above. When perceiving and recognizing biologically significant sounds, the auditory system interacts with other insect functional systems, some elements of which exhibit the properties of detectors of the conspecific signal features and can also participate in the process of its recognition [Zhantiev *et al*., 2004].

Conclusion

Despite significant advances in recent decades, many unresolved questions remain in insect bioacoustics, including the informative parameters of sound and vibrational signals used by a mating partner to identify a conspecific, the central mechanisms of conspecific signal recognition, the influence of stimuli of different modalities and other factors on the analysis of vibroacoustic signals in the central nervous system. In our opinion, the most promising areas of insect bioacoustics include studying the parameters and pathways of acoustic niche formation in representatives of different taxa, further research into the mechanisms of mechanoelectrical transduction in mechanoreceptors, the processes underlying mechanical amplification, algorithms for processing auditory information during the recognition of biologically important signals, and the development of applied aspects of bioacoustics, particularly vibroacoustic repellents and attractants.

Competing interests. The authors declare no competing interests.

Acknowledgements. Authors are very grateful to Prof. Dr. H. Römer, Prof. Dr. A. Stumpner, Prof. Dr. H. Ogawa and Dr. D. Lapshin for images provided. This article was written as a part of the Scientific Project of the State Order of the Government of Russian Federation to Lomonosov Moscow State University No. 121032300064-0.

References

Albert J.T., Göpfert M.C. 2015. Hearing in *Drosophila* // Current Opinion Neurobiology. Vol.34. P.79–85. https://doi.org/10.1016/j.conb.2015.02.001

Albert J.T., Nadrowski B., Göpfert M.C. 2007. Mechanical signatures of transducer gating in the *Drosophila* ear // Current Biology. Vol.17. P.1000–1006. https://doi.org/10.1016/j.cub.2007.05.004

Andrés M., Seifert M., Spalthoff C., Warren B., Weiss L., Giraldo D., Winkler M., Pauls S., Go M., Göpfert M.C. 2016. Auditory efferent system modulates mosquito hearing // Current Biology. Vol.26. P.1–9. https://doi.org/10.1016/j.cub.2016.05.077

Arjomandi I., Turchen L.M., Connolly A.A., Léveillée M.B., Yack J.E. 2024. Acoustic communication in bark beetles (Scolytinae): 150 years of research // Physiological Entomology. Vol.49. P.281–300. https://doi.org/10.1111/phen.12453

Atkins G., Pollack G.S. 1986. Age-dependent occurrence of an ascending axon on the omega neuron of the cricket, *Teleogryllus oceanicus* // Journal of Comparative Neurology. Vol.243. P.527–534. https//doi.org/ 10.1002/cne.902430407

Avcı C., Taylan M.S.2023. Bioacoustics of Tettigoniidae (Insecta, Orthoptera) Distributed in Hakkari (Eastern Anatolia) Province // Journal of the Entomological Research Society. Vol.25. No.2. P.371–386. https://doi.org/10.51963/jers.2023.95

Azevedo A.W., Wilson R.I. 2017. Active mechanisms of vibration encoding and frequency filtering in central mechanosensory neurons // Neuron. Vol.96. P.446–460. https//doi.org/ 10.1016/j.neuron.2017.09.004

Baden T., Hedwig B. 2007. Neurite-specific Ca2$^+$dynamics underlying sound processing in an auditory interneurone // Developmental Neurobiology. Vol.67. No.1. P.68–80. https://doi.org/10.1002/dneu.20323

Bailey N.W., Zuk M. 2009. Field crickets change mating preferences using remembered social information // Biological Letters. Vol.5. P.449–451. https://doi.org/10.1098/rsbl.2009.0112

Baker C.A., McKellar C., Pang R., Nern A., Dorkenwald S., Pacheco D.A., Eckstein N., Funke J., Dickson B.J., Murthy M. 2022. Neural network organization for courtship-song feature detection in *Drosophila* // Current Biology. Vol.32. P.3317–3333. https://doi.org/10.1016/j.cub.2022.06.019

Baker E., Chesmore D. 2020. Standardisation of bioacoustic terminology for insects // Biodiversity Data Journal. Vol.8. Art.E54222. https://doi.org/10.3897/BDJ.8.e54222

Balakrishnan R. 2016. Behavioral ecology of insect acoustic communication // G. Pollack, A. Mason, A. Popper, R. Fay (eds.). Insect hearing. Springer handbook of auditory research. Vol.55. Springer, Cham. https://doi.org/10.1007/978-3-319-28890-1_3

Barber J.R., Plotkin D., Rubin J.J., Homziak N.T., Leavell B.C., Houlihan P.R., Miner K.A., Breinholt J.W., Quirk-Royal B., Padrón P.S., Nunez M., Kawahara A.Y. 2022. Anti-bat ultrasound production in moths is globally and phylogenetically widespread // Proceedings of the National Academy of Sciences of the United States of America. Vol.119. No.25. Art.e2117485119. https://doi.org/10.1073

Bauer M., von Helversen O. 1987. Separate localization of sound recognizing and sound producing neural mechanisms in a grasshopper // Journal of Comparative Physiology A. Vol.161. P.95–101. https://doi.org/10.1007/BF00609458

Benediktov A.A. 2015. The possibility of computer analysis of the twilight soundscape of the orthopteran (Tettigoniidae, Gryllidae) community, by the example of an agrocenosis in Eastern Bulgaria // Entomological Review. Vol. 95. No.9. P.1174–1181. https://doi.org/10.1134/S0013873815090043

Boo K.S., Richards A.G. 1975. Fine structure of scolopidia in the Johnston's organ of male *Aedes aegypti* (L.) (Diptera: Culicidae) // International Journal of Insect Morphology and Embryology. Vol.4. P.549–566. https://doi.org/10.1016/0020-7322(75)90031-8

Boyan G.S., Fullard J.H. 1986. Interneurones responding to sound in the tobacco budworm moth *Heliothis virescens* (Noctuidae): morphological and physiological characteristics // Journal of Comparative Physiology A. Vol.158. P.391–404. https://doi.org/10.1007/BF00603623

Boyan G., Williams J. 1981. Descending interneurones in the brain of the cricket // Naturwissenschaften. Vol.68. No.9. P.486–487. https://doi.org/10.1007/BF01047530

Bukhvalova M. 2006. Partitioning of acoustic transmission channels in grasshopper communities // S. Drosopoulos, M.F. Claridge (eds.). Insect sounds and communication. Roca Baton: Taylor and Francis. P.199–205. https://doi.org/10.1201/9781420039337.ch14

Bukhvalova M.A., Zhantiev R.D. 1993. [Acoustic signals in grasshopper communities (Orthoptera, Acrididae, Gomphocerinae)] // Zoologicheskii Zhurnal. Vol.72. No.9. P.47–62 [in Russian with English summary].

Bura V.L., Rohwer V.G., Martin P.R., Yack J.E. 2011. Whistling in caterpillars (*Amorpha juglandis*, Bombycoidea): sound-producing mechanism and function // Journal of Experimental Biology. Vol.214. No.1. P.30–37. https://doi.org/10.1242/jeb.046805

Bush S.L., Schul J. 2006. Pulse-rate recognition in an insect: evidence of a role for oscillatory neurons // Journal of Comparative Physiology A. Vol.192. P.113–121. https://doi.org/10.1007/s00359-005-0053-x

Chesmore D. 2004. Automated bioacoustic identification of species // Anais da Academia Brasileira de Ciências. Vol.76. No.2. P.436–440. https://doi.org/10.1590/S0001-37652004000200037

Chesmore E.D., Ohya E. 2004. Automated identification of field-recorded songs of four British grasshoppers using bioacoustic signal recognition // Bulletin of Entomological Research. Vol.94. No.4. P.319–330. https://doi.org/10.1079/BER2004306

Chhaya V., Lahiri S., Jagan M.A., Mohan R., Pathaw N.A., Krishnan A. 2021. Community bioacoustics: studying acoustic community structure for ecological and conservation insights // Frontiers in Ecology and Evolution. Vol.9. Art.706445. https://doi.org/10.3389/fevo.2021.706445

Cigliano M.M., Braun H., Eades D.C., Otte D. 2025. Orthoptera Species File. Version 5.0/5.0. [2025-11-20]. http://Orthoptera.SpeciesFile.org

Cillov A., Stumpner A. 2022. Local prothoracic auditory neurons in Ensifera // Frontiers in Neuroscience. Vol.16. Art.1087050. https://doi.org/10.3389/fnins.2022.1087050

Clemens J., Schöneich S., Kostarakos K., Hennig R.M., Hedwig B. 2021. A small, computationally flexible network produces the phenotypic diversity of song recognition in crickets // Elife. Vol.10. Art.e61475. https://doi.org/10.7554/eLife.61475

Couldridge V.C.K., van Staaden M.J. 2004. Habitat-dependent transmission of male advertisement calls in bladder grasshoppers (Orthoptera; Pneumoridae) // Journal of Experimental Biology. Vol.207. No.16. P.2777–2786. https://doi.org/10.1242/jeb.01092

Creutzig F., Wohlgemuth S., Stumpner A., Benda J., Ronacher B., Herz A.V.M. 2009. Timescale-invariant representation of acoustic communication signals by a bursting neuron // Journal of Neuroscience. Vol.29. No.8. P.2575–2580. https://doi.org/10.1523/JNEUROSCI.0599-08.2009

Deily J.A., Schul J. 2006. Spectral selectivity during phonotaxis: a comparative study in *Neoconocephalus* (Orthoptera: Tettigoniidae) // Journal of Experimental Biology. Vol.209. No.9. P.1757–1764. https://doi.org/ 10.1242/jeb.02189

Deutsch D., Clemens J., Thiberge S.Y., Guan G., Murthy M. 2019. Shared song detector neurons in *Drosophila* male and female brains drive sex-specific behaviors // Current Biology. Vol.29. No.19. P.3200–3215.e5. https://doi.org/10.1016/j.cub.2019.08.008

Diwakar S., Balakrishnan R. 2007. Vertical stratification in an acoustically communicating ensiferan assemblage of a tropical evergreen forest in southern India // Journal of Tropical Ecology. Vol.23. P.479–486. https://doi.org/10.1017/S0266467407004208

Effertz T., Wiek R., Göpfert M.C. 2011. NompC TRP channel is essential for *Drosophila* sound receptor function // Current Biology. Vol.21. P.7592–7597. https://doi.org/10.1016/j.cub.2011.02.048

Farina A., Gage S.H. 2017. Ecoacoustics: a new science // A. Farina, S.H. Gage (eds.). Ecoacoustics: the ecological role of sounds. Oxford: John Wiley and Sons. 336 p.

Forrest T.G., Green D.M. 1991. Sexual selection and female choice in mole crickets (*Scapteriscus*: Gryllotalpidae): modelling the effects of intensity and male spacing // Bioacoustics. Vol.3. No.2. P 93–109. https://doi.org/10.1080/09524622.1991.9753166

Fullard J.H. 1984. Acoustic relationships between tympanate moths and the Hawaiian hoary bat (*Lasiurus cinnereus semotus*) // Journal of Comparative Physiology A. Vol.155. P.795–801. https://doi.org/10.1007/BF00611596

Ganchev T., Potramitis I., Fakotakis N. 2007. Acoustic monitoring of singing insects // IEEE International Conference on Acoustics, Speech and Signal Processing - ICASSP '07, Honolulu, HI, USA, 2007. P.IV-721–IV-724. https://doi.org/10.1109/ICASSP.2007.367014

Georgiades M., Alampounti C.A., Somers J., Su M., Ellis D., Bagi J., Terrazas-Duque D., Tytheridge S., Ntabaliba W., Moore S., Albert J.T., Andrés M. 2023. Hearing of malaria mosquitoes is modulated by a beta-adrenergic-like octopamine receptor which serves as insecticide target // Nature Communications. Vol.14. Art.4338. https://doi.org/10.1038/s41467-023-40029-y

Gomez-Morales D.A., Acevedo-Charry O.2022. Satellite remote sensing of environmental variables can predict acoustic activity of an orthopteran assemblage // PeerJ. Vol.10. Art.e13969. https://doi.org/10.7717/peerj.13969

Göpfert M.C., Albert J.T., Nadrowski B., Kamikouchi A. 2006. Specification of auditory sensitivity by *Drosophila* TRP channels // Nature Neuroscience. Vol.9. P.999–1000. https://doi.org/10.1038/nn1735

Göpfert M.C., Hennig M. 2016. Hearing in insects // Annual Review of Entomology. Vol.61. P.257–276. https://doi.org/10.1146/annurev-ento-010715-023631

Göpfert M.C., Humphris A.D., Albert J.T., Robert D., Hendrich O. 2005. Power gain exhibited by motile mechanosensory neurons in *Drosophila* ears // Proceedings of the National Academy of Sciences of the United States of America. Vol.102. P.325–330. https://doi.org/10.1073/0405741102

Göpfert M.C., Robert D. 2001. Biomechanics. Turning the key on *Drosophila* audition // Nature. Vol.411. P.908. https://doi.org/10.1038/35082144

Göpfert M.C., Robert D. 2003. Motion generation by *Drosophila* mechanosensory neurons // Proceedings of the National Academy of Sciences of the United States of America. Vol.100. No.9. P.5514–5519. https://doi.org/10.1073/pnas.073756410

Göpfert M.C., Surlykke A., Wasserthal L.T. 2002. Tympanal and atympanal 'mouth-ears' in hawkmoths (Sphingidae) // Proceedings of the Royal Society B. Vol.269. P.89–95. https://doi.org/10.1098/rspb.2001.1646

Greenfield M.D. 1988. Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity // Animal Behaviour. Vol.36. No.3. P.684–695. https://doi.org/10.1016/C0003-3472(88)80151-9

Greenfield M.D. 2013. Acoustic communication in the nocturnal Lepidoptera // Animal Signals and Communication. Berlin, Heidelberg: Springer-Verlag. P.81–100. https//doi.org/10.1007/978-3-642-40462-7_6

Greenfield M.D. 2014. Acoustic communication in the nocturnal Lepidoptera // B. Hedwig (ed.). Insect hearing and acoustic communication. Vol.1. Animal signals and communication. Berlin: Springer. P.81–100. https://doi.org/10.1007/978-3-642-40462-7

Guerten B., Spalthoff Ch., Göpfert M.C. 2013. Insect hearing: active amplification in tympanal years // Current Biology. Vol.23. No.21. P.R950–R952. http://dx.doi.org/10.1016/j.cub.2013.09.044

Gwynne D.T., Bailey W.J. 1988. Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae) // Behaviour. Vol.105. No.3–4. P.202–223. https://doi.org/10.1163/156853988X00025

Hedwig B., Stumpner A. 2016. Central neural processing of sound signals in insects // G. Pollack, A. Mason, A. Popper, R. Fay (eds). Insect hearing. Springer handbook of auditory research. Vol.55. Springer, Cham. P.177–214. https://doi.org/10.1007/978-3-319-28890-1_8

Hehlert P., Effertz T., Gu R.X., Nadrowski B., Geurten B.R.H., Beutner D., de Groot B.L., Göpfert M.C. 2025. NOMPC ion channel hinge forms a gating spring that initiates mechanosensation // Nature Neuroscience. Vol.28. P.259–267. https://doi.org/10.1038/s41593-024-01849-3

Heller K.-G. 1988. Bioakustik der europäischen Laubheuschrecken. Weikersheim: Josef Margraf. 358 S.

Heller K.-G., Baker E., Ingrisch S., Korsunovskaya O.S., Liu C.-X., Riede K., Warchałowska-Liwa E. 2021. Bioacoustics and systematics of *Mecopoda* (and related forms) from South East Asia and adjacent areas (Orthoptera, Tettigonioidea, Mecopodinae) including some chromosome data // Zootaxa. Vol.5005. No.2. P.101–144. https://doi.org/10.11646/zootaxa.5005.2.1

Heller K.-G., Hemp K., Ingrisch S., Liu C. 2015. Acoustic communication in Phaneropterinae (Tettigonioidea). A global review with some new data // Journal of Orthoptera Research. Vol.24. No.1. P.7–18. https://doi.org/10.1665/034.024.0103

Heller K.-G., von Helversen O. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats // Oecologia. Vol.80. P.178–186. https://doi.org/10.1007/BF00380148

Hemp K. 2021. A field guide to the bushcrickets, wetas and raspy crickets of Tanzania and Kenya. Frankfurt/Mein: Senckenberg. 451 p.

Huber F., Kleindienst H.-U., Moore T., Schildberger K., Weber T. 1990. Acoustic communication in periodical cicadas: neuronal responses to songs of sympatric species // G. Gribakin, K. Wiese, A. Popov (eds.). Sensory systems and communication in arthropods. Basel: Birkhäuser. P.217–231. https://doi.org/10.1007/978-3-0348-6410-7_38

Hummel J., Kössl M., Nowotny M. 2017. Morphological basis for a tonotopic design of an insect ear // Journal of Comparative Neurology. Vol.525. No.10. P.2443–2455. https://doi.org/10.1002/cne.24218

Jain M., Balakrishnan R. 2012. Does acoustic adaptation drive vertical stratification? A test in a tropical cricket assemblage // Behavioral Ecology. Vol.23. No.2. P.343–354. https://doi.org/10.1093/beheco/arr191

Kalmring K., Rössler W., Unrast C. 1994. Complex tibial organs in the fore-, mid- and hindlegs of the bushcricket *Gampsocleis gratiosa* (Tettigoniidae): Comparison of physiology of the organs // Journal of Experimental Zoology. Vol.270. No.2. P.155–161. https://doi.org/10.1002/jez.1402700205

Kawahara A.Y., Plotkin D., Espeland M., Breinholt J.W. 2019. Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths // Proceedings of the National Academy of Sciences of the United States of America. Vol.116. No.45. P.22657–22663. https://doi.org/10.1073/pnas.1907847116

Kaya S., Chobanov D, Ciplak B. 2014. Review of *Psorodonotus specularis* Group (Orthoptera, Tettigoniidae, Tettigoniinae): two new species from North-east Anatolia // Zootaxa. Vol.3895. No.3. P.367–400. https://doi.org/10.11646/zootaxa.3895.3.3

Kim T.W. 2010. A Sound Guide to Korean Tettigoniidae (Orthoptera: Ensifera). 136 p.

Kleyn T., Cruz Kaizer M., Passos L.F. 2021. Sharing sound: avian acoustic niches in the Brazilian atlantic forest // Biotropica, Vol.53. No.2. P.658–670. https://doi.org/10.1111/btp.12907

Korsunovskaya O., Berezin M., Heller K.-G., Tkacheva E., Kompantseva T., Zhantiev R. 2020. Biology, sounds and vibratory signals of hooded katydids (Orthoptera: Tettigoniidae: Phyllophorinae) // Zootaxa. Vol.4852. No.3. P.309–322. https://doi.org/10.11646/zootaxa.4852.3.3

Korsunovskaya O.S., Zhantiev R.D. 1992. [Auditory interneurons in the phaneropterid bush-crickets (Orthoptera, Phaneropteridae)] // Entomologicheskoe obozrenie. Vol.71. No.4. P.721–730 [in Russian with English summary]

Korsunovskaya O.S., Zhantiev R.D. 2022. Acoustic and vibrational signaling in true katydid *Nesoecia nigrispina*: three means of sound production in one species // PeerJ. Vol.10. Art.e13749. https://doi.org/10.7717/peerj.13749

Kössl M., Coro F. 2006. L1,L2 maps of distortion–product otoacoustic emissions from a moth ear with only two auditory receptor neurons // Journal of Acoustical Society of America. Vol.120. P.3822–3831. https://doi.org/10.1121/1.2363934

Kössl M., Möckel D., Weber M., Seyfarth E.-A 2008. Otoacoustic emissions from insect ears: evidence of active hearing? // Journal of Comparative Physiology A. Vol.194. No.7. P.597–609. https://doi.org/ 10.1007/s00359-008-0344-0

Kostarakos K., Hedwig B. 2012. Calling song recognition in female crickets: temporal tuning of identified brain neurons matches behavior // J. Neurosci. Vol.32. No.28. P.9601–9612. https://doi.org/10.1523/JNEUROSCI.1170-12.2012

Kostarakos K., Hedwig B. 2014. Pattern recognition in field crickets: concepts and neural evidence // Journal of Comparative Physiology A. Vol.201. No.1. P.73–85. https://doi.org/10.1007/s00359-014-0949-4

Kühne R. 1982. Neurophysiology of the vibration sense in locusts and bushcrickets: response characteristics of single receptor units // Journal of Insect Physiology. Vol.28. No.2. P.155–163. https://doi.org/10.1016/0022-1910(82)90123-8

Kumar T.M., Göpfert M.C. 2026. Hearing: insects // Encyclopedia of animal behavior. 3rd edition. Academic Press. In press.

Lai J.S., Lo S.J., Dickson B.J., Chiang A.S. 2012. Auditory circuit in the *Drosophila* brain // Proceedings of the National Academy of Sciences of the United States of America. Vol.109. P.2607–2612. https://doi.org/ 10.1073/1117307109

Lehnert B.P., Baker A.E., Gaudry Q., Chiang A.S., Wilson R.I. 2013. Distinct roles of TRP channels in auditory transduction and amplification in *Drosophila* // Neuron. Vol.77. No.1. P.115–128. https://doi.org/ 10.1016/j.neuron.2012.11.030

Lewis D.B. 1974. The physiology of the tettigoniid ear. I–IV. // Journal of experimental Biology. Vol.60. P.821–869. https://doi.org/10.1242/jeb.60.3.821

Li X., Ishimoto H., Kamikouchi A. 2018. Auditory experience controls the maturation of song discrimination and sexual response in *Drosophila* // Elife. Vol.7. Art.e34348. https://doi.org/ 10.7554/eLife.34348

Loh Y.M.M., Su M.P., Ellis D.A., Andrés M. 2023. The auditory efferent system in mosquitoes // Frontiers in Cell and Developmental Biology. Vol.11. Art.1123738. https://doi.org/10.3389/fcell.2023.1123738

Lomas K.F., Greenwood D.R., Windmill J.F.C., Jackson J.C., Corfield J., Parsons S. 2012 Discovery of a lipid synthesising organ in the auditory system of an insect // PLoS ONE. Vol.7. No.12. Art.e51486. https://doi.org/10.1371/journal.pone.0051486

Low M.L., Naranjo M., Yack J.E. 2021. Survival sounds in insects: diversity, function, and evolution // Frontiers in Ecology and Evolution. Vol.9. Art.641740. https://doi.org/10.3389/fevo.2021.641740

Lucas K.M., Windmill J.F., Robert D., Yack J.E. 2009. Auditory mechanics and sensitivity in the tropical butterfly *Morpho peleides* (Papilionoidea, Nymphalidae) // Journal of Experimental Biology. Vol.212. Pt.21. P.3533–3541. https://doi.org/ 10.1242/jeb.032425

Manley G.A. 2001. Evidence for an active process and a cochlear amplifier in nonmammals // Journal of Neurophysiology. Vol.86. P.541–549. https://doi.org/10.1152/jn.2001.86.2.541

Mann W., Erregger B., Hennig R.M., Clemens J. 2025. Resonant song recognition and the evolution of acoustic communication in crickets // iScience. Vol.28. No.2. Art.111695. https://doi.org/10.1016/j.isci.2024.111695

Mason A.C., Forrest T.G., Hoy R.R. 1998. Hearing in mole crickets (Orthoptera: Gryllotalpidae) at sonic and ultrasonic frequencies // Journal of Experimental Biology. Vol.201. P.1967–1979. https://doi.org/ 10.1242/jeb.201.12.1967

Matsuo E., Seki H., Asai T., Morimoto T., Miyakawa H., Ito K., Kamikouchi A. 2016. Organization of projection neurons and local neurons of the primary auditory center in the fruit fly *Drosophila melanogaster* // Journal of Comparative Neurology. Vol.524. No.6. P.1099–1164. https://doi.org/10.1002/cne.23955

Mhatre N. 2015. Active amplification in insect ears: mechanics, models and molecules // Journal of comparative physiology A. Vol.201. No.1. P.19–37. https://doi.org/10.1007/s00359-014-0969-0

Mhatre N., Robert D. 2013. A tympanal insect ear exploits a critical oscillator for active amplification and tuning // Current Biology. Vol.23. No.19. P.1952–1957. https://doi.org/10.1016/j.cub.2013.08.028

Minet J., Surlykke A. 2003. Sound producing and auditory organs // N.P. Kristensen (ed.). Lepidoptera, moths and butterflies, Bd.2: Morphology and Physiology. Handbook of Zoology/Handbuch der Zoologie IV, 35. P. Kap. 11. Berlin: De Gruyter.

Möckel D., Nowotny M., Kössl M. 2014. Mechanical basis of otoacoustic emissions in tympanal hearing organs // Journal of comparative physiology A. Vol.200. P.681–691. https://doi.org/10.1007/s00359-014-0914-2

Möckel D., Seyfarth E.A., Kössl M. 2011. Otoacoustic emissions in bushcricket ears: general characteristics and the influence of the neuroactive insecticide pymetrozine // Journal of Comparative Physiology A. Vol.197. P.193–202. https://doi.org/10.1007/s00359-010-0599-0

Moiseff A., Pollack G.S., Hoy R.R. 1978. Steering responses of flying crickets to sound and ultrasound: mate attraction and predator avoidance // Proceedings of the National Academy of Sciences of the United States of America. Vol.75. No.8. P.4052–4056. https://doi.org/10.1073/pnas.75.8.4052

Morris G.K., Ingrisch S., Willemse F., Willemse L., De Luca P.A., Klimas D. 2025. Stridulation songs of some Tettigoniidae (Ensifera, Orthoptera) from Papua New Guinea // Zootaxa. Vol.5600. No.1. P.1–81. https://doi.org/10.11646/zootaxa.5600.1.1

Mutanu L., Gohil J., Gupta K., Wagio P., Kotonya G. 2022. A review of automated bioacoustics and general acoustics classification research // Sensors. Vol.22. No.21. Art.8361. https://doi.org/10.3390/s22218361

Nadrowski B., Albert J.T., Göpfert M C. 2008. Transducer-based force generation explains active process in *Drosophila* hearing // Current Biology. Vol.18. P.1365–1372. https://doi.org/ 10.1016/j.cub.2008.07.095

Naskrecki P. 2000. Katydids of Costa Rica: Vol.1. Systematics and bioacoustics of the cone-head katydids (Orthoptera: Tettigoniidae: Conocephalinae sensu lato). Orthopterists' Society. 164 p.

Nocke H. 1972. Physiological aspects of sound communication in crickets (*Gryllus campestris* L.) // Journal of Comparative Physiology A. Vol.80. P.141–162. https://doi.org/10.1007/BF00696487

Ogawa H., Miller J.P. 2017.Optical recording methods: how to measure neural activities with calcium imaging // H.W. Horch, T. Mito, A. Popadić, H. Ohuchi, S. Noji (eds). The cricket as a model organism. Tokyo: Springer. P.285–302. https://doi.org/10.1007/978-4-431-56478-2_18

Oldfield B.P. 1982. Tonotopic organisation of auditory receptors in Tettigoniidae (Orthoptera: Ensifera) // Journal of Comparative Physiology A. Vol.147. No.4. P.461–469. https://doi.org/10.1007/bf00612011

Oldfield B.P., Hill K.G. 1986. Functional organization of insect auditory sensilla // Journal of Comparative Physiology A. Vol.158. No.1. P.27–34. https://doi.org/10.1007/BF00614517

Otte D. 1992. Evolution of cricket songs // Journal of Orthoptera Research. Vol.1. No.1. P.25–49. https://doi.org/10.2307/3503559

Perez M., Coro F. 1985. Physiological characteristics of the tympanic organ in noctuoid moths // Journal of Comparative Physiology A. Vol.156. P.689–696. https://doi.org/10.1007/BF00619118

Popov A., Shuvalov V.F. 1977. Phonotactic behaviour of crickets // Journal of comparative physiology A. Vol.119. P.111–126. https://doi.org/10.1007/BF00655876

Potamitis I., Ganchev T., Fakotakis N. 2007. Automatic acoustic identification of crickets and cicadas // Proceedings of the 20th IEEE International Symposium Signal Processing and Application, ISSPA-2007, Sharjah Millennium Hotel, United Arab Emirates (UAE), February 12–15, 2007. https://doi.org/10.1109/ISSPA.2007.4555462

Poulet J.F., Hedwig B. 2002. A corollary discharge maintains auditory sensitivity during sound production // Nature. Vol.418. No.6900. P.872–876. https://doi.org/10.1038/nature00919

Poulet J.F.A., Hedwig B. 2006. The cellular basis of a corollary discharge // Science, Vol.311. No.5760. P.518–522. https://doi.org/10.1126/science.1120847

Pulver C.A., Celiker E., Woodrow C., Geipel I., Soulsbury C.D., Cullen D.A., Rogers S.M., Veitch D., Montealegre-Z. F. 2022. Ear pinnae in a neotropical katydid (Orthoptera: Tettigoniidae) function as ultrasound guides for bat detection // eLife. Vol.11. Art.E77628. https://doi.org/10.7554/eLife.77628

Ragge D.R., Reynolds W.J. 1998. The songs of the grasshoppers and crickets of Western Europe. Colchester, Essex: Harley Books in association with the Natural History Museum. 596 pp.

Riede K., 1998. Acoustic monitoring of Orthoptera and its potential for conservation // Journal of Insect Conservation. Vol.2. P.217–223. https://doi.org/10.1023/A:1009695813606

Riede K. 2018. Acoustic profiling of Orthoptera: present state and future needs // Journal of Orthoptera Research. Vol.27. No.2. P. 203–215. https://doi.org/10.3897/jor.27.23700

Riede K., Balakrishnan R. 2025. Acoustic monitoring for tropical insect conservation // Philosophical Transactions of the Royal Society B. Vol.380. No.1938. Art.20240046. https://doi.org/10.1098/rstb.2024.0046

Riede K., Kroker A. 1995. Bioacoustics and niche differentiation in two cicada species from Bornean lowland forest // Zoologischer Anzeiger. Bd.234. P.43–51.

Riva F., Barbero F., Bonelli S., Balletto E., Casacci L.P. 2017. The acoustic repertoire of lycaenid butterfly larvae // Bioacoustics. Vol.26. No.1. P.77–90. https://doi.org/10.1080/09524622.2016.1197151

Roeder K.D., Treat A.E., Vande Berg J.S. 1970. Distal lobe of the pilifer: an ultrasonic receptor in choerocampine hawkmoths // Science. Vol.170. P.1098–1099. https://doi.org/10.1016/0022-1910(72)90255-7

Rogers S.M., Kostarakos K., Hedwig B. 2022. An auditory-responsive interneuron descending from the cricket brain: a new element in the auditory pathway // Journal of Comparative Physiology A. Vol.208. No.5–6. P.571–589. https://doi.org/10.1007/s00359-022-01577-8

Römer H. 2013. Masking by noise in acoustic insects: problems and solutions // H. Brumm (ed.). Animal communication and noise; animal signals and communication. Berlin, Heidelberg: Springer. Vol.2. P.33–63. https://doi.org/10.1007/978-3-642-41494-7_3

Römer H. 2019. Insect acoustic communication: The role of transmission channel and the sensory system and brain of receivers // Functional Ecology. Vol.34. No.2. P.310–321. https://doi.org/10.1111/1365-2435.13321

Römer H., Bailey W. 1998. Strategies for Hearing in Noise: peripheral control over auditory sensitivity in the bushcricket *Sciarasaga quadrata* (Austrosaginae: Tettigoniidae) // Journal of Experimental Biololy. Vol.201. No.7. P.1023–1033. https://doi.org/10.1242/jeb.201.7.1023

Römer H., Marquart V. 1984. Morphology and physiology of auditory interneurons in the metathoracic ganglion of the locust. // Journal of Comparative Physiology A. Vol.155. P.249–262. https://doi.org/10.1007/BF00612642

Rössler W., Jatho M., Kalmring K. 2006.The auditory–vibratory sensory system in bushcrickets // S. Drosopoulos, M.F. Claridge (eds). Insect sounds and communication. Roca Baton: Taylor and Francis. P.35–69. https://doi.org/10.1201/9781420039337.ch3

Rowell C.H., Reichert H. 1986. Three descending interneurons reporting deviation from course in the locust. II. Physiology // Journal of Comparative Physiology A. Vol.158. No.6. P.775–794. https://doi.org/10.1007/BF01324821

Ruggero M.A., Robles L., Rich N.C. 1992. Two-tone suppression in the basilar membrane of the cochlea: mechanical basis of auditory-nerve rate suppression // Journal of Neurophysiology. Vol.68. No.4. P.1087–1099.doi: 10.1152/jn.1992.68.4.1087

Savitsky V.Yu. 2000. Acoustic signals, ecological features, and reproductive isolation of grasshoppers of the genus *Dociostaurus* (Orthoptera, Acrididae) in semi-desert // Entomological Review. Vol.80. No.8. P.950–967.

Savitsky V.Yu. 2011. [Fauna, structure of communities and features of separation of ecological niches of grasshoppers (Orthoptera: Acridoidea) in the environs of the lake Baskunchak] // Russian Entomological Journal // Vol.19 (for 2010). No.4. P.267–304 [in Russian, with English summary]. https://doi.org/10.15298/rusentj.19.4.02

Schildberger K. 1984. Temporal selectivity of identified auditory neurons in the crickets brain // Journal of Comparative Physiology A. Vol.155. P.171–185. https://doi.org/10.1007/BF00612635

Schmidt A.K., Balakrishnan R. 2015. Ecology of acoustic signalling and the problem of masking interference in insects // Journal of Comparative Physiology A. Vol.201. P.133–142. https://doi.org/10.1007/s00359-014-0955-6

Schmidt A.K., Römer H., Riede K. 2013. Spectral niche segregation and community organization in a tropical cricket assemblage // Behavioral Ecology. Vol.24. P.470–480. https://doi.org/10.1093/beheco/ars187

Schöneich S., Kostarakos K., Hedwig B. 2015 An auditory feature detection circuit for sound pattern recognition // Science Advances. Vol.1. No.8. Art.e1500325. https://doi.org/10.1126/sciadv.1500325

Schwartzkopff J.1974. Principles of signal detection by auditory pathways of invertebrates and vertebrates // Abhandlungen der Rheinisch-Westfalische Akademie der Wissenschaften. Bd.53. P.331–344. Discuss. P.344–346. https://doi.org/10.1007/978-3-663-01719-6_24

Senthilan P.R., Piepenbrock D., Ovezmyradov G., Nadrowski B., Bechstedt S., Pauls S., Winkler M., Möbius W., Howard J., Göpfert M.C. 2012. Drosophila auditory organ genes and genetic hearing defects // Cell. Vol.150. No.5. P.1042–1054. https://doi.org/10.1016/j.cell.2012.06.043

Şirin D., Taylan M.S., Mol A. 2014. First song descriptions of some Anatolian species of Tettigoniidae Krauss, 1902 (Orthoptera, Ensifera) // ZooKeys. Vol.369. P.1–24. https://doi.org/10.3897/zookeys.369.5864

Skals N., Anderson P., Kanneworff M., Löfstedt C., Surlykke A. 2005. Her odours make him deaf: crossmodal modulation of olfaction and hearing in a male moth // Journal of Experimental Biology. Vol.208. P.595–601. https://doi.org/10.1242/jeb.01400

Somers J., Georgiades M., Su M.P., Bagi J., Andrés M., Alampounti A., Gordon Mills G., Ntabaliba W., Sarah J. Moore S.J., Spaccapelo R., Albert J.T. 2022. Hitting the right note at the right time: Circadian control of audibility in *Anopheles* mosquito mating swarms is mediated by flight tones // Science Advances. Vol.8. No.2. Art. eabl4844. https://doi.org/ 10.1126/sciadv.abl4844

Someya M., Ogawa H. 2018. Multisensory enhancement of burst activity in an insect auditory neuron // Journal of Neurophysiology. Vol.120. No.1. P.139–148. https://doi.org/10.1152/jn.00798.2017

Stange N., Ronancher B. 2012. Grasshopper calling songs convey information about condition and health of males // Journal of Comparative physiology A. Vol.198. P.309–318. https://doi.org/10.1007/s00359-012-0709-2

Stölting H., Stumpner A. 1998. Tonotopical organization of auditory receptors of the bushcricket *Pholidoptera griseoaptera* (De Geer 1773) (Tettigoniidae, Decticinae) // Cell and Tissue Research. Vol.294. No.2. P.377–386. https://doi.org/10.1007/s004410051187

Stout J.F., Huber F. 1972. Responses of central auditory neurons of female crickets (*Gryllus campestris* L.) to the calling song of the male // Zeitschrift für Vergleichende Physiologie. Bd.76. P.302–313. https://doi.org/10.1007/BF00303235

Stumpner A. 2002. A species-specific frequency filter through specific inhibition, not specific excitation // Journal of Comparative Physiology A. Vol.188. P.239–248. https://doi.org/10.1007/s00359-002-0299-5

Stumpner A., Gubert S., Knorr D.Y., Göpfert M.C. 2020. Auditory DUM neurons in a bush-cricket: Inhibited inhibitors // Journal of Comparative Physiology A. Vol.206. P.793–807. doi: 10.1007/s00359-020-01438-2

Stumpner A., Lakes-Harlan R. 1996. Auditory interneurons in a hearing fly (*Therobia leonidei*, Ormiini, Tachinidae, Diptera). // Journal of Comparative Physiology A. Vol.178. P.227–233. https://doi.org/10.1007/BF00188164

Stumpner A., Lefebvre P.C., Seifert M., Ostrowski T.D. 2019. Temporal processing properties of auditory DUM neurons in a bush-cricket // Journal of Comparative Physiology A. Vol.205. No.5. P.717–733. https://doi.org/10.1007/s00359-019-01359-9

Stumpner A., Molina J. 2006. Diversity of intersegmental auditory neurons in a bush cricket // Journal of Comparative Physiology A. Vol.192. P.1359–1376. https://doi.org/10.1007/s00359-006-0164-z

Stumpner A., Ronacher R. 1991. Auditory interneurones in the metathoracic ganglion of the grasshopper *Chorthippus* biguttulus. I. Morphological and physiological characterization // Journal of experimental Biology. Vol.158. No.1. P.391–410. https://doi.org/10.1242/jeb.158.1.391

Sueur J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae) // Biological Journal of the Linnean Society. Vol.75. Is.3. P.379–394. https://doi.org/10.1046/j.1095-8312.2002.00030.x

Sueur J., Farina A. Ecoacoustics. 2015. The ecological investigation and interpretation of environmental sound // Biosemiotics. Vol.8. P.493–502. https://doi.org/10.1007/s12304-015-9248-x

Sueur J., Mackie D., Windmill J.F.C. 2011. So small, so loud: extremely high sound pressure level from a pygmy aquatic insect (Corixidae, Micronectinae) // PLoS ONE. Vol.6. No.6. Art.E21089. https://doi.org/10.1371/journal.pone.0021089

Sugai L.S.M., Silva T.S.F., Ribeiro J.W., Llusia D. 2019. Terrestrial passive acoustic monitoring: review and perspectives // BioScience. Vol.69. No.1. P.15–25. https://doi.org/ 10.1093/biosci/biy147

Sun L., Gao Y., He J., Cui L., Meissner J., Verbavatz J.M. , Li B., Feng X., Liang X. 2019. Ultrastructural organization of NompC in the mechanoreceptive organelle of *Drosophila* campaniform mechanoreceptors // Proceedings of the National Academy of Sciences of the United States of America. Vol.116. P.7343–7352. https://doi.org/10.1073/181937111

Sun P., Mhatre N., Mason A.C., Yack J.E. 2018. In that vein: inflated wing veins contribute to butterfly hearing // Biology Letters. Vol.14. Art.20180496. http://doi.org/10.1098/rsbl.2018.049

Surlykke A. 1984. Hearing in notodontid moths: a tympanic organ with a single auditory neurone // Journal of Experimental Biology. Vol.113. No.1. P.323–335. https://doi.org/10.1242/jeb.113.1.323

Surlykke A., Yack J.E., Spence A.J., Hasenfuss I. 2003. Hearing in hooktip moths (Drepanidae: Lepidoptera) // J. Exp. Biol. Vol.206. P.2653–2663. http://doi.org/doi:10.1242/jeb.00469

Swain B., von Philipsborn A.C. 2021. Sound production in *Drosophila melanogaster*: Behaviour and neurobiology // Advances in Insect Physiology. Vol.61. P.141–187. https://doi.org/10.1016/bs.aiip.2021.08.001

Tauber E., Cohen D., Greenfield M.D., Pener M.P. 2001. Duet singing and female choice in the bushcricket *Phaneroptera nana* // Behaviour. Vol.138. P.411–430. https://doi.org/10.1163/156853901750382089

Tauber E., Pener M.P. 2000. Song recognition in female bushcrickets *Phaneroptera nana //* Journal of Experimental Biology. Vol.203. No.3. P.597–603. https://doi.org/10.1242/jeb.203.3.597

Ter Hofstede H.M., Symes L.B., Martinson S.J., Robillard T., Faure P., Madhusudhana S., Page, R.A. 2020. Calling songs of neotropical katydids (Orthoptera: Tettigoniidae) from Panama // Journal of Orthoptera Research. Vol.29. P.137–201. https://doi.org/ https://www.jstor.org/stable/26996700

Tishechkin D.Yu., Bukhvalova M.A. 2009. Acoustic communication in grasshopper communities (Orthoptera: Acrididae: Gomphocerinae): segregation of acoustic niches // Russian Entomological Journal. Vol.18. No.3. P.165–188.

Tootoonian S., Coen P., Kawai R., Murthy M. 2012. Neural representations of courtship song in the *Drosophila* brain // Journal of Neuroscience. Vol.32. No.3. P.787–798. https://doi.org/10.1523/JNEUROSCI.5104-11.2012

van Staaden M.J., Rieser M., Ott S.R., Papst M.A., Römer H. 2003. Serial hearing organs in the atympanate grasshopper *Bullacris membracioides* (Orthoptera, Pneumoridae) // Journal of Comparative Neurology. Vol.465. P.579–592. https://doi.org/10.1002/cne.10871

van Staaden M.J., Römer H. 1998. Evolutionary transition from stretch to hearing organs in ancient grasshoppers // Nature. Vol.394. P.773–776. https://doi.org/10.1038/29517

Vavakou A., Scherberich J., Nowotny M., van der Heijden M. 2021. Tuned vibration modes in a miniature hearing organ: Insights from the bushcricket // Proceedings of the National Academy of Sciences of the United States of America. Vol.118. No.39. Art.e2105234118. https://doi.org/10.1073/pnas.2105234118 (2021)

Vedenina V.Yu., Zhantiev R.D. 1990. [Recognition of acoustic-signals in sympatric species of locusts] // Zoologicheskii Zhurnal. Vol.69. No.2. P.36–45 [in Russian with English summary].

Vorontsov D.D., Lapshin D.N. 2023. [Effect of octopamine on the frequency tuning of the auditory system in *Culex pipiens pipiens* mosquito (Diptera, Culicidae)] // Sensornye sistemy.

Vol.37. No.3. P.244–257 [in Russian]. https://doi.org/10.31857/S0235009223030071

Vorontsov D.D., Lapshin D.N. 2024. Effect of octopamine on the frequency tuning of the auditory system in *Culex pipiens pipiens* mosquito (Diptera, Culicidae) // Neuroscience and Behavioral Physiology. Vol.54. P.319–328. https://doi.org/10.1007/s11055-024-01600-2

Waters D.A. 2003. Bats and moths: what is there left to learn? // Physiological Entomology. Vol.28. P.237–250. https://doi.org/10.1111/j.1365-3032.2003.00355.x

Wit H.P., Bell A. 2024. Something in our ears is oscillating, but what? a modeller's view of efforts to model spontaneous emissions // Journal of the association for research in otolaryngology. Vol.25. No.4. P.313–328, erratum: P.407. https://doi.org/10.1007/s10162-024-00940-7

Xu M., Shaw K.L. 2019. Genetic coupling of signal and preference facilitates sexual isolation during rapid speciation // Proceedings of the Royal Society B: Biological Sciences. Vol.286. No.1913. Art.20191607. https://doi.org/10.1098/rspb.2019.1607

Yack J.E. 2004. The structure and function of auditory chordotonal organs in insects // Microscopy Research and Technique. Vol.36. P.315–337. https://doi.org/10.1002/jemt.20051

Yack J.E., Otero L.D., Dawson J.W., Surlykke A., Fullard J.H. 2000. Sound production and hearing in the blue cracker butterfly *Hamadryas feronia* (Lepidoptera, Nymphalidae) from Venezuela // Journal of Experimental Biology. Vol.203. No.24. P.3689–3702. https://doi.org/10.1242/jeb.203.24.3689

Zhang X., Hedwig B., 2023. Sound processing in the cricket brain: evidence for a pulse duration filter // Journal of Neurophysiology. Vol.130. No.4. P.953–966. https://doi.org/10.1152/jn.00252.2023

Zhantiev R.D. 1979. [Bioacoustics of insects. Sound signaling and orientation]. Doctoral dissertation (Doctor of Science), Moscow: Lomonosov Moscow State University. [In Russian]

Zhantiev R.D. 1981. [Bioacoustics of Insects]. Moscow: Moscow University Press. 256 pp. [In Russian]

Zhantiev R.D., Kalinkina I.N., Chukanov V.S. 1975. [Characteristics of the directional sensitivity of tympanal organs in *Gryllus bimaculatus* Deg. (Orthoptera, Gryllidae)] // Entomologicheskoe Obozrenie. Vol.54. No.2. P.249–257 [in Russian with English summary].

Zhantiev R.D., Korsunovskaya O.S. 1977. [Reaction to sound of descending nerons in cervical connectives of the cricket *Gryllus bimaculatus* Deg. (Orthoptera, Gryllidae)] // Entomologicheskoe Obozrenie. Vol.56. No.2. P.248–257 [in Russian with English summary].

Zhantiev R.D., Korsunovskaya O.S. 1978. [Morphofunctional organization of tympanal organs in *Tettigonia cantans* (Orthoptera: Tettigoniidae)] // Zoologicheskii Zhurnal. Vol.57. No.7. P.1012–1016 [in Russian with English summary].

Zhantiev R., Korsunovskaya O. 1986. [Sound communication in bushcrickets (Tettigoniidae, Phaneropterinae) of the European part of USSR] // Zoologicheskii Zhurnal. Vol.65. No.1. P.1151–1163 [in Russian with English summary].

Zhantiev R.D., Korsunovskaya O.S. 1997. [Suppression of spike activity of receptors in the tympanal organ of bushcrickets (Orthoptera, Tettigoniidae)] // Sensornye Systemy. Vol.11. No.2. P.118–127 [in Russian with English summary].

Zhantiev R., Korsunovskaya O. 2014. On recognition of sound communication signals in bush crickets (Orthoptera, Tettigoniidae) // Entomological Review. Vol.94. No.6. P.815–819. https://doi.org/10.1134/S0013873814060025

Zhantiev R.D., Korsunovskaya O.S. 2021. Functions of chordotonal sensilla in bushcrickets (Orthoptera, Tettigoniidae // Entmological Review. Vol.101. P.755–766. https://doi.org/10.1134/S0013873821060038

Zhantiev R., Korsunovskaya O. 2023. Bimodality of auditory receptors in bush-crickets. Continued discussion. It's time to experiment // Journal of Experimental Zoology A. Vol.339. No.3. P.961–966. https://doi.org/10.1002/jez.2745

Zhantiev R.D., Korsunovskaya O.S., Chukanov V.S. 2004. Effect of sound signals on spontaneous activity in bush-cricket's interneurons (Orthoptera, Tettigonidae) // Journal of Evolutionary Biochemistry and Physiology. Vol.40. P.653–661. https://doi.org/10.1007/s10893-005-0022-6