

Functions of Chordotonal Sensilla in Bushcrickets (Orthoptera, Tettigoniidae)

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Abstract—Acoustic and vibrational sensitivity of single identified auditory receptors in bushcrickets was studied by electrophysiological methods. In the intermediate organ, some neurons were identified whose response to acceleration did not depend on the stimulus frequency over a significant frequency range; along with them, there were cells showing increased sensitivity to frequencies of 0.4–0.8 kHz for displacement, and/or 0.1–0.3, 1–1.2, and 1.4–3 kHz for all the vibration parameters. In addition, most of the studied receptors had a zone of increased sensitivity to high-frequency vibrations at 1.5–2.5 kHz. In the sensilla of the crista acustica, increased sensitivity was recorded at frequencies of 0.1–0.3, 0.4–0.8, 1–1.2, and 1.4–2.5 kHz. The best frequencies of a single sensillum may lie in different frequency ranges for different vibration parameters. Such differences in sensitivity to vibration acceleration, vibration velocity, and displacement, and also the different best frequencies in the receptors of the intermediate organ and the crista acustica were probably determined by differences in size, position, and morphological details of the sensilla, their own resonances, and reactions to resonance vibrations of the trachea section bearing the vibroreceptors. Thus, the chordotonal sensillum is a bifunctional mechanoreceptor which, along with auditory sensitivity, can combine the functions of both a displacement receiver and an accelerometer due to the different mechanical properties of its cells and the surrounding structures.

Keywords: bushcrickets, tympanal organ, bifunctional auditory receptors, vibrational sensitivity

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Perception of acoustic and vibrational stimuli plays a significant role in the life of insects. Sounds and substrate vibrations warn insects of the approaching predators. Besides, acoustic and vibrational cues are used by many insects during mating behavior and by predators when seeking prey (for reviews, see Zhantiev, 1981; Yack, 2016; Virant-Doberlet, 2019). The most advanced vibroacoustic communication is found in Auchenorrhyncha (Hemiptera) and in Orthoptera, in particular bushcrickets (Tettigoniidae). The male singing on a plant is located by the female first by sound and then by vibrations of the branch (Latimer and Schatral, 1983). In some cases, vibrations spreading over the substrate function as calling signals, for example, in *Meconema thalassinum* (De Geer, 1773) (Sismondo, 1980), or as premating and postmating signals, as in *Siliquofera grandis* (Blanchard, 1853) (Korsunovskaya et al., 2020).

The use of vibrational signals reduces the risk of attracting predators which locate prey by the emitted sounds.

Bushcrickets perceive sounds with their tympanal hearing organs positioned in the proximal part of the fore tibiae. The specialized vibrosensitive organs of insects, including bushcrickets, are the subgenual chordotonal organs (Fig. 1, A). Apart from them, vibrations can be perceived by the receptors of the femoral and tibiotarsal chordotonal organs (for review, see Field and Matheson, 1998) and by campaniform sensilla (Kuehne, 1982), but vibrational sensitivity of these organs and individual receptors is usually much lower than that of the subgenual organs.

Vibrational sensitivity of individual chordotonal receptors was studied earlier in locusts and bushcrickets (Kuehne, 1982; Kalming et al., 1994, 1996); yet the

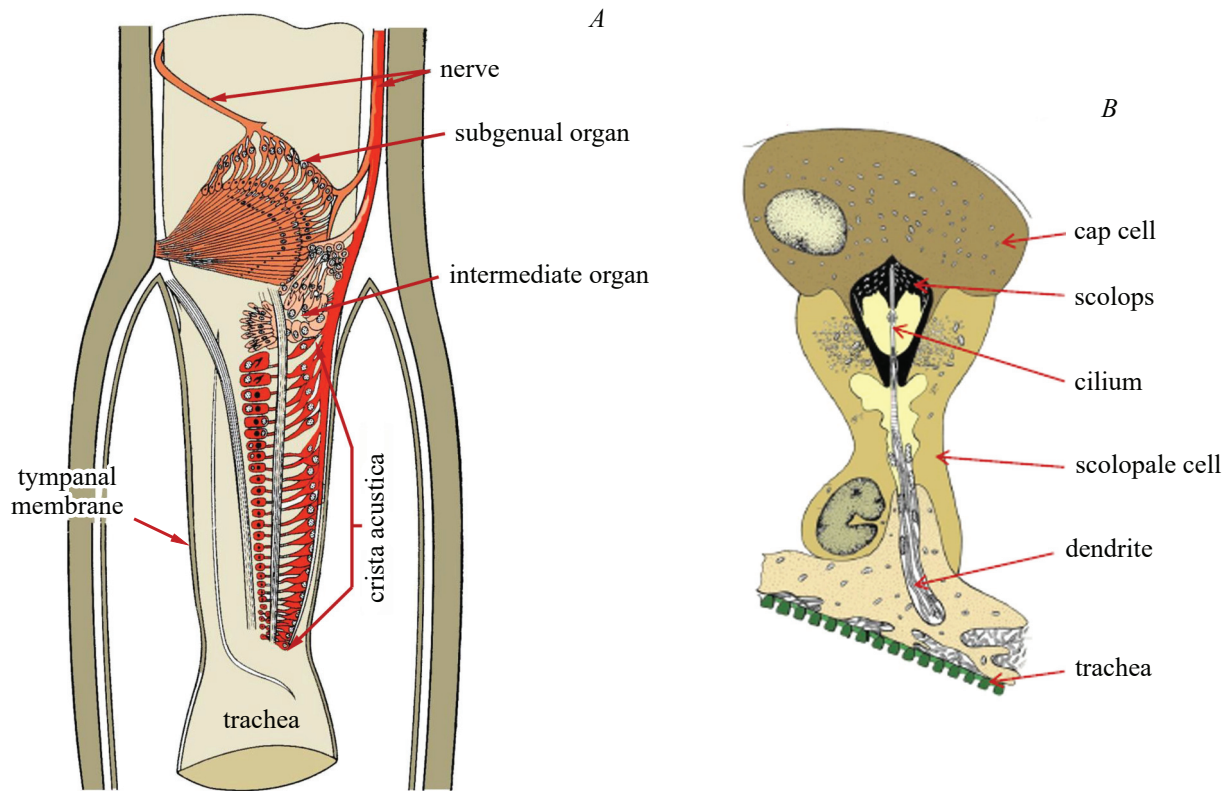


Fig. 1. Structure of the tibial chordotonal organs in the bushcricket *Decticus verrucivorus* (L.) (A; after Schwabe, 1906) and the sensillum of the crista acustica (B; after Zhantiev, 1969).

cited authors could not determine which vibrosensitive organs included these receptors.

Our preliminary study using a combination of electrophysiological and morphological methods (Korsunovskaya and Zhantiev, 2011) showed that some of the vibrosensitive receptors belong to the hearing organ; in other words, these receptors are bifunctional.

In this paper we consider the acoustic and vibrational sensitivity of individual receptors in the tympanal hearing organ of bushcrickets.

MATERIALS AND METHODS

The experiments were carried out with males and females of the bushcricket *Tettigonia cantans* (Fuessly, 1775); in some experiments we also used *Decticus verrucivorus* (Linnaeus, 1758). The insects were collected in Moscow and its environs and kept in the laboratory in cages measuring $30 \times 30 \times 30$ cm. Their diet consisted of dandelion, clover, and lettuce leaves,

chunks of fruit, and a mixture of oat flakes and dried *Gammarus*.

The activity of the tympanal organ receptors was recorded using electrophysiological equipment which included a custom-made amplifier coupled to a tape recorder or, via an E14-440 AD/DA converter (L-Card, Russia), to a PC. When necessary, the physiological signal was passed through a low-frequency filter built into the amplifier to filter out noise pickup from the AC network. The stimulating signals were produced by an analog or digital audio generator (SoundGen software, DiSoft, Russia) with a Fostex FT17H horn tweeter (Japan) and by a 11073 portable vibration shaker (Robotron-Messelektronik "Otto Schön," DDR). When using the virtual generator, the setup included a Pioneer A-10 amplifier (USA) and a UR12 audio interface (Japan). The neural activity records and the acoustic stimuli were digitized at 10 kHz sampling frequency, using the L-Graph (L-Card, Russia) or PowerGraph (DiSoft, Russia) software. Stimulation was performed by acoustic

or vibrational signals 40–80 ms long with the amplitude increasing and decreasing over 10 ms. The stimulus was presented at a rate of 1 s^{-1} . The stimulus level at which the receptor produced a single pulse in response to 1 out of 3 consecutive stimuli was considered the threshold intensity.

The response of receptors to vibrational and acoustic stimuli was studied in a detached fore leg fixed in such a way that the femur was positioned at 90° to the tibia, the tarsus touched the vibrator, and the vibrational wave spread along the longitudinal axis of the tibia. For reliable contact, the first tarsomere was glued to the vibrator with a droplet of wax/colophony mixture; the tibio-tarsal joint remained movable, while the tibial spines and spurs did not touch the vibrator. The tarsus was also positioned at 90° to the tibia.

A glass microelectrode was inserted through a small hole made in the cuticle on the dorsal surface of the tibia. The tip of the microelectrode was filled with 5% aqueous solution of Lucifer Yellow CH vital dye, and the cylindrical part of the micropipette was filled with 1.5 M solution of LiCl. The spike activity of the receptors was recorded intracellularly. The electrode resistance at its tip was 10–40 mOm. After recording, the tympanal organ preparation was examined and, when necessary, documented under an ML 40 Axioscop fluorescence microscope (Germany). The threshold values of the sound pressure level (SPL) and vibration amplitude were expressed in dB, with 0 dB corresponding to 20 μPa for sound and to 0.00005 mm/s for vibrations.

The experiments were performed in an anechoic chamber at 22–26°C. The data were statistically processed and visualized using the Origin 6.1.6 software.

The results presented herein were obtained by studying 66 receptors.

RESULTS

The hearing organ of bushcrickets consists of two parts: the intermediate organ (pars intermedia) and the crista acustica (Fig. 1, *A*). Sensilla of the intermediate organ are much smaller than those of the crista acustica to which they are adjacent; they lie on the trachea in a fan-like pattern, and the cap cells of some of them are connected to the tibial cuticle. As shown earlier (Zhantiev, 1971; Zhantiev and Korsunovskaya, 1978),

the intermediate organ perceives sounds in the low frequency range from 1 to 12–14 kHz, and its receptors have a relatively low sensitivity, the minimal response thresholds at their best frequencies being 60 dB or greater.

Sensilla of the crista acustica (Fig. 1, *B*) are located on the trachea; their cap cells are covered with the tectorial membrane and are not connected to the cuticle of the tibia. The bodies of the receptor cells lie in a small recess between the tibial trachea and the tympanal membrane, while their axons form the tympanal nerve going into the femur and then, through the trochanter and coxa, into the prothoracic ganglion. The crista acustica is composed of receptors more sensitive to sound and has a tonotopic arrangement of sensilla (Zhantiev and Korsunovskaya, 1978; Oldfield, 1982, 1985; Stoelting and Stumpner, 1998): its proximal sensilla are the most sensitive to low-frequency sounds, the distal ones, to ultrasound, and the middle ones, to sounds in the intermediate frequency range.

Our experiments revealed no differences between males and females of *T. cantans* in their response to stimuli.

Threshold Curves of the Intermediate Organ Sensilla for Acoustic and Vibrational Stimuli

The studied receptors responded to sounds within a range of 1–12 kHz (less often 14 kHz), and had best frequencies of 5–7 kHz.

The threshold curves of the intermediate organ receptors for vibrational stimuli may be conditionally divided into three groups (Fig. 2). In the first group, the response to acceleration (Fig. 2, *A, B: 1*) was the strongest at low frequencies (in our tests, at 0.1–0.2 kHz); as the stimulus frequency increased to 0.8 kHz, the response gradually decreased and then either remained at a relatively stable level or decreased further. At the same time, the sensitivity of these receptors to displacement (Fig. 2, *A, B: 3*) increased over the entire range tested, while their sensitivity to velocity remained approximately constant within a range of 0.06–0.2 mm/s (Fig. 2, *A, B: 2*).

The second group (Fig. 2, *C, D*) united the threshold curves characterized by the lowest threshold values of acceleration in the low-frequency stimulus range.

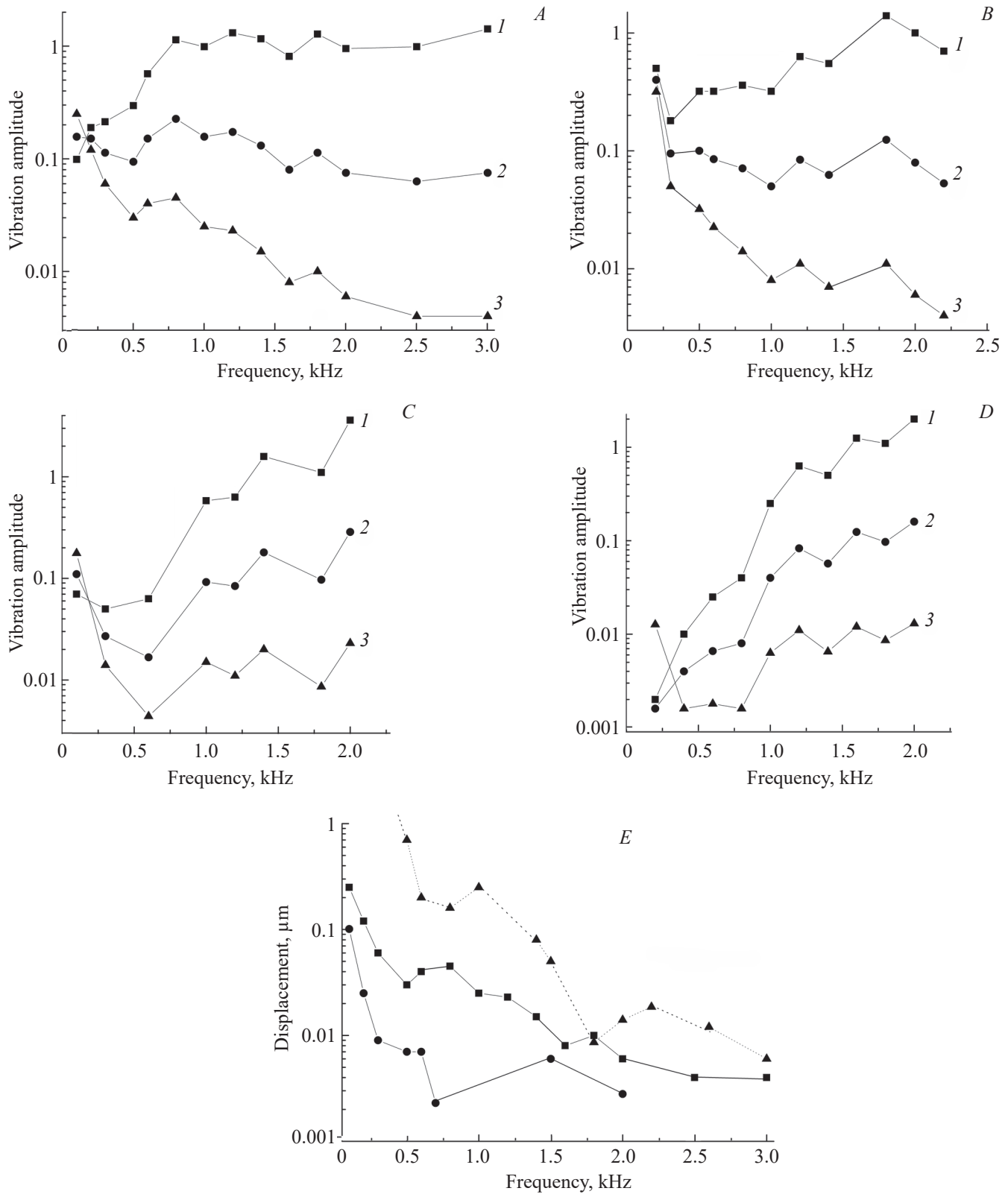


Fig. 2. Threshold curves for vibrational stimulation of receptors of the intermediate organ of *Tettigonia cantans* (Fuessly): (A) receptor c308io of group 1; (B) receptor d269io of group 1; (C) receptor d209io of group 2; (D) receptor c289io of group 2; (E) response to displacement in three receptors of group 3. Response: 1, to acceleration (m/s^2); 2, to velocity (mm/s); 3, to displacement (μm).

Table 1. Best frequencies (kHz, in parentheses) and the lowest threshold values of vibrations perceived by receptors of the tympanal organ of *Tettigonia cantans* (Fuess.)

Parameters	Intermediate organ	Crista acustica		
		proximal receptors	middle receptors	distal receptors
Zones of increased sensitivity, kHz	0.3; 0.4–0.8; 1–1.2; 1.6–>2	0.2–0.3; 0.4–0.6; 1–1.2; 1.4–2.5	0.06–0.2; 0.5–0.8; 2	0.1–0.3; 0.4–0.8; 1–1.2; 1.4–2
Lowest thresholds for acceleration, m/s ²	0.03 (0.3)	0.005 (0.4–0.6)	0.006 (0.8)	0.001 (0.8)
Lowest thresholds for velocity, mm/s	0.014 (1)	0.006 (0.6)	0.0015 (0.8)	0.008 (2)
Lowest thresholds for displacement, μm	0.001 (1.8)	0.002 (0.6)	0.0002 (0.8 and 2)	0.0035 (1.6)

An additional minimum was sometimes observed at 0.4–0.8 kHz, either in response to all the vibration parameters (Fig. 2, *C: 1–3*) or only in response to displacement (Fig. 2, *D: 3*).

The threshold curves of the third group showed that the sensitivity of receptors to all the vibration parameters increased with their frequencies. The curves had several minima: at 0.6–0.8 or 1–1.2 kHz and at 1.4–3 kHz. The threshold curves for displacement are shown in Fig. 2, *E*.

The minimal threshold values of acceleration, velocity, and displacement, and also the best frequencies of vibration perception by receptors of the intermediate organ and the crista acustica are given in Table 1.

Threshold Curves of Sensilla of the Crista Acustica (Fig. 3, A–C)

The *proximal* receptors of the crista acustica showed the highest sensitivity to sound within a frequency range of 8–10 kHz.

In most of the tested proximal sensilla, the threshold curves of response to vibration had a minimum within a range of 0.4–0.6 kHz. Two receptors were the most sensitive at 0.3 kHz (sensillum no. 9) and at 1 kHz (sensillum no. 5). These best frequencies were marked by the minima of the threshold curves for all the parameters of the vibrational stimulus: velocity, acceleration, and displacement.

Similar to the receptors of the intermediate organ, an increased sensitivity to higher frequencies was observed along with the optimum within 0.1–1 kHz. In particular, at 2 kHz some cells showed threshold displacement values of 0.0015–0.0030 μm.

In the *middle* part of the crista acustica, responses to acoustic and vibrational stimuli were recorded in the zone of sensilla nos. 10–14. These receptors were the most sensitive to sounds at frequencies above 12–14 kHz (sensilla nos. 10–13).

In cells of this group, the sensitivity to displacement typically increased in a relatively uniform manner as the stimulus frequency increased to 0.6–1 kHz (sensillum no. 11; see Fig. 3, *B: 1*) and often up to 2 kHz (sensillum no. 14; see Fig. 3, *B: 2*). The threshold curves of the same sensilla for velocity and/or acceleration showed additional, much weaker minima within a frequency range of 0.6–1.2 kHz. Sometimes the middle sensilla of the crista acustica had the highest vibration sensitivity at frequencies of 0.6 or 0.8–1 kHz both for displacement and for velocity or acceleration (sensilla nos. 10, 11); the corresponding threshold curves were approximately V-shaped (Fig. 3, *B: 4*).

The minimal threshold values of receptors of this group are given in Table 1.

The receptors in the *distal* third of the crista acustica were smaller than the more proximal ones but still arranged in a single row. The distalmost sensilla formed

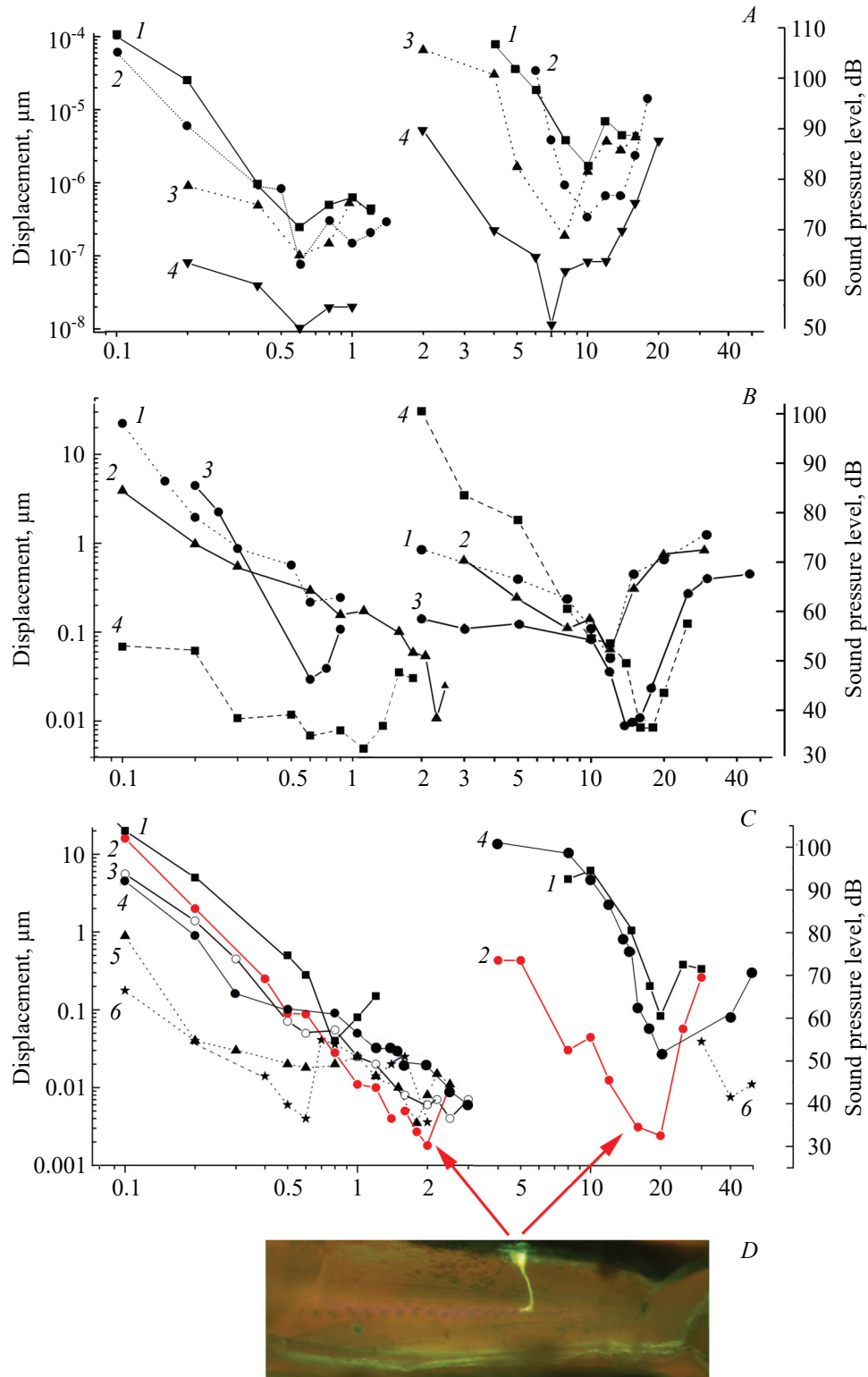


Fig. 3. Threshold curves for vibrational (left) and acoustic (right) stimulation of the crista acustica receptors in *Decticus verrucivorus* (L.) (A: 2) and *Tettigonia cantans* (Fuessly) (all the other diagrams): (A) proximal part; (B) middle part; (C) distal part of crista acustica; (D) crista acustica of *T. cantans* with stained receptor no. 15. The responses of the same receptor cell are marked with identical numbers. The following receptors were morphologically identified: in A, receptor no. 2 (1), no. 4 (2), no. 5 (4); in B, receptor no. 11 (1), no. 12 (3), no. 14 (2); in C, receptor no. 15 (2), no. 18 (5), no. 20 (3).

a double row, with densely packed neuron bodies and very short axons entering the tympanal nerve, so that responses of individual cells were difficult to record. Correspondingly, our work was restricted to the sensilla with best frequencies varying from 20 to 40 kHz; judging by the physiological and morphological characteristics, these were sensilla nos. 15–30.

All the distal sensilla of the crista acustica tested for vibration sensitivity shared the following features. The sensitivity peaks were observed both in the low frequency range (below 1 kHz) (e.g., see Fig. 3, C: 1, 5, 6) and at higher frequencies (Fig. 3, C: 2–6). The best frequencies were 0.6, 0.8, and 1 kHz in the first case, and about 2 kHz in the second case; some cells had a single or an additional maximum at 1.2 or 1.4 kHz (see Table 1). The threshold curves for all the vibration parameters were similar in shape but differed in the degree of expression of the maxima. The minimal threshold values of the most sensitive receptors are given in Table 1. In most sensilla the thresholds for acceleration were no greater than 0.9 m/s², those for velocity were within a range of 0.008–0.07 mm/s, and those for displacement were within a range of 0.004–0.02 μm.

Intensity Response Function of Sensilla of the Tympanal Organ

The study of response of the intermediate organ and crista acustica receptors depending on the stimulus intensity yielded the following results. The responses of the same neuron to sound and vibration differed in the maximum number of spikes, this number being greater in response to sound nearly in all the receptors tested (Fig. 4, A, B). The responses were tonic, with after-effects developing at high intensity of both acoustic and vibrational stimuli (Fig. 5). In some experiments the response was produced with pauses (Fig. 5, A) described in our earlier paper (Zhantiev and Korsunovskaya, 1997). No saturation was observed in the responses to vibrations (Fig. 4, B, C). The response of some cells only slightly changed as the amplitude of vibrational stimuli increased (Fig. 4, C: 3, 4).

DISCUSSION

It is known that the response of vibrosensitive organs can be affected by a number of factors (for review, see Strauß et al., 2019); correspondingly, the details of material preparation and testing technique are of great

significance. Our experiments were carried out with a detached fore leg, which was connected to the vibrator in such a way that the vibrational wave spread along the longitudinal axis of the tibia that was positioned at 90° to the femur. Previously it was determined that the direction of the vibrational stimulus (vertical or horizontal) affected the amplitude of mechanical response of the tibial cuticle but did not change its frequency selectivity.

The amplitude of mechanical response of the tibia in the cave cricket *Troglophilus neglectus* Krauss, 1879 was recorded at vibrations spreading in the vertical direction, along the longitudinal axis of the tibia. The strongest mechanical response of the leg was observed when the angle between the femur and the tibia was 45° (Stritih-Peljhan and Strauß, 2018); therefore, it is quite possible that this angle may also affect the response of vibroreceptors in *Tettigonia cantans*. The angle between the femur and the tibia changes constantly during walking. Besides, the response of vibroreceptors may also be influenced by the absence of load (in our case, the insect's body weight). It was found out that when the hind leg of a cricket resting against the substrate was loaded, its vibration sensitivity somewhat increased at frequencies below 0.5 kHz and decreased within a range of 0.7–2 kHz, but the optimum in the threshold curve did not shift (Dambach, 1972). According to our data, the intensity values corresponding to the minima in the vibroreceptor threshold curve may change inconsiderably in the detached leg, while the frequency tuning of the sensilla remains the same. The absence of the insect's body in our experiments could potentially affect the threshold curve of the receptors for sound. However, the results of our previous experiments (our unpublished data) are consistent with the previously established facts (Chukanov and Zhantiev, 1978) that the acoustic tracheal sacs in the prothorax of *Tettigonia cantans* only increase the sensitivity of the hearing organ (mostly in the ultrasonic range) but have no significant effect on its frequency tuning: the best frequencies of the tympanal organ lie in a range of 12–20 kHz both in the intact insect and in the detached leg. At the same time, the high-frequency receptors in the detached leg remain sufficiently sensitive to ultrasound (Fig. 3, C: 1, 6).

Thus, the angle between the femur and the tibia, the direction of the vibrational wave, and the position of the leg on the substrate may affect the vibration sensitivity of the tympanal organ receptors; yet these influences

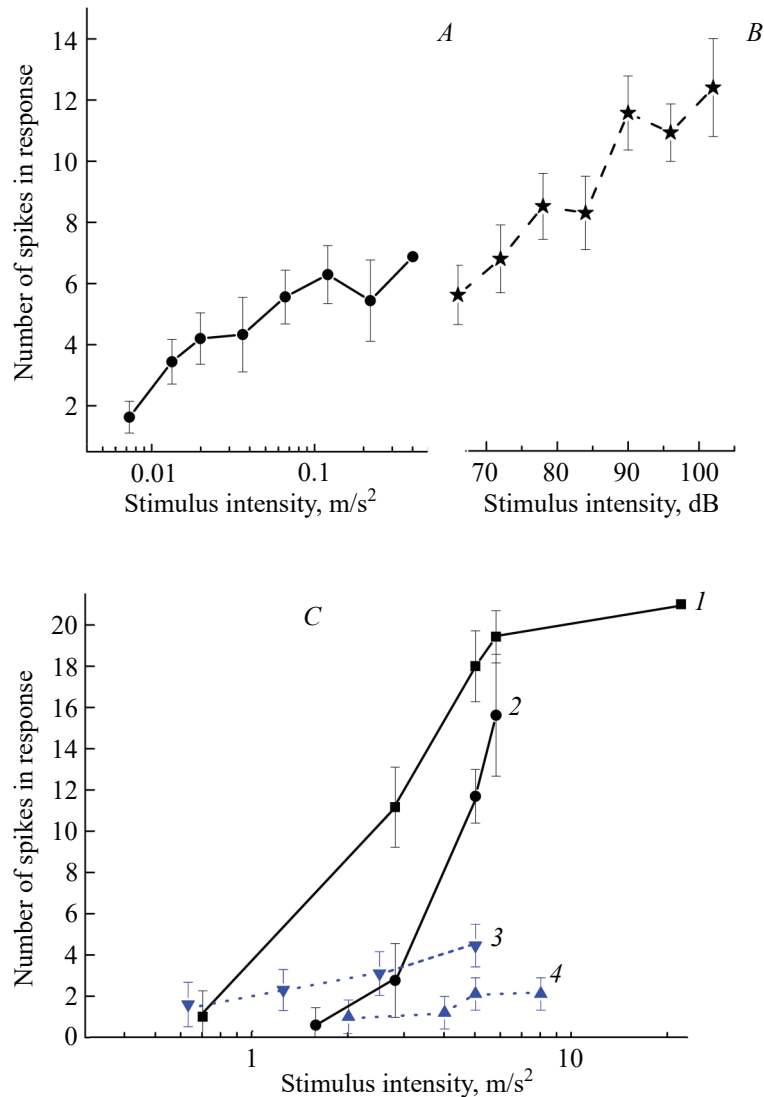


Fig. 4. Intensity response function of three auditory receptors of *Tettigonia cantans* (Fuessly) in response to vibratory and sound stimuli (means and standard deviations): (A) receptor no. 5 of the crista acustica responding to vibration at 0.6 kHz; (B) the same receptor responding to sound at 8 kHz, stimulus duration 55 ms; (C) receptors of the intermediate organ: 1 and 2, receptor c298io responding to vibrations at 1.6 kHz (1) and 0.5 kHz (2), stimulus duration 80 ms; 3 and 4, receptor b99io responding to vibrations at 0.2 kHz (3) and 0.4 kHz (4), stimulus duration 40 ms.

appear to be inconsiderable and do not affect the threshold curve of the chordotonal sensilla. The most stable response to different vibrational stimuli seems to be characteristic of the subintegumental sensilla of the intermediate organ and crista acustica, since these sensilla perceive the cuticular vibrations indirectly via the leg hemolymph, along the trachea under the sensilla and along the tectorial membrane above them. Besides, it should be borne in mind that while perceiving vibrations, the insect can be moving on various substrates

positioned at varying angles to the longitudinal axis of the tibia, and the leg itself is constantly flexed and extended during locomotion. Therefore, the conditions of stimulation, fixation to the vibrator, and the position of the leg preparation during our experiments did not essentially differ from the natural conditions.

As noted earlier, the frequency tuning and sensitivity of vibroreceptors are affected by the position of the insect's leg (Stritih-Peljhan and Strauß, 2018; Strauß

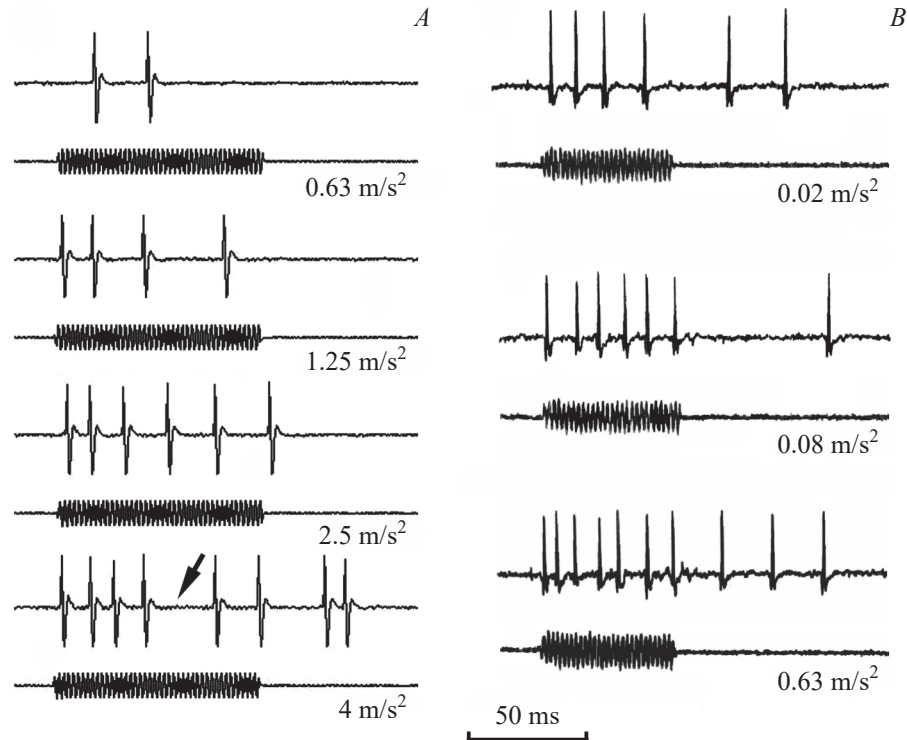


Fig. 5. Responses of the tympanal organ receptors of *Tettigonia cantans* (Fuessly) to vibrations: (A) intermediate organ, stimulus at 1.6 kHz; (B) crista acustica, stimulus at 0.6 kHz. Arrow marks a pause in response.

et al., 2019). However, since bushcrickets have receptors that retain their sensitivity over a wide frequency range (see Fig. 2, A, B), the moving insect can still reliably locate the sources of various vibrations. Besides, the presence of tympanal organ receptors with different best frequencies for velocity, acceleration, and displacement suggests that the vibration sensitivity of bushcrickets is sufficient to ensure their reaction to a wide range of vibrations spreading along any surface and in any substrate.

Comparison of the threshold curves for vibrational stimuli in the tympanal organ receptors has shown that their best frequencies mostly lie at 0.1–1 kHz and 2–3 kHz. Increased sensitivity of the bifunctional sensilla ensures detection of biotic and abiotic noise (usually occurring in a low-frequency range below 0.2 kHz), as well as vibrational components of species-specific acoustic signals, which in *Tettigonia cantans* have frequencies from 30 Hz to 5 kHz. Thus, the tympanal organ of bushcrickets is a multifunctional organ capable of perceiving any vibration along with sound.

The intermediate organ and the crista acustica were found to contain elements varying in their sensitivity to vibration parameters (acceleration, velocity, and displacement), and also receptors with different best frequencies. These differences may be determined by certain factors acting both separately and in combinations. The receptors of the tympanal organ are positioned on the trachea and covered with the tectorial membrane. Some sensilla of the intermediate organ are integumental, i.e., attached to the cuticle of the tibia. Most of the receptors in the crista acustica are arranged in a single row and decrease in size toward the distal end; the distalmost sensilla are the smallest and lie in a double row on the membrane. Besides, the scolops inclination angle also varies along the crista acustica (Kalmring et al., 1993). All these morphological and topographic features can certainly affect the properties of the bifunctional receptors in the hearing organ of bushcrickets.

When analyzing the sensitivity of receptors to different parameters of the vibrational stimulus, it would be

feasible to compare them with technical instruments for measurement and analysis of vibrations. Such instruments include various types of sensors: velocimeters, accelerometers, and displacement receivers, and different sensors are used for different purposes: displacement receivers, for analysis of low-frequency vibrations; accelerometers, for high-frequency vibrations; and velocimeters, for frequencies in the medium range. All these instruments utilize different mechanisms. By analogy, we may suppose that bushcrickets also obtain information through receptors responding to different parameters of vibrations.

Mechanosensory transduction is realized in this case by the mechanically activated ion channels in the dendrite membrane that undergoes deformation. However, mechanical action on this membrane can be exerted by different elements, both directly and indirectly. A chordotonal sensillum is a complex of several cells, each representing a distinct mechanical system. During perception of the vibrational stimulus these cells are affected by the vibrational wave either directly (for instance, cap cells of the subgenual organ) or via the cap cells of the subintegumental sensilla contacting the hemolymph, sheath cells, and bodies of neurons. In addition, these cells have their own natural resonances and can respond to the resonance vibrations of the trachea section bearing the sensillum. Correspondingly, a chordotonal sensillum can act both as a displacement receiver and an accelerometer, due to different mechanical properties of its cells and the surrounding structures. This hypothesis is indirectly supported by the threshold curves of some intermediate organ receptors, in which the threshold acceleration values at first increase with the stimulus frequency and then reach a plateau, and also by the presence of increased sensitivity zones at specific frequencies in some receptors of the tympanal organ.

Bifunctional receptors of the intermediate organ and the crista acustica are highly sensitive to mechanical oscillations over a wide frequency range. Due to increased sensitivity to high-frequency vibrational stimuli, insects can detect the vibrational components of communication sound signals or the conspecific vibrational signals, for instance, those emitted by the orthopteran species studied by us earlier (Benediktov et al., 2020; Korsunovskaya et al., 2020). The abiotic sounds and also the vibrations caused by locomotion and other activities of other animals usually belong to a low-

frequency range of 0.1–2 kHz. They also can induce responses in the corresponding receptors even at very low amplitudes.

Differentiated response to different vibration parameters was demonstrated earlier for receptors of the femoral chordotonal organs in stick insects and locusts (for reviews, see Field and Matheson, 1998; Eberl et al., 2016), and also of the hearing organs in locusts and bushcrickets (Kuehne, 1982). However, no direct analogies which would clarify this phenomenon can be drawn in this case, since the femoral chordotonal organ is mainly involved in controlling the leg movement in the femur-tibia joint, i.e., its main function is different from that of the tympanal hearing organ. As mentioned above, the results reported by Kuehne (1982) add little to understanding the perception of vibrations by receptors, since the exact position of the receptors was not determined in the cited research. It should also be remembered that the mechanosensory transduction mechanisms in the dendrites of the chordotonal receptors in insects are still vaguely understood; therefore, we can only illustrate some features of the sensilla that may be relevant to these processes.

The presence of bifunctional mechanoreceptors, namely the chordotonal sensilla in the hearing organ of bushcrickets, considerably expands the possibility of analysis of biologically important cues, increasing the efficiency of conspecific communication (in particular, during mating behavior) and the probability of escaping predators. Such adaptations, along with other specific morphofunctional traits, determine the current status of insects as one of the most prosperous groups of living organisms.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. All the applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All the procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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