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Short Communication

THE DEPENDENCE OF BEHAVIORAL AUDITORY THRESHOLDS ON THE DELAY OF ECHO-LIKE SIGNALS IN NOCTUID MOTHS (LEPIDOPTERA, NOCTUIDAE)

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The auditory system of noctuoid moths capable to respond to ultrasounds has long been a model for anti-predator studies in neuroethology. Many moths avoid hunting bats by listening for their echolocation calls and taking evasive manoeuvres to escape predation. Besides these flight defences, certain tiger moths (Arctiidae) emit high-frequency clicks to jam the echolocator of an attacking bat. Another suggested function for ultrasonic audition in moths along with their capability to emit loud ultrasonic clicks was pulse echolocation. However, it seemed difficult to arrange sufficient temporal resolution in a simple invertebrate auditory system. Here we present an evidence of moth's capability to perceive an echo following its own click with a very short delay. The behavioral responses of moths to the acoustic pulses imitating echoes of their own clicks were investigated under conditions of tethered flight. It has been found that such echo-like stimulation evokes an increase in average emission rate of own acoustic signals in moths. Auditory thresholds were measured in two noctuid species (*Enargia paleacea* Esp. and *Blepharita satura* Schiff.) at stimulus delays 0.2, 0.3, 0.5 and 1 ms in relation to the respective moth clicks. Our findings reveal the ability of these moths to perceive echoes of their own signals, thus demonstrating potential possibility for use of pulse echolocation.

Keywords: Temporal resolution; noctuid moths; echolocation; auditory thresholds.

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1. Introduction

Noctuid moths (Noctuidae) are able to produce brief ultrasonic clicks during flight. This phenomenon was first described by Roeder and Treat [17]. In addition, these moths have well developed auditory system which is adapted to ultrasound reception, thus the authors proposed that the moths were capable to echolocate. Kay [6] suggested that the generators of clicks were of a tymbal type and were situated bilaterally on metepisternites, like in closely related family of arctiids [2]. Nevertheless, using stroboscopic observation of flying moths, Agee [1] concluded that the acoustic pulses recorded by Kay either were produced due to the flap of one wing on the other at the highest point or were artefacts. Later on, the conclusions of Agee have also been revised: it was shown that the wings were positioned near horizontally at the moments of clicking [13, 23] thus the ultrasonic emission in these experiments was not consequent upon the wing flaps.

It should be noted that in noctuid moths ultrasounds could really be produced during flight when the wings are situated at the highest point [22] but, as a rule, their amplitude does not exceed 65 dB SPL, i.e., they are three times weaker than the clicks registered by Roeder, Treat, Kay, Agee and Lapshin (by 10 dB, at least).

We have proposed a mechanism of acoustic emission in noctuids based on the interaction of two adjacent complementary structures, situated at the base of a forewing and on the metascutum, which have been morphologically described before [7]. We have repeated the morphological studies of these structures in view of their possible role for generation of ultrasounds. The structures are capable to couple; when they uncouple, a short broadband click is emitted [13]. To date the acoustic emission has been described in most detail in *Amphipyra perflua* F. [12]. This moth generates ultrasonic clicks with a very short rise time and duration of 25 to 100 μs while waveform and spectrum can vary significantly even in one specimen.

Noctuids are prey species the bats feed on and at the present time there are no facts suggesting that acoustic signals of noctuid moths can scare the attacking bat or jam its echolocator. Such a strategy of acoustic behavior was demonstrated only in arctiids [4]. If one takes into consideration the echolocation hypothesis then it should be noted that (i) the echolocation system can be effective for orientation if it is capable of working at the distances commensurable with a moth's size and (ii) the use of impulse echolocator is possible only if the auditory system do not respond to the moth's own probing click, otherwise the moment of receiving echo coincides with either the spike generation or the refractory time of the auditory receptor.

The decrease in responses of auditory receptors to the loud stimuli was described in noctuids [16]. We believe that the own click of a moth causes paradoxical reaction of the tympanic auditory receptors, namely, the suppression of their activity. Such a reaction to the artificially evoked tymbal clicks was demonstrated for the Al receptor in arctiids (which are closely related to noctuid moths) while the B-cell of the tympanic organ demonstrated steady response consisting of three spikes to every evoked click [11].

After a short-time impact caused by the moth's own click the tympanic membrane will perform damped oscillation for some time [18]. For the echolocator to work properly, the restoration of receptor sensitivity must extend gradually according to the damping of membrane oscillations down to the subthreshold level. The dependence of the auditory thresholds on the delay of echo-like stimulus which follows the moth's own click could reflect the restoration of receptor sensitivity. In the design of our experiments, it was important to determine which patterns of noctuids' behavior may be thought of as their response to echo. In the past, similar problem arose and was solved in the course of investigation of bats' responses to artificial stimuli. An increased emission of the probing pulses turned out to be a good indicator of increased attention of a bat to biologically significant echolocation signals [5]. Such changes in bat emission were reproducible and could be easily registered. How do the noctuid moths behave in analogous situations? One could suggest that echolocation stimuli would also evoke similar responses in moths, i.e., the noctuids would increase the repetition rate of their own clicks. Indeed, we have demonstrated the increase in moth acoustic emission in response to echo-like stimulation [10,12]. Here we consider this effect as an indication of the moth's reaction when measuring behavioral thresholds.

The results of preliminary studies in a single species [14] encouraged us to continue the work using specimens of two noctuid subfamilies. The purpose of the present study was to measure the auditory thresholds to the echo-like stimuli given with different delays relative to the moth's own clicks.

2. Material and Methods

Noctuid moths of two species, namely, *Enargia paleacea* Esp. (Amphipyrinae) (31 specimens) and *Blepharita* (*Crino*) *satura* Schiff. (Cuculliinae) (37 specimens), male and female, were used in the experiments. Wild specimens were captured from a trap with food attractant, i.e., a birch cortex greased with a mixture of beer and honey which started to ferment. Only those specimens which maintained ultrasonic emission under experimental conditions were used (about 60% of the total number captured).

The method was based essentially on the principle of retransmission of the stimuli imitating echo from a non-existent (virtual) obstacle to the moth. The scheme of experimental setup is represented in Fig. 1. The click produced by a moth was recorded by the microphone. The electrical impulse from the microphone output was amplified, filtered (bandpass 10-100 kHz), converted to a square pulse to be used for starting up the echo-like stimulus which was emitted back toward the moth after certain delay in relation to the initial signal. Such stimulation system did not contain any movable details at all and thereby guaranteed the independence of the obtained results from the visual and tactile sensitivity of the insect.

The moth was glued by warm wax to one end of a long (15 cm) thin wire serving as a leash of mechano-optical sensor of horizontal shift which allowed registration

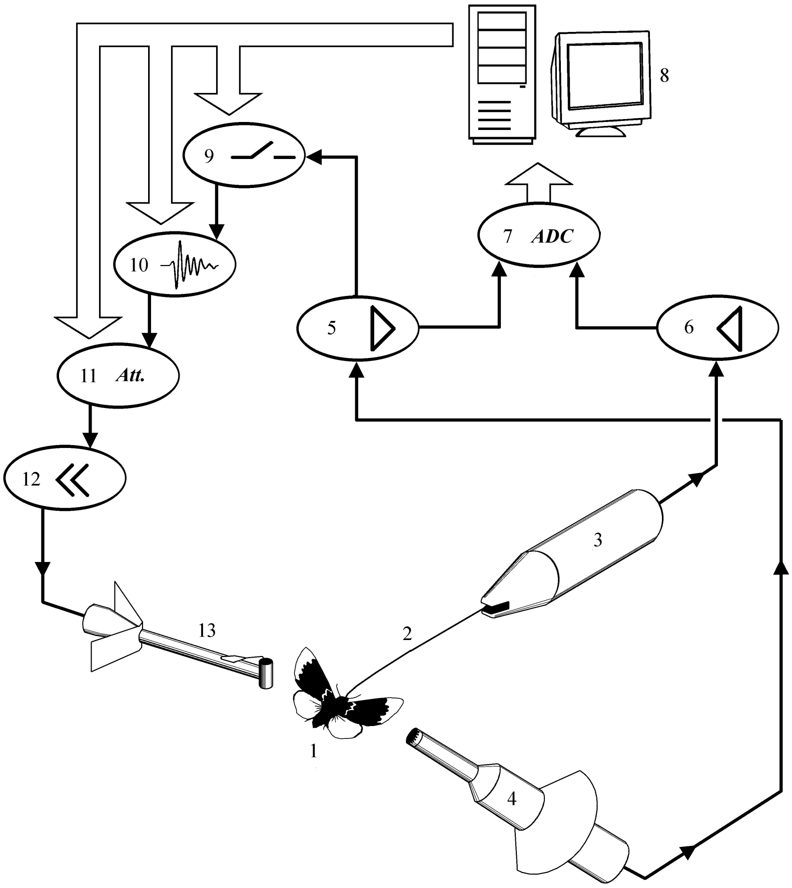


Fig. 1. The scheme of experimental set-up. The moth (1) attached to the leash (2) of the horizontal shift sensor (3) is flying and producing ultrasound clicks which are recorded by the microphone (4). The signals from the outputs of the shift sensor and the microphone come to amplifiers (5 and 6) and from there to the analogue-to-digital converter (7) connected to the computer (8). Computer controls the electronic switch (9). In its open state, the switch allows the signals produced by the moth to trigger the generator of echo-like stimuli (10). After the attenuator (11) and power amplifier (12), stimulating pulses come to the condenser loudspeaker (13) which emits signals in the direction of the moth. In additional series of experiments the condenser loudspeaker was replaced by piezocrystal.

of the moth's manoeuvres concurrently with its acoustic emission. In the course of the experiment, the shifts of the moth from its equilibrium position were as little as several millimetres. The elasticity coefficient of the detector at the position to be occupied by the insect was equal to 300 dyn/cm. We expected that echo-like stimulation would evoke motor responses like those recorded earlier [8]. However, in our current work the results on motor responses were not statistically significant, at least for near-threshold amplitudes of the stimulus. Some of the moths demonstrated spontaneous manoeuvres which were accompanied by click emission. It was important to control and timely cull out the specimens with such behavior, so we

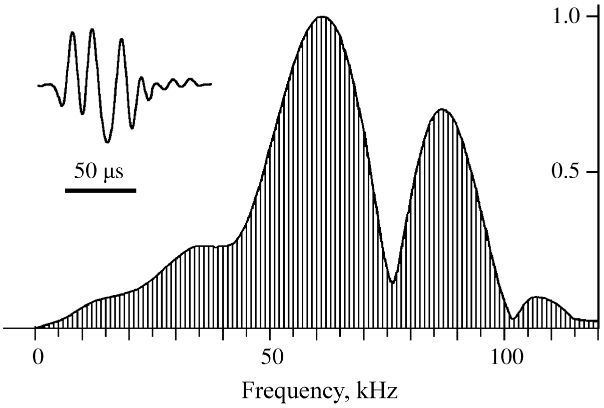


Fig. 2. The artificial click: waveform and spectrum. Waveform: time scale — 50 *μ*s; spectrum: peak normalized, vertical scale — amplitude of harmonic components in linear scale, relative units.

aimed to control the motor activity of a moth during its click emission to prevent interpretation of the clicks as by-products of the manoeuvres.

To record acoustic clicks produced by the moth, a condenser microphone (quarter inch Brüel & Kjær 4135) was placed below the moth at a distance of 2-2.5 cm. After amplification, the signal from the microphone output was fed to the electronic switch controlled by a computer. When the switch was unlocked, each click of the moth (provided that it exceeded 73 dB SPL) started up a generator of click stimuli. The output signal of a generator was similar (from 1 to 100 kHz) to the natural click [15]. Its waveform and spectrum are shown in Fig. 2. Once a stimulating click has been emitted, the emitter was blocked for about 6 ms. Thereby, the effects of direct action of the sounds produced by the loudspeaker onto the microphone and, as a consequence, the generation of stimuli not related to the moth ultrasonic emission was prevented.

To imitate natural changes in acoustic environment around the moth, the cycle of apparatus' readiness to respond (i.e., the interval when the electronic switch was unlocked) was divided into four parts of 0.2 s in duration each (Fig. 3). Beyond these intervals of readiness (i.e., during the three intervening intervals) the apparatus could not reply to the insect by producing "echo". Overall duration of one stimulation episode, including the silent intervals, was 1.4 s. The sequence of readiness phases corresponded approximately to the dynamics of the moth flight past four plane juxtaposed obstacles. The moment of the first acoustic contact (i.e., in the linked pair of events: own click of the moth — echo signal) was assumed as an automatic onset of the stimulation time counting. Although the stimulus amplitude and echo delay did not change during one stimulation episode as they do in nature, the kind of stimulation program we used, according to our experience, more often evokes moth's reactions compared to the uninterrupted stimulation episode [12]. The intervals between stimulation episodes were varied at random in the range 6-12 s.

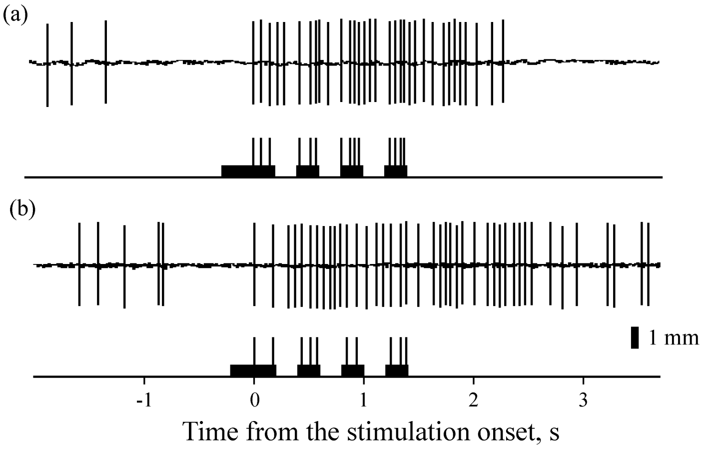


Fig. 3. Examples of responses of noctuid moths to the echo-like stimulation. Continuous waveform represents deviations of the moth in the horizontal plane. Superimposed vertical lines correspond to the moments of click emission by the moth. Abscissa represents time scale, "0" corresponds to the moment of the first acoustic contact of the insect with the stimulator. Black bars above abscissa indicate the intervals of readiness of the apparatus to retransmission; vertical strokes above these bars represent the moments of acoustic stimulation (echo-signals).

Every moth was presented with at least 20 stimulation episodes at certain delay of the stimulus. At the stimulus volume determined as the threshold, the number of clicks recorded during the stimulation episode (1.4 s) had to be significantly higher than the number of clicks during the interval of the same length preceding the stimulation. Similarly, this difference had to be non-significant at the subthreshold level (usually 2dB lower than the initial threshold estimate). Statistical significance was determined using the non-parametric Wilcoxon paired signed-ranks test, $p < 0.05$. The moth's own clicks which actuated the stimulation program were attributed to the preceding background acoustic emission.

We used four values of the stimulus delay in relation to the respective moth's clicks: 0.2, 0.3, 0.5 and 1 ms. These intervals include the click transit time from the moth to the microphone, the delay due to signal transformation in the electronic generator, and stimulation click travel time from the emitter to the moth. Eight experiments per one delay value were conducted with moths of either species. In every new experiment the delay value was changed and a new one was chosen from a set of four. In most cases a single specimen was used only in one experiment except two specimens with enormously stable acoustic emission (one of *B. satura* and one of *E. paleacea*) which allowed measurement of auditory thresholds at three values of the stimulus echo delay (0.3, 0.5 and l ms).

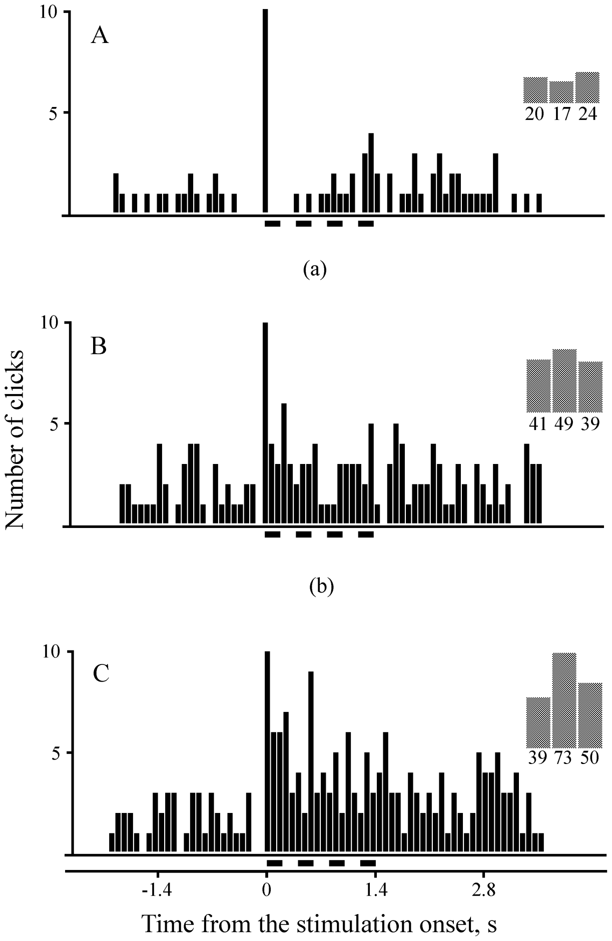
In the main series of experiments a home-made cylindrical condenser loudspeaker served as a source of stimulating clicks (external diameter 7 mm, generatrix of the cylinder 15 mm). Its emitting membrane was made of 35 μm thick metallopolymeric film with the polarization voltage of 180 V. The loudspeaker was placed on one side of the moth at a distance of 3.5 cm. As every material object (the loudspeaker and the microphone) that we used produced a passive echo after the moth's click, the microphone was situated at an angle to the moth in such a way that it reflected acoustic wave aside. The level of an echo from the loudspeaker surface measured at the position of the moth was equal to —17 dB compared to the test signal level. To estimate the influence of this unavoidable echo on the results obtained, additional series of experiments with six specimens of *B. satura* was performed. In these experiments, the condenser loudspeaker which is described above was replaced by the piezocrystal with a diameter of 3 mm and a length of 5 mm oriented to the moth by its flat end. We failed to measure the echo level from the piezocrystal, which means that it was — 30 dB or lower.

The signal emitted by the piezocrystal was a fast-fading (with a time constant of 60 μs) sine wave with its carrier frequency depending on the crystal resonance (75 kHz). Acoustic stimuli emitted by the piezocrystal differed from the natural moth clicks in spectral and temporal parameters, therefore, since we did not know whether these characteristics of an echo were important to the noctuids, the usage of such stimulation was confined to these additional experiments. The delay of stimulus in relation to the moth click in this series was set to 0.2 ms. The control of the stimulus waveform and level was fulfilled by the use of the microphone (Brüel & Kjær 4135) with protecting grid put out, and the amplifier (Brüel & Kjær 2235) in conjunction with the digital oscilloscope (Hewlett Packard 51604B). To control the measuring hardware the calibrator 05 000 MMF (VEB Metra Meβ Frequenztechnik) was used. All the sound pressure levels (SPL) were measured at their peak values and are given in dB (re 20 μPa). The experiments were carried out at the biological station "Kropotovo" of the Institute of Developmental Biology Russian Academy of Science (RAS) (105 km south-east of Moscow) during August-September from 4 p.m. to 0 a.m., local astronomic time, at the air temperature of 18-20°C.

3. Results

The presentation of echo-like stimuli with suprathreshold levels caused not only the increase of the acoustic emission rate soon after the first acoustic contacts (fast kind of response, Fig. 3) but also a general activation of acoustic emission that lasted for several minutes. The effect of increase in click rate was especially pronounced in the near-threshold area. It was rather difficult to consider the moth's jerking movement as an indication of the response to the echo, so we did not use these reactions for the threshold measurement. The example of distribution of acoustic emission rate at different levels of stimulation is shown in Fig. 4.

In both species the minimal threshold values were obtained at the stimulus delay being equal to 0.5 ms: 31 dB SPL in *E. paleacea* and 25 dB SPL in *B. satura* (see Fig. 5). At 1 ms delay the sensitivity to the echo-like stimuli was slightly reduced (by 1-3 dB) while at shorter delays the thresholds rose with increasing slope: by 16-18 dB from 0.5 ms to 0.3 ms and by 29 dB to 0.2 ms. The trend of threshold-delay



(a)

(b)

(c)

Fig. 4. Distributions of moth acoustic emission rate at near-threshold levels of stimulation in *B. satura* (data from a single experiment): (a) 24 dB SPL, (b) 26 dB SPL, (c) 28 dB SPL (the threshold value). The delay of stimuli was set to 0.5 ms. Every histogram is built from ten responses to stimulation. Abscissa represents time scale, "0" corresponds to the moment of the first acoustic contact of the insect with the stimulator (i.e., the first pair "natural click — echo-stimulus"). The four black bars (from 0 to 1.4 s) indicate the intervals of readiness of the apparatus to retransmit echo. The bin width is 80 ms. The height of each of the three shaded bars to the right of the distribution histogram corresponds to the total number of clicks during the following intervals of 1.4 s duration each: (-1.4—0 s) — background emission, (0—1.4 s) — emission during stimulation, (1.4—2.8 s) — after-effect.

curve was the same in those experiments when stable acoustic emission of a moth allowed us to measure individual thresholds at different delay values.

The amplitude of natural clicks varied from 70 to 90 dB SPL in 4 cm from the moth with the most typical values being from 78 to 82 dB SPL. We have not found any relation between the threshold values and the amplitude of natural clicks.

In additional series of experiments we aimed to estimate the influence of a passive echo from the loudspeaker to the results obtained. These experiments were

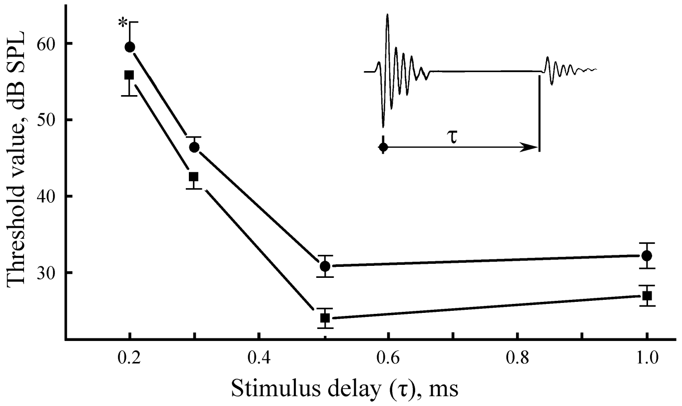


Fig. 5. Mean behavioral thresholds depending on the delay of echo-stimulus in *Enargia paleacea* (●) and *Blepharita satura* (■). Each point of the figure represents eight similar experiments, data are presented as means ± SE. The method of echo-stimulus delay (*τ*) estimation is shown in the upper part of the figure.

performed with *B. satura* which had shown higher auditory sensitivity compared to *E. paleacea.* The thresholds obtained from these experiments when a piezocrystal was used as a source of acoustic stimulation were by 6 dB higher at 0.2 ms delay of the stimulus (62 dB SPL, an asterisk in Fig. 5 represents the mean) than those determined using the electrostatic loudspeaker (56 dB SPL).

4. Discussion

During the emission of a natural click the tympanic organ is affected by two physical factors: (i) vibrational impact which spreads through the cuticle after the click has been generated and (ii) the acoustic click itself which goes to the tympanic membrane through the air. It seems most likely that for auditory receptors the main distinction of a moth's own click is the effective amplitude that significantly exceeds the average level of outside sounds.

The dependence of the auditory thresholds on the echo-like stimulus delay can be explained if one assumes that a strong mechanical influence to the receptor causes abrupt fall of its membrane resistance. The increased conductance of the membrane, in its turn, will lead to (i) suppression of the receptor potential due to shorting of the depolarizing currents and (ii) reduction of the membrane time constant. The latter effect will shorten the time needed for restoration of receptor normal sensitivity after the click emission.

The shape of the curve plotted in Fig. 5 supports this hypothesis. For the auditory receptor to restore its normal sensitivity for as little as 0.3 ms the time constant of the receptor membrane must be several times lower than the restoration time, i.e., of the order of 0.1ms. The time constant of the auditory receptor membrane in *Noctua pronuba* was found to be 34 ms [21], that is at least 30 times higher than what we would expect from our results on restoration of receptor sensitivity after the moth's own click (0.1 ms). Such a drastic decrease of membrane time constant is possible only if transmembrane conductance is proportionally increased and that might happen after a strong mechanical influence is imposed on the membrane.

In our experiments, after the emission of natural ultrasonic click, the tympanic organ of the moth at first received the passive echo from the loudspeaker (delayed by ca. 0.2 ms) and then the synthesized echo-like stimulus (the delay of the latter was controlled by an experimenter). Unfortunately, it was not possible to completely suppress the passive echo from the loudspeaker; however, we could estimate its influence on the results obtained.

When artificial echo-stimulus is delayed by 0.2 ms it comes to the tympanic organ simultaneously with the passive echo. At this delay the threshold level of the stimulus might be close to the amplitude of the passive echo. Due to superposition of the two signals with a random phase, the resultant signal may lead to an error in threshold measurements. The results of additional experiments demonstrated that the decrease in the level of passive echo caused the auditory thresholds to rise. Thus, it can be concluded that superposition of two echo-signals led to the underestimation of auditory threshold values by ca. 6 dB. However, these results should be considered as preliminary ones since the waveform and the spectrum of the stimulus produced using the piezocrystal significantly differed from the respective parameters of the natural moth clicks. The ability of moths to detect echo-like signals in such unfavorable conditions allows us to assume that they possess some mechanisms to detect the anticipated signal in damping noise after the emission of a click.

When the delay is set to 0.3 ms and more, the echo-stimulus and passive echo are separated in time. It was shown that the sensitivity to paired clicks of equal amplitude is about 3 dB higher compared to the sensitivity to a single click [9, 20]. The fact that passive echo may be louder than the following stimulus does not make a substantial difference since the signals which appear after 0.2 ms following the moth's click fall on a high threshold of the receptor and are perceived faintly compared to the stimulus. So, the actual threshold values at the stimulus delay of 0.3 ms and more could be at most 3 dB higher than those that we have measured. This correction is commensurable with the accuracy of the threshold estimation carried out in this work.

The ability of noctuid moth to respond to a short stimulus that follows its own click with a very short delay suggests a possible use of the impulse echolocation. This conclusion is in agreement with our earlier results when moths were tested in so-called carousel set-up [8]. It was shown that under conditions of partially restricted flight, the moth had rarely collided with obstacles which had possessed higher reflecting power for ultrasound. This effect was demonstrated when the moth emitted ultrasonic clicks. During the silent flight the probability of collision with an obstacle did not depend on acoustic properties of the obstacle. The shape of the curves shown in Fig. 5 allows us to make a rough estimate of the actual distance for echolocation: delays from 0.3 to 1 ms correspond to a distance range from 5 to 16.5 cm (according to the assumed acoustic speed being equal to 333 m/s), i.e., the flying moth can use its echolocator for interrogating surroundings to locate nearby objects.

The use of auditory sense by the moths during echolocation does not contradict the task of timely detection of bats in the air. The pulse reflected from an obstacle should obligatorily be preceded by the own pulse, and this feature permits the moth to distinguish between its own echo and all the other sounds. Supposedly, degree of correlation between the probing signal and the subsequent acoustic signals determines the type of behavior response of the moth. Our previous findings support this supposition: echo-like stimulation at 70 dB SPL evoked an increase in average emission rate while the stimuli having similar acoustic parameters but not correlated in time with own clicks of a moth, as a rule, brought about a reversal in response, i.e., the suppression of acoustic activity [12].

Responses of the noctuid moths to external sounds are quite opposite to those in the arctiid moths [3,4]. In this connection, it would be interesting to investigate in more detail acoustic behavior of the noctuid moths dwelling in isolation from bats (on some islands, for instance) as it was done earlier in the course of investigation of hearing in these insects [19]. The role of echolocation among other sensory systems, particularly, its relationship with visual system, has yet to be discovered. Conceivably the short-range echolocation might serve in noctuids to ensure a safe "obstacle-free corridor" for flying in vegetation where on the one hand, the intensity of illumination at night is much less than in open, uncluttered areas, and on the other, the appearance of hunting bats is highly improbable.

Acknowledgments

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