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GENERAL BIOLOGY

Activation of Echolocation Signal Emission by Noctuid Moths (Noctuidae, Lepidoptera) in Response to Retranslation of Echo-Like Stimuli

D. N. Lapshin and D. D. Vorontsov

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Noctuid moths (Noctuidae) are the only group of invertebrates for whom echolocation was demonstrated [2, 3]. The probing signals of these insects are short-wavelength ultrasonic clicks that are emitted during flight at a close to horizontal wing position. The maximum radius of the echolocation system sensitivity is 10 to 35 cm according to different authors [2-4].

Studies of the capability for echolocation in noctuid moths demonstrated no definite responses to echo [2, 3]: the moths either flew toward the object discovered by echolocation or around it. Moreover, the motivation changed several times during the experiment. Such a variation in the insect's behavior introduced uncertainty into experimental results, and the problem of searching for more stable parameters arose for the moth's ability to respond to echo.

Similar problems appeared and were then solved in studies of bat responses to model stimuli. The increase of emitted probing signals may be used as an indicator of an increased attention of bats to biologically important echolocation information [1]. These changes were reproducible and could be easily recorded. The question of how noctuid moths behave in similar situations arises. We suggested that echolocation stimulation induces a similar increase in the frequency of acoustic signals emitted by a noctuid moth. Here, we verify this suggestion.

To record emitted signals, a moth was fixed on a long thin wire of a horizontal shift detector and stimulated with acoustic signals that simulated the echo of its own clicks. The scheme of the experimental setup is shown in Fig. 1. An amplified natural signal from the microphone output was transmitted to a computer-operated electronic switch. When the switch was turned on, each moth's click triggered a generator of echo-like stimuli. This scheme allowed us to stimulate moths with determined acoustic signals. In our experiments, a single stimulating click was similar to the expected echo from a plane barrier (signal duration, 80 µs; frequency, 60 kHz). The signal amplitude (71 dB SPL, ultrasonic region) was either ten times higher or lower than the amplitude of the moth's own click. The delay of the retranslated stimuli relative to the probing signals was 0.5 ms, which corresponded to the distance to the virtual obstacle of 8 cm.

To simulate natural variations in the echolocation situation near a flying moth, the moths readiness to respond (i.e., when the electronic switch was turned on) was divided into four intervals, each 0.2 s (Fig. 2). During the intermediate periods, no echo signals were

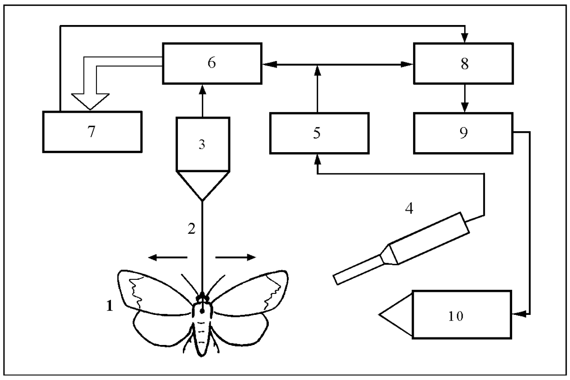

Fig. 1. The scheme of the experimental setting used for studying the response of noctuid moths to echolocation signals. The moth (1) fixed on the wire (2) of the horizontal shift detector (3) is flying and emitting ultrasonic clicks that are registered with the microphone (4). Signals from the detector (3) and microphone amplifier (5) are transmitted to the integrator (6) connected to the computer (7). The electronic switch (8) is operated by the computer (7). When the switch is turned on, it triggers the generator of echo-like stimuli (9) from the moth's own signal. The acoustic stimulus is emitted toward the moth through the condenser speaker (10).

Institute for information transmission problems,
Russian Academy of Sciences,
B. Karetnyi per. 19, Moscow, 127994 Russia

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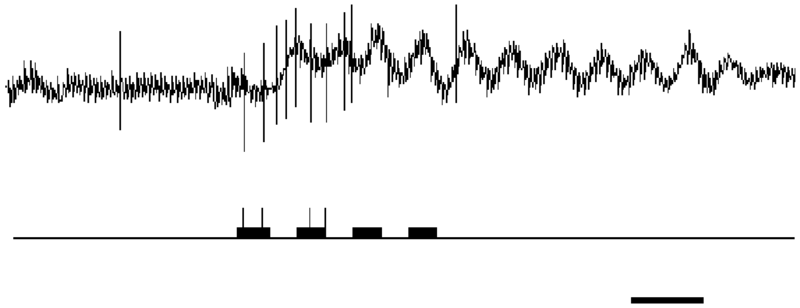

Fig. 2. The response of the noctuid moth *(C. satura)* to stimuli that simulated the echo of its own clicks (retranslated signals). Solid line, moth's movement in a horizontal plane; its rapid fluctuations, wing flaps; vertical lines, moments of echolocation signal emission by the moth; black boxes, periods of readiness of the setting to retranslation; vertical lines (against the background of stimulation), moments of appearance of retranslated signals. Time scale, 1 s. In response to stimulation, the moth changed the direction of its flight toward the echo source and noticeably increased the frequency of emission of probing clicks.

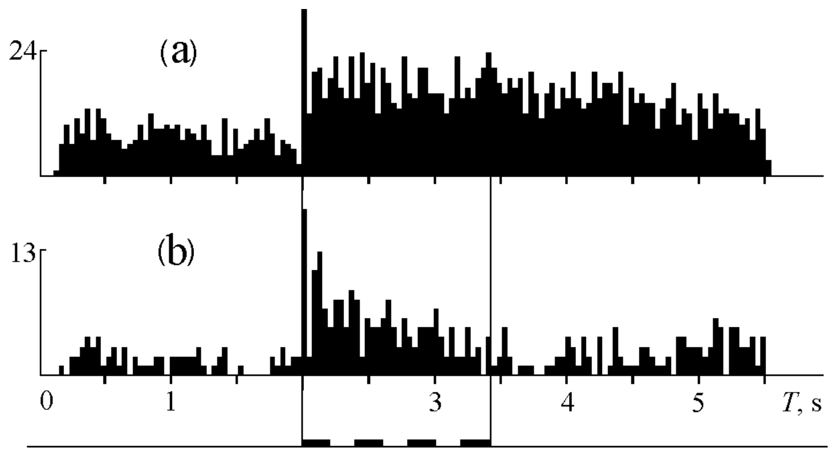

Fig. 3. Distribution of acoustic signals (clicks) of noctuid moths before stimulation (0.3-2 s), upon echo simulation (2-3.4 s), and after simulation: (a) *C. satura* (10 experiments, 100 stimuli); (b) *X. c-nigrum* (one experiment, 35 stimuli). Horizontal axis, time; vertical axis, number of impulses in the accumulation channel (width, 40 ms).

simulated. The rhythm of readiness corresponded approximately to the dynamics of moth flight along four plane obstacles. Thereafter in the text, we refer to the whole cycle of readiness as stimulus, when at least one acoustic contact (i.e., coupled moth's own click and the corresponding stimulus) was observed. The moment of first contact was used as the initial one.

The studies of the dynamics of acoustic signal emission in response to echolocation stimulation were performed most extensively on the noctuid moth *Crino satura* Schiff. (both male and female moths). A total of 20 experiments were performed; one moth was studied in each experiment.

Initially, the moths emitted clicks very rarely: the average impulse emission frequency did not exceed 3 impulses per s. However, it increased to 5-30 impulses per s after the first acoustic contacts (Fig. 3a).

Each moth received no less than ten stimuli. We found that the increase in average impulse emission frequency after stimulation was statistically significant in nine moths from 20 specimens studied ($H < 5\%$ according to the χ^2-criterion). In six moths, acoustic activity also increased several times against a background of stimulation; however, these differences were not significant because of low frequency of impulse emission. Since no opposite responses were observed in these experiments, we concluded that *C. satura* noctuid moths perceived echolocation signals and responded to them with an increase in the average frequency of probing signal emission. Therefore, we demonstrated for the first time that this species of noctuid moths is capable of echolocation. It was also found that the increase in the frequency of acoustic signal emission is the most reliable criterion of the insect's response to echo. It should be noted that analysis of the motor responses of moths to echolocation stimulation (Fig. 2) did not allow us to draw conclusions on the significance of these responses (both spontaneous and upon stimulation) because of the great variability in maneuvering the moths.

The studies described above were performed on a species characterized by stable flight. However, many Noctuidae species are rare in the Moscow region. It was interesting to study single specimens of these species for their capacity to respond to stimuli (echo) by the same method. Here, we show the results obtained for a single specimen (Fig. 3b) of *Xestia c-nigrum* L. (only two specimens of this species were caught in summer, 1997; one of the moths flew badly under experimental conditions).

As is seen in the histogram shown in Fig. 3b, the stimulation with echo-like clicks caused rapid and statistically significant increases in the frequency of signal emission immediately after the first acoustic contact. Note that motor responses to echoes were observed for the first time for this species of noctuid moths [3]. Hence, it may be concluded that *X. c-nigrum* is also capable of echolocation.

A question arises whether the stimulating effect of acoustic stimuli is related to their synchronicity to the moth's own probing clicks or if a similar effect may be achieved by stimulating the moths with nonsynchronized acoustic impulses. The specificity of perception of acoustic signals by insects was verified in the following series of experiments. The moths were stimulated with the same signals and within the same cyclic time intervals, but the impulse emission was triggered with a frequency of 30 Hz from a computer timer. We found that, upon this stimulation mode, nine of ten experimental moths ceased click emission after 3-4 stimuli and then ceased their flight upon subsequent stimulation. One moth responded with an increase in frequency of click emission. These data correlate well with the hypothesis of Roeder [5], who suggested that, in noctuid moths, audition plays an important role in the defensive behavior upon attack of bats. It seems reasonable that stimuli, which did not correlate with moths' own clicks, were perceived by the moths as echolocation signals of bats, and noctuid moths ceased emissions of clicks in order not to be found by bats.

In conclusion, stimulation of noctuid moths with stimuli simulating the echo of their own clicks caused an increase in the average frequency of echolocation signal emission. The use of this increase as a criterion of the insect's response to echo allowed us for the first time to demonstrate the capability for echolocation in moths *C. satura*.

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